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Bella S. Galil
Paul F. Clark
James T. Carlton
*Editors*

# In the Wrong Place – Alien Marine Crustaceans: Distribution, Biology and Impacts

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Volume 6

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# In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts

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# Preface

While humans have facilitated the movement of marine and estuarine (brackish water) crustaceans for millennia to regions where ocean currents would never have taken them, it is perhaps only in the past 200 years, with the creation of interoceanic canals and the advent of global shipping that a "sea change" has truly taken place in the distribution of hundreds, some might argue *thousands*, of species of crustaceans. We present here, in 25 chapters by contributors from around the world, the first global, comprehensive review of alien marine crustaceans. Our concept of "alien", as used in this volume, includes species that are commonly also referred to as exotic, introduced, invasive, non-indigenous, and non-native.

Much remains to be learned about the breadth and depth of how human activity has altered the biogeography of crustaceans in the world's oceans. The best-known marine crustacea are the decapods; crabs, shrimps, crayfish (crawfish), lobsters, and their relatives. The present work reflects that knowledge: 12 of the 25 chapters here focus entirely or largely on decapods. Similarly, the historical biogeography of crustaceans in European, North American, Atlantic South American, and Australasian waters are far better known than many other regions of the world, and the contributions geographically reflect that knowledge base.

In turn, the lacunae of the present work reflect the well-known gaps in our knowledge of alien marine crustacea: the history, diversity, distribution, and impacts of, for example, alien marine species of amphipods, isopods, tanaids, cumaceans, ostracodes, mysids, and many other groups are simply not sufficiently well known to present either comprehensive regional analyses for most areas of the world or global perspectives. While our goal at the outset was not to create a world encyclopedia of alien marine crustacean invasions (as useful as that would be), and while we are acutely aware that we present here no reviews of invasions in the sea by such important crustaceans as copepods, we are nevertheless pleased that a number of chapters cover some species in these lesser-studied groups, serving to plant the necessary seeds for future work.

We highlight here the pervasiveness, importance, and impacts of alien crustacea on many of the world's shores; even so, for most species – even many larger species now occurring in great abundance where they did not evolve – we know little to nothing about their impact. And for many of those species that have been studied, we frequently still lack basic information about their reproduction, feeding, and interactions with native species that would provide the basis for both our understanding of how communities and ecosystems have changed over time, and for management and control decisions. We have little doubt that of critical and increasing concern in coming decades will be those marine crustaceans that are commercially important in fisheries and aquaculture; including not only their diseases and parasites, but their propensity to establish populations in the wild. It is our hope that this volume points the way toward productive research directions and arenas on alien marine crustaceans.

We are indebted to our colleagues for their contributions to this volume. As authors and editors we are aware of the unseen and unsung labours of many more colleagues whose reviews and comments on the manuscripts enhanced and improved them. We are grateful to them all, acknowledged here: Pere Abelló, Shane Ahyong, Fernando Alvarez, Gail Ashton, Ashley Baldridge, Matt Bentley, John Bishop, Karin Boos, Geoff Boxshall, Benny Chan, Earl Dawe, Carlo Froglia, Graham Gillespie, Stephan Gollasch, Sammy De Grave, Mark Hanson, Richard Hartnoll, Jens Høeg, Johan Hollander, Paul Jivoff, Arbačiauskas Kęstutis, Rafael Lemaitre, Erkki Leppäkoski, Donald Lovett, Enrique Macpherson, Colin McLay, Christopher McQuaid, Dan Minchin, Alan Myers, Peter Ng, Pierre Noël, Ferran Palero, Vadim Panov, Richard Piola, Phil Rainbow, Tzachi Samocha, David Smith, Marcos Tavares, Sven Thatje, Martin Thiel, Cédric d'Udekem d'Acoz, Keiji Wada, Sylvia Yamada and Darren Yeo.

Bella S. Galil, Paul F. Clark, and James T. Carlton
Haifa, London, and Mystic
February 2010

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# Part I
# In the Beginning

# The Global Dispersal of Marine and Estuarine Crustaceans

**James T. Carlton**

> *... que l'homme a pris possession de la surface des mers.*
> *(... when man took possession of the surface of the seas.)*
>
> Catta (1876) on the occasion of a fouled ship arriving in the Port of Marseilles from India

> *It is almost impossible for a landsman to gain any idea of the amount of stuff that collects upon the hull of a seagoing ship – millions of tiny shell fish, barnacles, whelks, minute clam-like molluscae ... against which nothing as yet known in the art of ship-building is proof. All these clinging to the hull below the water line will form in an incredibly short time a coating so thick that it will make a difference of from four to six knots in the vessel's speed ... Indeed, it is chiefly for the sake of scraping the hull of the ship that these immense dry docks have been built ...*
>
> – Fitting Cruisers for Service: A Day Spent at the Mare Island Dry-Dock [San Francisco Bay, California, USA], December 5, 1896 (Norris 1896)

**Abstract** The scale of invasions by crustaceans in marine and estuarine waters globally has been vastly underestimated. This underestimation derives from two primary sources: First, most of the species distributed in the first 400–500 years of global shipping have escaped recognition, potentially strongly skewing our perceptions of the evolution and history of many nearshore communities. Second, invasions are rarely reported amongst smaller-bodied and taxonomically more challenging taxa. The combination of the two suggests that many fundamental but overlooked shifts have occurred in marine ecosystems in only the past few centuries. While a still all-too-common statement in the literature is that most invasions are benign and have no impact, no experimental or quantitative data are available that support that conclusion.

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# 1 Introduction

As long as humans have taken to the sea, they have taken marine life with them, intentionally and unintentionally. For thousands of years, primitive and early watercraft, with living organisms on and in them, moved along coastlines and within ocean basins, and to a limited extent between adjacent oceans, such as the many early voyages between the Indian and Pacific Oceans (Riley et al. 1971; Finney 1977; Natkiel and Preston 1986; Hattendorf 2007). Significant global inter-oceanic voyages did not commence, however, until the 1500s, when European explorers with well-fouled and well-bored wooden ships, began sailing throughout the Atlantic Ocean and into the Indian and Pacific Oceans as well (Wolff 2005; Hattendorf 2007). In most areas of the world where these ships touched, marine biologists were not to arrive for several centuries. How many thousands of ship-borne species were to lead to enduring assumptions (that persist today) of natural cosmopolitanism of many marine invertebrates and algae has hardly begun to be explored (Carlton 2009).

The impacts of these and related assumptions on our modern-day understanding of marine invertebrate biogeography are examined here, using, in concert with the rhythm of the present volume, marine crustaceans as a model group. Crustaceans are the second best known group of marine invertebrates, next to molluscs. Both molluscs and crustaceans have enjoyed millennia of human subscription, the former exceeding the latter in global knowledge largely because of shell collectors attracted to the diversity, beauty, and preservability of seashells. Crustaceans (also diverse and beautiful, but not as easily preservable) nevertheless have long been prominent in the public arena: they serve as food (decapods), are persistently annoying (fouling organisms, boring organisms, and fish lice, among other nuisances), and in more modern times, provide both pet food and entertainment (dried krill and live brine shrimp). All of these have important economic benefits or consequences. Further, copepods, euphausiaceans, mysids, amphipods, decapods, and other taxa often form the foundation of many food webs. Many other crustaceans are “ecological engineers,” regulating the structure and function of communities. The fundamental ecological, environmental, economic, and societal roles of crustaceans have thus propelled long interest.

For hundreds and tens of millions of years the natural processes of plate tectonics, isolation (interrupted gene flow), and limited dispersal, shaped the biogeography, evolution, and structure of marine systems. In a profoundly short time (ca. 500 years) global homogenization commenced as marine life from the North Atlantic arrived after a few months journey in the South Pacific Ocean, or as the biota of the North Pacific was mixed with that of the South Atlantic, and after estuaries and bays everywhere became converted to ports and harbours, creating a global corridor of animals and plants upon which uncounted species began to flow. In due course, no shore remained untouched.

## 2 Vectors

Numerous works explore the sobering diversity of the means by which humans have altered the natural distribution of marine, freshwater, and terrestrial organisms (Carlton 1985, 1992; Carlton and Geller 1993; Gollasch 2002; Coutts et al. 2003; Ferreira et al. 2006; Carlton and Cohen 2007). Some vectors transcend all three of these biomes; others are unique to one habitat. Few of these vectors do not apply to crustaceans, whose breadth of life styles, physiological repertoires, and reproductive strategies encompass those of most marine invertebrates. Two great endeavours have led this anthrophoretic charge: global *shipping* and the global movement of *oysters*. Despite the predominance of these vectors, seemingly "minor" vectors (such as seaweed packed with bait worms) can lead to "major" invasions (Cohen et al. 1995), such that due attention must be paid to all of the means by which species were, and are, transported, in order to understand historic, modern and future invasions.

Table 1 summarizes many (but not all) of the vectors that have or could transport, or are transporting, marine and estuarine crustaceans along coastal corridors,

**Table 1** Human-mediated vectors or corridors that have or could transport, or are transporting, marine and estuarine crustaceans along coastlines, across oceans, and between oceans

| | |
|---|---|
| Vessels and other watercraft (including drilling platforms) | Solid ballast (sand, rocks, intertidal or beach debris); water ballast and sediments, and fouling organisms in ballast tanks; wet wells and wet boxes (including fouling and entrained nekton); fouling, boring, trapped, and entrained organisms on hulls, anchors, anchor chains, sea chests, seawater pipe systems, deck basins and scuppers; bathroom water; saltwater swimming pools on cruise ships |
| Other maritime activities: equipment, sea planes, and commerce | Movement and transportation of floats (pontoons), sea buoys, dry docks, sea planes, amphibious planes, log booms: all with associated organisms, as above |
| Movement, holding and release of living organisms including associated biota in containers and packing material (dunnage) | Aquaculture, mariculture, live sea food (including temporary outplanting and open-sea storage of animals and plants); aquarium industry (public and private); intentional stocking (legal or illegal) for enhancement, introduction, or forage food; release of transgenics; biological supply; biomonitoring; education and teaching; bait industry; movement of kelp to attract deposition of fish eggs for harvesting |
| Contaminated gear and footwear | Gear and footwear associated with commercial fisheries, sport fishing, aquaculture, diving, swimming, other water sports, research, exploration, tourism, nature-watching, and other activities |
| Marsh restoration | Movement of salt marsh plants and saline soils, with associated organisms |
| Floating plastic debris | Fouling or entrained organisms on semi-permanent substrates floating in neritic and oceanic waters |
| Canals | Active transport on water moving through canal, in addition to passive transport on vessels or other conveyances as above |

transoceanically, and interoceanically. These are summarized in seven major categories: (1) vessels and other watercraft (including drilling platforms), (2) a host of miscellaneous maritime activities (including the movement of equipment, sea planes, and commercial products), (3) the movement of living organisms, and holding or releasing these in the open sea, or holding them in such a way that they could be inadvertently released to the open sea, (4) gear and footwear with associated living organisms, (5) salt marsh restoration projects, (6) floating plastic debris (which provides a novel nearly *permanent* oceanic substrate), and (7) sea level or lock canals. The specific means or mechanisms by which these vectors operate are detailed in Table 1. Canals are included here, but noted as a *corridor*, not a *vector,* following the terminological framework erected by Carlton and Ruiz (2005).

Excluded from Table 1 is a vector that may come into play in the twenty-first century: the intentional translocation of threatened and endangered species to novel locations in order to establish new populations. This activity is variously referred to as "assisted migration" or "managed relocation" (Ricciardi and Simberloff 2009; Richardson et al. 2009). As yet, no marine or estuarine crustaceans are on this relocation radar.

As a further example of the challenges faced by understanding the depth and breadth of the abilities of humans to move marine organisms long distances, Table 2 presents data from what might be called the "bioweb": the availability of living organisms for purchase on the internet. For this vector (for which it would take a small monograph to do justice to the number of species available) a few examples of edible seafood have been selected, and one example of the range of species available from a biological supply company. An important "between the lines" aspect, noted in the table title, is that a large number of other organisms typically come along with the target species. A particularly rich source of living marine crustaceans, for example, might be to simply order the water or "communities" shown on Table 2-B. The management challenge from the unregulated shipment of living organisms is that a very large number of species are now able to be placed in private hands, for such use (or for dissemination and release) as seems fit to whoever has purchased these animals and plants.

The global expansion of the live seafood industry, facilitating the movement of living crabs, lobsters, shellfish, and other species anywhere in the world within 24 h, is a related vector that remains poorly explored. Of particular interest, for example (other than the obvious movement of living edible crustaceans) are fouled shellfish also in global flow. Thus living oysters (such as *Crassostrea ariakensis*) are flown daily from Puget Sound, Washington (via Seattle International Airport) to Washington, D.C., to be served in seafood restaurants and bars (a measurable reflection on the state of the Chesapeake Bay oyster industry itself). The oysters are transported in such a way as to maximize their survival such that they can be served alive. Thus, any species on the oyster shells may survive as well: the Pacific coast barnacle *Balanus glandula* has been intercepted alive on such oyster shipments, remaining viable for as long as 13 days out of water (Carlton, unpubl. obs.).

Presumably such episodes are repeated daily worldwide, but the extent to which such shellfish (and their epibiota; molluscan, crustacean, or both) ends up in the sea

**Table 2** Live crustacea directly or unintentionally available via the internet (*examples only*, as of March 2010)

| Website | Species available for live shipment (with associated water and packing materials) |
|---|---|
| A. Edible seafood | |
| www.mainelobsterdirect.comwww.thefreshlobstercompany.com/ (and many others) | American lobster, *Homarus americanus* |
| www.aqualife.nu/lobster-canada-europe.html | American lobsters (*Homarus americanus*) ==> shipped to Europe |
| www.crawfishcoofcentralflainc.com/Live-Blue-Crab-Delivered.html | (Louisiana) blue crab (*Callinectes sapidus*) |
| www.ordercrabs.com/ | (Maryland) blue crab (*Callinectes sapidus*) |
| www.berwickshellfish.com/ordering.html | European lobster (*Homarus gammarus*) |
| | Brown crab (*Cancer pagurus*) |
| | Velvet crab (*Necora puber*) |
| | Green crab (*Carcinus aestuarii*) |
| | Spider crab (*Maja squinado*) |
| | Squat lobster (*Pleuroncodes monodon*) |
| | Norway lobster (langoustine) (*Nephrops norvegicus*) |
| B. Biological supply companies | |
| Ward's natural science 2010 biology & chemistry catalogue (http://wardsci.com/) | "Pond water" (1 gal): "Nonsterile; may contain organisms" |
| | "Sea water" (1 gal): "Nonsterile, from our marine tanks" |
| | Flame scallops, *Lima scabra*, and associated biota |
| | "Feather duster" polychaete worms, and associated biota |
| | "Marine hermit crab" *Pagurus* sp. and fiddler crabs, *Uca* sp |
| | Sea urchin, *Strongylocentrotus* sp., and associated biota |
| | "Sea peach" tunicate, *Halocynthia pyriformis*, and associated biota |
| | "Marine animal aquarium Set"(invertebrates and fish) |
| | "Living rock community": "amphipods, other crustaceans, sponges, bryozoans, and even algae" |
| | "Marine invertebrate symbiosis set" (includes crabs) |
| | "Invertebrate set 1" (includes scallops, and presumably associated biota) |
| | "Invertebrate set 2" (includes hermit crabs) |
| | Red algae (*Callithamnion, Corallina, Gigartina, Polysiphonia, Porphyra, Porphyridium*, *Bangia*) |
| | Green algae (*Ulva, Cladophora*) |
| | Brown algae (*Fucus, Dictyota, Ectocarpus, Laminaria*) and associated biota with all algae |

and not in rubbish dumps is unknown. The fact that living, foreign shellfish are found alive in the wild suggests that landfills are not always the final repository. Thus Atlantic blue crabs (*Callinectes sapidus*) are occasionally found living in San Francisco Bay (California) and in Kaneohe Bay (Oahu, Hawaii), and Pacific Dungeness crabs (*Cancer magister*) can on occasion be found in the open ocean off Gloucester, Massachusetts. Eastern *Callinectes* and Western *Cancer* are both actively shipped, west and east respectively, as part of the live seafood industry, and are thus available for live purchase in San Francisco and Boston. Some of these crabs are evidently then released into adjacent waters, perhaps with the intention of establishing reproducing populations (the *Cancer* are, however, a male-only fishery).

Of interest is to compare the vectors (Table 1) to major groups of crustaceans, and ask the extent to which different taxa are susceptible to anthropogenic dispersal. Table 3 contrasts 16 groups of crustaceans to the seven categories of vectors/corridors from Table 1. Column and row totals are presented. *Shipping* and *canals* are clearly significant relative to their dispersal potential across all taxa, although other mechanisms are also potentially of virtually equal weight (*other maritime activities, the movement of living organisms, contaminated maritime equipment and footwear*, and *marsh restoration*). Fortunately *floating plastic debris*, for crustaceans, has the potential to transport fewer groups of crustaceans, which however does not imply that this vector is any less important for the species that are transportable or successfully transported.

Of further interest, and awaiting continental-scale, ocean-scale, or global analysis, is that the row totals suggest that there are groups of crustaceans (and by extension other marine invertebrates) whose distributions should be less susceptible than other groups to widespread alteration and modification. At one extreme, many vectors are capable of transporting, for example, barnacles, copepods, ostracodes, decapods, isopods, tanaids, and amphipods. It is thus amongst these groups that many undetected invasions may have occurred or are occurring. At the other extreme, it appears that cephalocarids, branchiurans, mystacocarids, euphausiaceans, stomatopods, and leptostracans have the least interface with synanthropic dispersal vectors, and we would expect relatively fewer invasions amongst these groups.

Tempering these predictions, however, are three realities: one, that intensive vector activity involving any of these latter groups could lead to successful invasions. Thus while Branchiura (fish lice) do not interface with many vectors, the increasing movement of fish for aquaculture or stocking purposes, and the presence of fish in ballast water, may more than compensate for the lack of vector diversity. Two, while we might expect fewer (for example) stomatopod (mantis shrimp) invasions based upon this vector matrix, little is known of the role of those vectors that do operate, and how they may have modified mantis shrimp biogeography. Thus stomatopod larvae occur in ballast water (Carlton and Geller 1993), opening up a potentially complex window into how stomatopod ranges (virtually all of which are assumed to be natural) may have been cryptically altered by over 100 years of the movement of ballast water. Three, we work at the mercy of taxonomists, who are

**Table 3** Marine and estuarine crustaceans transportable by human-mediated vectors and corridors along coastlines, across oceans, and between oceans

| Taxon | Vector | | | | | | Corridor | |
|---|---|---|---|---|---|---|---|---|
| Class, infraclass, superorder, or order | Vessels | Other maritime activities | Movement, holding of living organisms | Contaminated gear / footwear | Marsh restoration | Floating plastic debris | Canals | Total |
| Cladocera | x | x | x | x | x | | x | 6 |
| Cephalocarida | x | | | x | | | x | 3 |
| Cirripedia | x | x | x | x | x | x | x | 7 |
| Branchiura | x | | x | | | | x | 3 |
| Mystacocarida | x | | | x | | | x | 3 |
| Copepoda | x | x | x | x | x | x | x | 7 |
| Ostracoda | x | x | x | x | x | x | x | 7 |
| Decapoda | x | x | x | x | x | x | x | 7 |
| Euphausiacea | x | x | | | | | x | 3 |
| Mysidacea | x | x | x | | x | | x | 5 |
| Cumacea | x | x | x | x | x | | x | 6 |
| Isopoda | x | x | x | x | x | x | x | 7 |
| Tanaidacea | x | x | x | x | x | x | x | 7 |
| Amphipoda | x | x | x | x | x | x | x | 7 |
| Stomatopoda | x | x | x | | | | x | 4 |
| Leptostraca | x | x | x | | | | x | 4 |
| Total | 16 | 13 | 13 | 11 | 10 | 7 | 16 | – |

x = potentially transportable by vector or corridor shown the *sine qua non* of understanding and measuring changes in biodiversity. The availability of taxonomists and the impact of such availability, or the lack thereof, is discussed below.

## 3 History of Recognition of Human-Altered Biogeography of Marine Crustaceans

Early workers were aware of the potential for non-indigenous crustaceans to arrive on their shores from across the seas. For the review here, literature for a 100 year period, from the 1820s to the 1910s, has been selected to capture a sense of the extent to which largely nineteenth century scientists were aware of the human-mediated dispersal of marine crustaceans.

Roux (1828) wrote for example, in describing the littoral isopod *Ligia exotica* from the Mediterranean,

> Quoique j'aie trouve' à Marseille cette nouvelle espèce, j'ai lieu de penser cue la Provence n'est point sa patrie, et que c'est par un navire venant de Cayenne, où elle doit être originaire, qu'elle a e'te apportée. Il paraîtrait qu'elle a pu vivre durant la traversée, à fond de cale, dans le voisinage de quelque petite voie d'eau propre à entretenir l'humidité que ces Crustacés recherchent. [1]

Although (Catta 1876: 6, footnote) implied that Roux had actually found this isopod in the hold of a ship, Roux was clearly speculating. Nevertheless, Roux's insight that *Ligia* could have been carried across the sea from South America (French Guiana), and his apparent awareness of the damp recesses of a vessel that could maintain the proper viable conditions, are compelling for the time.

Gould (1841), based in Boston, Massachusetts, and writing of the New England marine fauna, commented that as barnacles can affix themselves to floating and "locomotive" objects, they,

> ... are, therefore, extensive voyagers, and hail from no particular sea. During the last summer, two vessels lay side by side at one of our wharves, one from India, the other from Sweden, and their bottoms were occupied by similar species of barnacles. In long voyages, especially in warm climates, and still more certainly where vessels are not sheathed with copper, the barnacles adhere in incredible numbers, and grow to such a size, as materially to impede the course of the vessel. Conveyed in this way, they are brought in contact with their food, and are seen in every port.

Gould thus implies that ships have aided and abetted in the creation of what was to be recognized by the twentieth century as a "port biota." He further noted that

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[1] "Although I found this new species at Marseille, I have reason to think that its provenance is not this country, and that it is from a ship which brought it here from Cayenne, where it must be originally from. It would appear that it was able to live during the crossing, at the bottom of the hold, in the vicinity of some small amount of water which properly maintained the humidity that these crustaceans require."

"*Balanus tintinnabulum*" [= *Megabalanus tintinnabulum*] was one of the common species "found on vessels arriving from warmer regions", that he had collected *Balanus eburneus* [= *Amphibalanus eburneus*] "from the bottom of a ship of war from the West India station", and that lepadid barnacles were regularly found on ship bottoms.

Bell (1844–1853), while not directly referring to human-mediated accidental dispersal, noted the long-distance movement of live crabs (*Cancer pagurus*) from Norway to the London markets by means of "well boxes", which were attached to vessels, and which had "holes in all the sides to admit of continued change of water". This is one of the earliest references to the existence of wet boxes and wet wells associated with coastal vessels, structures that we now know to be capable of transporting living organisms, both fouling and nektonic (Carlton, unpubl. obs.). Coincidentally, De Kay (1844), in the same year, noted that a "car full" of American lobsters (*Homarus americanus*) had been introduced about 1814 into Charleston harbour, South Carolina (a few individuals were still found 10 years later). Although rarely noted as vectors for the first half of the nineteenth century, it is likely that such moderately long-distance movements of large edible crustaceans were common, in a pre-ballast water era when we generally assume that water-borne organisms were rarely (or never) transported by human-mediated mechanisms.

Catta (1876), reported on the fouling community on the iron ship *Karikal* that had arrived in Marseille, via the Cape of Good Hope, from Puducherry (Pondicherry), India. Crabs, isopods, and amphipods were found amongst a rich covering of the barnacle *Lepas* and the green alga *Bryopsis*; the peracarids had apparently been acquired locally in France, but the four crabs had been entrained along the voyage (Schmitt [1965], in a well-known popular work on crustaceans, misreported the amphipod *Ampithoe* as having been carried on the *Karikal* from India to France). The crabs on the *Karikal* were *Pachygrapsus transversus* (as *Pachygrapsus advena*), *Planes minutus* (as *Nautilograpsus minutus*), *Plagusia depressa* (as *P. squamosa*) and *Plagusia chabrus* (as *P. tomentosa*). Catta commented that the crabs had survived great variations in temperature and water chemistry, and felt that such observations "sont certainement destines a modifier nos idees sur la resistance vitale de certaines especies animales".[2] More intriguing, however, are Catta's thoughts on the potential for the "hand of man" in altering the global distributions of marine life; his comment is a rare one for the nineteenth century:

> L'observation actuelle, tout isolée qu'elle est, nous montre combien il est nécessaire, dans les études zoologiques, telles qu'on les entend aujourd'hui, de tenir compte de pareilles causes de modifications des faunes, surtout si l'on songe que ces causes agissent d'une façon constante depuis que l'homme a pris possession de la surface des mers.[3]

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[2] "are certainly destined to change our notions on the fundamental resistance of certain animal species."

[3] "The present observation, although isolated, shows us how necessary it is in zoological studies, as we understand them today, to take account of similar causes of faunal changes, especially if we think that these causes operate in a manner consistent with when man took possession of the surface of the seas."

Not surprisingly, one of the first clear and extensive expositions on the role of international shipping in influencing the distribution of marine crustaceans are Charles Darwin's monographs on barnacles. Darwin (1851), reported at least seven species of lepadomorph barnacles on ships, while Darwin (1854), noted the occurrence of at least 16 species of balanomorph barnacles in ship fouling. Some of Darwin's observations are apropos today, although they appear to have been rarely cited, buried in what most workers assume to be purely taxonomic treatments. For example, (Darwin 1854: 163), wrote,

> ... those species ... which seem to range over nearly the whole world ... are species which are habitually attached to ships, and which could hardly fail to be widely transported. Indeed, it appears to be surprising, that such species as *Balanus psittacus* and *eburneus*, which often become attached to vessels, should still be confined, the one to Southern, and the other to Northern America.

Darwin (1854: 192) appears to have specifically had in mind species such as *Balanus tintinnabulum* [= *Megabalanus tintinnabulum*] and *Balanus amphitrite* [= *Amphibalanus amphitrite*]. Since Darwin, *Austromegabalanus psittacus* has been introduced to New Zealand (Hosie and Ahyong 2008) where it was first found in 2006; thus it remains a poor global colonizer for reasons that remain unknown. *Amphibalanus eburneus*, however, has dispersed globally since the nineteenth century.

Darwin (1854: 197), further speculated on whether transport "to new and distant localities" might explain the morphological variation seen in ship-borne populations of *Megabalanus tintinnabulum*, and specifically wondered if interbreeding among populations could produce intermediate forms. Henry and McLaughlin (1986) have since sorted out which of these intermediate forms and variations are in fact distinct species.

Of no small interest is Darwin's observation on how ships accumulated different species over the course of a voyage; his remarks (1854: 200, 209), in this regard appear not to have been mentioned since. Darwin reported upon a guano ship that had left England for Ichaboe (Namibia, Africa), then sailed to Patagonia, and returned through the South Atlantic to England: " ... it was interesting to see the manner in which numbers of *B[alanus] psittacus*, a Patagonian species, had become attached on the African *B[alanus] tintinnabulum* ... and subsequently during the voyage home, some of the latter had adhered on *B. psittacus*" (apparently this second *Megabalanus tintinnabulum* cohort had been acquired on the voyage home).

Henry Pilsbry (1916: 64), a half century later, painted an even more complex bioaccumulation picture, based upon a collection made in the 1870s:

> A large series from a whaler, Cape Cod, September 3, 1879, collected by Prof. A. E. Verrill, is interesting for its associates and coloration. In all probability the vessel was a Provincetown schooner whaling in the West Indies, and the barnacles were gathered in course of the usual short (six months) voyage. The wooden bottom was first rather copiously covered with *Balanus trigonus* up to about 8 mm. diameter. These were then mostly covered by flat, thin oysters (*Ostrea folium* Linnaeus), mainly under 25 mm. in length, and by the *Balanus tintinnabulum antillensis*, which seem to have settled down at the same time. Upon these

> oysters and barnacles *Tetraclita radiata* sits, the specimens reaching a diameter of about 8 mm. There are also a few extremely young *Balanus eburneus*, 1 to 2 mm. diameter, which were clearly the last settlers, after the vessel returned to Massachusetts.

In the Caribbean the vessel was thus colonized by *Balanus trigonus* (a recent invasion at the time from the Atlantic Ocean), upon which *Megabalanus tintinnabulum* (which now includes *antillensis*) and an oyster (probably *Dendostrea frons*, which in Pilsbry's time was being referred to by the Indo-Pacific name *Ostrea folium*), and upon which *Newmanella radiata* (= *Tetraclita radiata*) then settled. Pilsbry was then able to detect that the New England barnacle *Amphibalanus eburneus* was the last to settle. The building of fouling communities over a cruise track, resulting in a vessel arriving in a port with multiple species from multiple locations has rarely been discussed, and was not to be experimentally addressed until the 1980s (Carlton and Hodder 1995).

Pilsbry (1896), further noted that, after studying a collection of barnacles from a vessel that had travelled from San Francisco, California, to Hong Kong, and then to Java and India, before arriving at Philadelphia, Pennsylvania, " ... the Balanidae themselves have been so widely diffused by commerce that alone they afford but little evidence of their original *patria*". But it appears to have remained for Fulton and Grant (1900) to have expanded the concept (based upon a suggestion from a government official) of what could be transported by ships. They suggested that the arrival of the European shore crab *Carcinus maenas* in Australia may have been mediated by carriage in spaces *inside* a vessel's hull, specifically in wooden ships that had been bored by shipworms (teredinid bivalve mollusks), and then fitted with "false bottoms" that could provided sanctuaries large enough, and sufficiently stable, to transport errant crustaceans, otherwise not associated with external ship fouling, around the world.

In a particularly interesting discourse on the decapods of Bermuda, Verrill (1908) took some interest in ships and the potential for the invasion of non-native crabs. Verrill reported that while no decapods from Europe, including the Mediterranean, were found in Bermuda," such are known to occur in other orders, especially in those groups that habitually cling to the foul bottoms of vessels". Verrill noted that, (1) the *opportunities* for introduction have been "unusually good" for many species, because of the "great dry dock (that) has existed at the naval station for many years", and further emphasized that "even from the first settlement" Bermuda was a "favorite place" for ships to be beached and their hulls cleaned, and, (2) "probably hundreds of species have been" carried to the islands by ships, but either "became too separate to find their mates at breeding season" or were eaten by the "voracious fishes".

Thus, Verrill considered the potential for massive and multiple inoculation of invasions, the challenges of establishing a reproductive population, and that predation exerted in tropical climates may have lead to the lack of non-native decapods; all considerations that are regularly visited and discussed in modern-day invasion ecology literature. The "massive/multiple" inoculations hypothesis would resurface again for ship-mediated invasions about a half-century later, when Bishop (1951) introduced the "convoy proposition", suggesting that the invasion of the Australasian barnacle *Elminius modestus* in the European theatre ca. World War II was facilitated by the "accumulation of vessels into convoys (which) would tend to increase the population density of larvae of fouling organisms in a given locality at a given time".

Rarely mentioned in modern literature are Verrill's remarkable extolments on the virtues of intentionally introducing edible crabs to Bermuda. Verrill wrote:

> It would be of great scientific interest, as well as evident, economical benefit, to experiment with the introduction of edible East American and West Indian crustacea that do not now exist at the Bermudas. Among those that might succeed are the large Southern Rock Crab (*Menippe mercenaria*); the West Indian Rock Crab *Carpilius corallinus*); the southern variety of the Edible Blue Crab (*Callinectes sapidus*), and many others. Probably their fertilized eggs could be transported far more easily than the adults, and in vastly greater numbers. With suitable arrangements at the new Bermuda Biological Station, such eggs could easily be hatched and the young liberated in great numbers, in suitable places ... there seems to be no reason why any species from the Carolina coasts or the Florida Keys should not flourish in Bermuda if once introduced there in considerable numbers and protected from their enemies at first ... Aside from edible species, the introduction of the smaller kinds would afford a large additional supply of food for useful fishes, and thus benefit the fisheries. Probably there is no locality in the world so well adapted by nature for experiments in the naturalization of marine animals as Bermuda. There are here numerous deep basins and ponds, of pure sea water, due to fallen caverns, which have subterranean connections with the sea through pores and crevices in the porous limestone, by which the sea water is constantly renewed. In such places large numbers of marine creatures could be protected and allowed to breed till well naturalized, and numerous enough to be safely liberated. The equable temperature of the climate is also particularly favorable for such experiments. That any given species of the West Indian marine fauna is not now found in Bermuda does not prove that it is not able to live there, but rather that it has lacked the opportunity or means of arriving there. There is a large field open here for enterprising naturalists and biologists.

Again of no small interest here is Verrill's observations that limited larval dispersal capabilities of some taxa have played a role in the construction of the Bermudan biota. Of equal interest (for words written in 1907!) are Verrill's propositions that edible crabs should be introduced via fertilized eggs and grown in mariculture operations, and that forage crabs should also be considered for introduction to enhance fisheries.

Chilton (1910), in a widely-cited paper, again commented on the potential of ships to introduce foreign species, repeating earlier observations and suggestions, particularly those of (Catta 1876) and Fulton and Grant (1900). The motivation for Chilton's paper was the arrival of the British Antarctic vessel *Terra Nova* in Lyttelton, New Zealand, in October 1910, "with a plentiful growth of seaweed, barnacles, etc." Chilton read about the arrival of the fouled ship in the newspapers, and went down to the dry dock but found the vessel already scraped. He recovered balanids and lepadids from the dock floor, and found Australian isopods in a plank that had been removed from the ship.

It is thus clear that a number of both general marine zoologists and systematists, and carcinologists in particular, throughout the 1800s were aware of shipping (at least) as a mediator of long-distance accidental dispersal across otherwise insurmountable barriers. Darwin in particular was convinced that ship-mediated dispersal of barnacles had long been in play.

How, then, did this awareness translate into the more general carcinological literature? If we examine nineteenth century monographs on crustaceans, to what extent was the role of the previous 400–500 years of global shipping invoked in explaining interesting, anomalous, or unusual distributions? Table 4 reviews the extent of mention or discussion of human-mediated dispersal of marine crustaceans in 12 well-known nineteenth century monographs from 1834 to 1895. Other than the barnacle distributions discussed (and already reviewed above) in Gould (1841) and Darwin (1851, 1854) there are, remarkably, no statements on the dispersal of crustaceans by human activities, by any means, in such classic works as those of Milne-Edwards, Bate and Westwood, Stebbing, and Sars.

It is thus tempting to suggest that because a fundamental sense of the potential role of shipping (and other vectors) in altering species distributions was lacking in many of the major works of nineteenth century carcinology, this cast an influence upon the thinking, and writings, of many if not most twentieth century workers. Thus, in much of the systematic and biogeographic literature of many common marine crustaceans, such as copepods, ostracodes, isopods, tanaids, and amphipods (the latter with the exception of the papers of J. Laurens Barnard), humans are absent in the formula of seeking to explain why species were where they are.

**Table 4** Mention of human-mediated dispersal of crustaceans in selected nineteenth century monographs, 1834–1895[a]

| Reference (title abbreviated; full citation in literature cited) | Mention or discussion of synanthropic dispersal |
|---|---|
| Milne-Edwards (1834, 1837, 1840) *Histoire naturelle des Crustacés* | No remarks |
| Gould (1841) *Invertebrata of Massachusetts....Crustacea* | Role of ships in barnacle dispersal |
| De Kay (1844) *Zoology of New-York (Crustacea)* | No remarks (but see discussion in this chapter) |
| Bell (1844-1853) *History of British Stalk-Eyed Crustacea* | No remarks (but see discussion in this chapter) |
| Darwin (1851) *Monograph on the Cirripedia: Lepadidae* | Role of ships in barnacle dispersal |
| Darwin (1854) *Monograph on the Cirripedia: Balanidae* | Role of ships in barnacle dispersal |
| Bate and Westwood (1863, 1868) *History of British Sessile-Eyed Crustacea* | No remarks |
| Boeck (1871) *Crustacea amphipoda borealia et arctica* | No remarks |
| Haswell (1882) *Australian Stalk- and Sessile-Eyed Crustacea* | No remarks |
| Stebbing (1893) *History of Crustacea: Recent Malacostraca* | No remarks |
| Sars (1895) *Crustacea of Norway: Amphipoda* | No remarks |
| Faxon (1895) *Albatross: The Stalk-Eyed Crustacea* | No remarks |

[a] Searchable pdfs of these books and monographs were downloaded from http://www.biodiversitylibrary.org/, http://www.archive.org/index.php, and http://books.google.com/. Search terms used were: ship, vessel, boat, carried/carry, transport, hull, foul(ing), and harbor, their French equivalents for Milne-Edwards (1834–1840), and their Latin equivalents for Boeck (1871).

While individual zoologists of the 1800s were aware of ship-mediation, that awareness failed to transcend to the "big picture", and thus did not became part of any explanatory paradigm of crustacean biogeography, let alone a *cause célèbre* to explain unusual, disjunct, or other distributions.

## 4 The Scale of Modern-Day Recognition of Crustacean Invasions

To what extent, then, is the legacy of these perspectives reflected in modern-day treatments of marine and estuarine crustaceans invasions around the globe? Table 5 provides insight: catalogued here are the introduced and cryptogenic crustaceans recognized in selected regions of the world: Europe (Belgium, Netherlands, Ireland, England, and the Azores), Atlantic South America (Uruguay/Argentina), Pacific South America (Chile), Japan, and the Hawaiian Islands.

Despite the numerous different approaches of these studies, the variable background of authors, and variable data quality, the patterns are clear. Only three groups of crustaceans are even modestly recognized globally as including introduced species: decapods, barnacles, and amphipods. Copepods appear in most lists, but rarely are more than three introduced species listed for any given location. Mysids are vastly underreported, with only one introduced species being reported from each of three separate regions. If we eliminate the Hawaiian Islands (the subject of intensive study for nearly 15 years), and South Africa (the subject of a recent but short-term intensive examination), isopods rank with copepods in the level of recognition of non-indigenous species.

The situation then becomes even more grim: absent from all lists are introduced marine and brackish water cladocerans (water fleas), branchiurans (fish lice), euphausiaceans (krill), cephalocarids, mystacocarids, and leptostracans, and, with one or two rare exceptions, ostracodes, stomatopods, and cumaceans.

Several of these lacunae are explicable by the simple lack of taxonomists: there are few workers who study cephalocarids and mystacocarids, so that despite the high probability that they were transported for centuries in sand ballast (Carlton 2007), a lack of knowledge renders them inaccessible for resolution. Another explanation for the lack of reported invasions, or the reporting of few invasions, among many crustacean groups is the absence of a sufficient number of interested, dedicated investigators who pose questions about the historical biogeography of specific taxa. Thus, there seems little question that ostracodes are severely underreported as invasions, given that they are highly transportable (Table 3), including arriving alive at the end of voyages in ship fouling and in ship ballast water (Carlton and Geller 1993; Carlton and Hodder 1995). Rarely cited in this regard is the cogent paper by Teeter (1973), who noted that the "recent dispersal of widespread ostracode species may have been aided by transoceanic shipping". Rarer still are ostracode biogeographers who have questioned the distribution of species in the world's bays, harbours, ports, and estuaries.

**Table 5** Introduced (I) and cryptogenic (C) marine and brackish-water (estuarine) crustaceans reported from selected locations, and numbers of species

| | Atlantic Ocean | | | | | | Atlantic/Indian | Pacific Ocean | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Belgium | Netherlands | Ireland | Britain | Azores | Uruguay/Argentina | South Africa | Chile | Japan | Hawaii |
| | (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) |
| Cladocera | | | | | | | | | | |
| Cephalocarida | | | | | | | | | | |
| Cirripedia | I(7), C(1) | I(2), C(1) | I(2) | I(2) | I(2),C(1) | I(3),C(2) | I(2) | | I(6) | I(4) |
| Branchiura | | | | | | | | | | |
| Mystacocarida | | | | | | | | | | |
| Copepoda | I(3) | I(4) | I(2),C(9) | I(1) | | | I(1) | I(3) | | I(3), C(1) |
| Ostracoda | | | | I(1) | | | | | | |
| Decapoda | I(6) | I(5) | | I(2) | C(2) | I(1),C(2) | I(2) | | I(2) | I(10) |
| Euphausiacea | | | | | | | | | | |
| Stomatopoda | | | | | | | | | | I(1) |
| Leptostraca | | | | | | | | | | |
| Mysidacea | I(1) | I(1) | | | | C(1) | | | | I(1) |
| Cumacea | | | | | | | | | | I(2) |
| Isopoda | | | C(1) | | I(1),C(1) | I(4) | I(6), C(5) | | | I(18) |
| Tanaidacea | | | | | C(1) | C(2) | | | | I(2),C(1) |
| Amphipoda | I(3),C(1) | I(6),C(1) | I(4),C(3) | I(1) | | I(1),C(9) | I(9),C(8) | | | I(20),C(5) |

*References*:
(1) Belgium: Kerckhof et al. 2007
(2) Netherlands: Wolff 2005
(3) Ireland: Minchin 2007
(4) Britain: Eno et al. 1997
(5) Azores: Cardigos et al. 2006
(6) Uruguay/Argentina: Orensanz et al. 2002
(7) South Africa: Mead et al. 2011
(8) Chile: Castilla et al. 2005
(9) Japan: Otani 2006
(10) Hawaiian Islands: Carlton and Eldredge 2009

A useful illustration of the underreporting of crustacean invasions comes from examining regions (of which there are few) that are well-studied relative to the history of their community assembly. San Francisco Bay, in central California, has been the focus of studies on marine invasions since the 1960s (Carlton 1965, 1967, 1979; Cohen and Carlton 1995). Ten species of introduced copepods, all from Asia, have been identified in the Bay (Cohen and Carlton 1995), more than the combined total of marine copepod invasions from several continents. Five species of introduced mysids, all also from Asia, are now known from San Francisco Bay (Cohen and Carlton 1995; Modlin 2007), again more than all the marine or estuarine mysid invasions known from other continents. Rather than San Francisco Bay being an unusual sink for non-native copepods and mysids, it seems more probable that the application of adequate sampling, investigator interest, and robust systematics, have resulted in a more fine-tuned resolution of the number of invasions in these taxa, and should signal workers in other regions of the world that there are likely a plethora of undetected invasions present in their regions. That these are not necessarily obscure or rare species is illustrated by the example, below, of the invasion of the North American mysid *Neomysis americana* in South America. All this said, a necessary caveat is that even in well-studied San Francisco Bay, entire groups of copepods (as an example) remain unexplored, such as the abundant benthic and fouling harpacticoids, or the parasitic clausidiid and notodelphyid copepods of introduced ascidians.

Even among those groups that are modestly well studied, the reported numbers likely represent a small fraction of the actual number of introductions, particularly among the amphipods and barnacles, and among smaller decapods.

## 5 Discussion

Carlton (2009) recognized more than a dozen sources of error that lead to the number of alien species being underestimated. These include,

*Cryptogenic species*: species that are not known to be native or introduced.

*Pseudoindigenous species*: species mistaken as native, including introduced species misidentified as previously known native species. A particular and enduring phenomenon here is that the scale of invasions remains elusive in part because of the inadvertent re-description of newly-discovered species as new species, leading to hundreds of introduced species being redescribed, often again and again, around the world, as native species (Carlton 2009). This situation, an overestimate of endemicity based upon introduced species being interpreted as native, remains unrectified for a number of taxa.

*Unidentified species*: species that are unidentified or unidentifiable.

*Small species*: species less than 1.0 mm in size that because they are small are considered native.

*Uninvestigated species*: taxonomic groups that are never or rarely studied.

*Known but unreported species*: introductions known to scientists but never published.

*Widespread intraoceanic species*: species that are widespread within an ocean and presumed to be native wherever they occur.

*Widespread interoceanic species*: species that occur in two or more ocean basins and are presumed to be native wherever they occur ("cosmopolitan" species).

*Pseudo-oceanic species*: species that are presumed to drift with ocean currents, such as estuarine hydromedusae, coastal teredinid bivalves, or estuarine caprellids, but do not.

*Parasitic, commensal, or symbiotic species.*

*Undersampled taxa in microhabitats and ecotones.*

These systematic, historic, sampling, and related challenges result in a profound obfuscation of the actual numbers of non-native species. Two broad categories capture many of the above phenomena: One, invasions that occurred between the 1500s and early 1900s, and two, invasions amongst taxa that are cryptic, small-bodied and taxonomically challenging. For the first, it is clear that for all regions of the world we are missing the first 400–500 years of introductions, a sobering reflection on our understanding of the evolution and history of most marine and estuarine communities. For the second, a vast number of cryptic (underexplored habitats and biological associations) and small-bodied invasions are simply overlooked.

Why is it important to know about "older" invasions of the seemingly distant past, or invasions of small species? For the latter, "small" does not mean unimportant. For the former, species that arrived decades or centuries ago could have had a profound impact on the structure and function of communities, communities that we have erroneously presumed are the result of long-term evolutionary processes. Equally important is that fundamental to invasion science are invasion rates, the characteristics of invaders, the nature of changing vectors over time, the susceptibility or resistance of different geographic areas to invasion (in terms of both numbers of species and of functional groups), and an understanding of invasions over space and time as potential signals of significant environmental changes (such as water quality, overfishing, or climate change). Possessing only a fractional grasp of the actual number of invasions severely limits our ability to approach any of these questions.

The ease by which single species insertions can both be overlooked and profoundly alter ecosystems is illustrated by the case history of the North American mysid *Neomysis americana* which ranges (presumably naturally) from the Gulf of St. Lawrence (Canada) to Florida (Heard et al. 2006; but see Carlton and Hodder 1995, who discuss how seemingly natural confluent ranges may have been altered in historical time). *Neomysis americana* was first reported from the Atlantic coast of South America in Uruguay by Gonzalez (1974), and it has since spread to Argentina (Vinas et al. 2005). Despite this remarkable disjunct distribution, and its historical absence in South American estuaries, it has not been recognized as an alien species by South American workers (Orensanz et al. 2002, list it as cryptogenic; while Schiariti et al. (2006) and Vinas et al. (2005) mention nothing of its history). Remarkably, *Neomysis americana* has become, in a matter of a few decades, a major component of South American coastal food webs: it is the most abundant mysid in Rio de la Plata on the Argentine-Uruguay border, and is "the main food item for juvenile fishes in this estuary" (Schiariti et al. 2006). While Jumars (2007) correctly notes that it was introduced from North to South America, here we have a species which has assumed a fundamental role in Argentinean and Uruguayan ecosystems, but passes without notice in the invasion ecology literature. It is difficult to begin to imagine how many other overlooked *Neomysis*-like case histories have occurred over the past 30 years; let alone the past 300 years.

Finally, a widespread misperception in the literature is that most invasions are benign: that they have little or no impact in the new communities they have colonized. This conclusion is sometimes linked to the "tens rule", which states that only 10% of invasions have an impact, which statistic not only has little to no ecological bearing on marine systems (Carlton 2003), but is, more importantly, not supported by any data. Since most marine invasions (including perhaps 95% or more of all known invasions of marine crustaceans) have been the subject of no qualitative, quantitative, or experimental studies to determine their ecological or other impacts, it is simply not possible to conclude that only 10% (or fewer) of these species have had an impact.

McGeoch et al. (2006) have called for understanding the number of invasions as one measure for assessing the goal of reducing the current rate of global biodiversity loss, specifically relative to "the progress of nations toward the targets of stabilizing invasive alien species (IAS) numbers and the implementation of IAS management plans". Using invasions as a metric for understanding the scale of biodiversity change and loss is, as Richardson et al. (2000) have also emphasized, and as underscored above, highly dependent upon the level of taxonomic expertise available and the funding available for thorough, continuous surveys. Our ability to resolve the scale of invasions both historically and now, to be able to adequately detect future invasions, and thus to monitor changes in global marine biodiversity as we look down the long road of global climate change (Carlton 2000; Occhipinti-Ambrogi 2007; Sorte et al. 2010) is, in turn, dependent on our ability to rebuild and expand to unprecedented levels, the fields of morphological and molecular (Geller et al. 2010) taxonomy and systematic biology in not only museums but in universities as well.

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# Part II
# Global Dispersal

# Human-Mediated Spread of Alien Crabs

**Annette Brockerhoff and Colin McLay**

**Abstract** The introduction and spread of alien species is now recognized as one of the most significant modifiers of biodiversity. In the absence of their normal predators and parasites, alien crabs often establish high population densities and tend to compete fiercely with local fauna for food and shelter. A total of 73 species of brachyuran and crab-like anomuran decapods are known as alien species, of which 48 (65.8%) have become established. Three groups stand out with their high number of alien species: namely the Portunoidea (swimming crabs, such as *Carcinus maenas*), Grapsoidea (shore crabs, such as *Hemigrapsus takanoi*) and Majioidea (spider crabs, such as *Pyromaia tuberculata*). Canals, ballast water and hull fouling are the primary vectors/routes by which crabs are spread. Transfer of crabs with shellfish, combined with the live seafood trade, are also important. The Mediterranean Sea has the highest number of alien brachyuran species as many have invaded through the Suez Canal, making the Mediterranean the meeting place of Atlantic and Indo-West Pacific faunas. We used egg size as an indicator of life history strategies and a comparison of established alien species with a matched control group of crabs shows that mean egg size of alien crabs is smaller, but it shows wide variation. The Erythrean invaders from the Red Sea are a representative sample of aliens that shows the same pattern even though their transfer agent was a canal rather than shipping. Deliberate transfers to establish new fisheries has been successful in some cases (e.g., *Paralithodes camtschaticus* to the Barents Sea), but some species are still expanding their range and so their ultimate effects are unknown. The impact of most aliens remains uncertain, but recent work on *Hemigrapsus sanguineus* provides an excellent model of the kind of experimental field work that needs to be done. The current focus of attention on coastal aliens has resulted in the unfortunate agreement, at the international level, that ballast water can be dumped with impunity on the high seas, without any knowledge of its impact.

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# 1 Introduction

The introduction and spread of marine alien species is now recognized as one of the most significant global modifiers of marine biodiversity along with marine pollution, habitat alteration and overexploitation. The Mediterranean Sea, for example, has been colonized by large numbers of alien species, the current total standing at 573 and increasing at the rate of ten species per year (Galil 2007, 2009). Many of these are Indo-Pacific species which have gained access by the Suez Canal (Holthuis and Gottlieb 1958). Brachyura are playing a major part in marine bioinvasions which are occurring worldwide and at an increasing speed over the last century (Cohen and Carlton 1998; Ruiz et al. 2000). Of the approximately 6,800 described brachyuran crabs (Ng et al. 2008) many have invaded new regions, particularly in areas where there is a high density of maritime traffic, but there are still some parts of the world where alien crabs remain unknown. The global invasive species database (Invasive species specialist group, http://www.issg.org/database) holds a list of the world's 100 worst (an emotive term incapable of scientific definition and therefore best avoided) invasive alien species (Lowe et al. 2000) including two brachyurans, the European green crab *Carcinus maenas* (Decapoda: Portunidae) and the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Varunidae). These two crab species have been widely studied and their biology, impact and invasion history has recently been comprehensively summarised (Klassen and Locke 2007; Veilleux and de Lafontaine 2007). Most of these introductions are thought to be anthropogenic, often in ballast water or hull fouling, and their impacts have been diverse, from being an aggressive competitor for food and shelter with native species, to affecting aquaculture facilities and harvests and causing structural damage to river banks (see biological synopsis of Klassen and Locke 2007; Veilleux and de Lafontaine 2007). However, for most alien species we do not have any evidence that their impact will be disruptive but this should not lead to complacency. For most alien species there have been no qualitative, quantitative, or experimental studies on impact: such studies are only just beginning (see for example Sect. 5.8 *Hemigrapsus sanguineus*). Herein, absence of any statement about impact does not mean that presence of the species is benign. Several deliberate introductions of these crustaceans have resulted in profitable fisheries, but others have not.

Biological invasions are synergistic processes which are influenced by the characteristics of the invading species and by the effects of the transport vector and the recipient environment. Whether more diverse native marine communities are less vulnerable to invasion, depends upon the spatial scale at which you examine the problem (Fridley et al. 2007). It is impossible to make exact and quantitative prediction of the next marine invaders, but establishing biological trends will be an important ingredient allowing better understanding of marine invasions. For example, it is generally believed that high fecundity, planktonic dispersal, broad spectrum of habitat and food preferences, tolerance to a wide range of environmental conditions, longevity and a large size are usually good traits for being a successful marine invader (Hutchings et al. 2002). However, a particular invader typically does not comprise all of these traits and it is not always clear which of those are the most influential for successful invasion. As a rule of thumb it has been proposed that 10% of introduced species will settle and 1% will become invasive in the terrestrial environment (Williamson and Fitter 1996). Streftaris et al. (2005) and Zenetos et al. (2005) have proposed that 55% (456 of 828 species) and 52% (385 of 745 species) have become established in 'European Seas' and the Mediterranean respectively. However, caution is required when drawing conclusions about the chances of successful establishment because the actual number of species "inoculated" into the 'European Seas' and the Mediterranean remains unknown and the estimates may well be far too high because the total number of species arriving is underestimated (J. Carlton, pers. comm. 2010). Miller and Ruiz (2009) provide an elegant analysis of the consequences of defining the species pool in different ways.

Here, a world overview is provided of the 73 alien brachyuran and crab-like anomuran decapods, some of which became established others not. The authors are particularly interested in comparing the decapod species that became successful invaders versus the ones that were detected but have failed to become established so far. What are the contributing factors in their biology that make the difference or is it all just a matter of chance? This study comprises detailed information for about a third of the species, the most invasive ones, but less tends to be known about some of the other aliens. Egg-size has been used to compare life histories of the crabs that have become established with others that have not been detected outside their native range. Hines (1982, 1992) has provided an analysis of the determinants of brood characters of some crabs. In the absence of any exhaustive world-wide literature search we examined the reprint collection of one of us (CLM, more than 7,000 papers on Brachyura and Anomura) and assembled a dataset of the egg size of some 200 crab species that have never been recorded as alien and used this as a control group for comparison with the aliens. Only data has been used from the same families as the aliens, so the control group is not entirely representative of crabs as a whole. These data were not available for some aliens so we used data from the same genus or in a few cases the same family to estimate their egg size. Egg volume ($mm^3$) was estimated from egg diameter by assuming that the shape was spherical. Egg size usually increases as development proceeds and where authors gave a range of sizes we used mean egg diameter.

Besides the scientific literature there are a number of regularly updated databases which provide the most recent information: ISSG: Invasive Species Specialist Group (http://www.issg.org/database/), CIESM: Atlas of exotic crustaceans in the Mediterranean (http://www.ciesm.org/atlas/index.html), NIMPIS: National Introduced Marine Pest Information System (http://crimp.marine.csiro.au/nimpis), USGS (http://nas.er.usgs.gov/) and others (see reference list for more details).

This review includes a few freshwater species, but deals primarily with marine species as well as brackish water and catadromous species, such as *Rhithropanopeus harrisii* and *Eriocheir sinensis*, as they have parts of their lifecycle in the marine environment. For brachyuran classification we follow the annotated checklist of extant brachyuran crabs of the world from Ng et al. (2008), and other recent references when available. The anomuran king crab, *Paralithodes camtschaticus* has also been included because its deliberate introduction into the Bering Sea has been well documented and a porcellanid *Petrolisthes armatus*.

The following definitions are used: “native species”, within its natural range; “alien”, outside its natural geographic range; “established species”, species with self maintaining populations (producing their own recruits) or with many records; “not established species”, species with sporadic recordings in place and time outside their native range; we reserve the term “invasive/pest species” for those which have spread far from their putative release point and have a serious community impact. The alien species seen occasionally are mostly one-off records that indicate a potential for transportation, but not necessarily colonization. We do not include records of species “in transit” as fouling or in ballast water. The authors only include species found in the new environment and free of the means of transport. The term “crab” is used to include all brachyurans plus crab-like anomurans (Lithodidae and Porcellanidae) and qualify it when referring specifically to one of these groups.

## 2 Alien Marine Crabs

Currently there are 93 described brachyuran families which include 6,793 described species (Ng et al. 2008). Of these crabs 73 species (in 26 families including Porcellanidae and Lithodidae) have been recorded as alien species, of which 48 (65.8%) have become established in various seas and countries (Table 1, Fig. 1). The families with the largest number of alien representatives are Portunidae (15), Grapsidae (6), Pilumnidae (6) and Epialtidae (5). The species that have become established belong to the Portunidae (10), Grapsidae (5), Panopeidae (4), Varunidae (3), Pilumnidae (3), Epialtidae (3) and Leucosiidae (3).

In their normal range these alien species live at depths ranging from the intertidal to 1,400 m (Table 2). By plotting all alien species on a composite depth scale and recording all species whose range encompasses each depth zone we obtain a depth profile (Fig. 2). We assumed that species could occur at any depth between the two limits. The greatest number of aliens is found in shallow waters (11–20 m zone) followed by 31–40, 21–30 and 0–10 zones. From there onwards the numbers of aliens gradually decline until 151–160 m, below which the attrition rate changes to its lowest. The distribution of established aliens in relation to depth follows a similar trend. The discrepancy between the total and established aliens is greatest in shallow waters because the greater ease of sampling enhances the probability of detection of an alien. Given that the Mediterranean has by far the greatest number of alien crab species of any sea, we wanted to know whether it had a similar profile to the rest of the world. In the Mediterranean there are more non-established shallow water alien species than found at comparable depths in the rest of the world’s oceans (Figs. 3 and 4).

Alien crabs have been recorded in most of the common coastal marine habitats. The generic habitats Sand, Rock and Mud are the most common places to find alien species while the biogenic habitats like fouling, shellfish, corals and mangroves cater for species with more specialized requirements. The biogenic habitats not

**Table 1** Overview of native and alien distribution and likely vectors of alien marine brachyuran decapods worldwide

| Family | Species | Origin (Native range) | Alien range | Likely vector/ route | Recent reference |
|---|---|---|---|---|---|
| R – Raninidae | *Notopus dorsipes* | Indo-west Pacific, Red Sea to Malay Archipelago | Mediterranean | Suez Canal | Galil (2007) |
| Cl – Calappidae | *Calappa hepatica* | Indo-Pacific, Red Sea to Hawaii, Clipperton Island | Mediterranean | Suez Canal | Balkis and Çeviker (2003) |
| Cl – Calappidae | ***Calappa pelii*** | Tropical East Atlantic | Mediterranean | Unknown | CIESM |
| Cl – Calappidae | *Cryptosoma cristatum* | Tropical East Atlantic | Mediterranean | Unknown | Garcia-Raso (1993) |
| Cl – Matutidae | *Ashtoret lunaris* | Indo-West Pacific, Red Sea to Australia | Mediterranean | Suez Canal | Galil and Golani (1990) |
| Cc – Cancridae | *Glebocarcinus amphioetus* | Northwest Pacific (E China Sea, Yellow Sea, Sea of Japan), Northeast Pacific (Gulf of California) | Southwest Pacific (New Zealand) | Hull fouling or ballast water | Brockerhoff and McLay (2008) |
| Cc – Cancridae | *Metacarcinus magister* | Northeast Pacific | Northwest Atlantic (Massachusetts), Northwest Pacific (Japan) | Accidental release? | Abe (1981) |
| Cc – Cancridae | ***Metacarcinus novaezelandiae*** | Southwest Pacific (New Zealand) | Southwest Pacific (South Australia, Tasmania) | Accidental transfer with oysters | McLay (1988) |
| Cc – Cancridae | *Romaleon gibbosulum* | Northwest Pacific (E China Sea, Yellow Sea, Sea of Japan) | Southwest Pacific (New Zealand) | Hull fouling or Ballast water | Brockerhoff and McLay (2008) |
| Da – Dairidae | *Daira perlata* | Indo-west Pacific | Mediterranean | Suez Canal | Enzenross and Enzenross (1995) |

(continued)

**Table 1** (continued)

| Family | Species | Origin (Native range) | Alien range | Likely vector/ route | Recent reference |
|---|---|---|---|---|---|
| Do – Dorippidae | ***Dorippe quadridens*** | Indo-west Pacific (Red Sea to Australia and China) | Mediterranean | Suez Canal | Galil (2005) |
| E – Menippidae | *Sphaerozius nitidus* | Indo-west Pacific | Mediterranean | Suez Canal | Ramadan and Dowidar (1972) |
| Go – Euryplacidae | ***Eucrate crenata*** | Indo-Pacific (Red Sea to Hawaii) | Mediterranean | Suez Canal | Enzenross and Enzenross (2000) |
| L – Leucosiidae | ***Ixa monodi*** | Red Sea | Mediterranean | Suez Canal | Holthuis and Gottlieb (1956); Galil and Kevrekidis (2002) |
| L – Leucosiidae | ***Coleusia signata*** | Indo-west Pacific | Mediterranean | Suez Canal | Grippa (1982) |
| L – Leucosiidae | ***Myra subgranulata*** | Western Indian Ocean (Red Sea to Madagascar) | Mediterranean | Suez Canal | Corsini Foka and Kondilatos (2006) |
| M – Epialtidae | ***Herbstia nitida*** | Tropical East Atlantic (Gulf of Guinea) | Mediterranean | Unknown | Galil (2007) |
| M – Epialtidae | *Hyastenus hilgendorfi* | Indo-west Pacific (Red Sea to Malay Archipelago) | Mediterranean | Suez Canal | Galil (2006) |
| M – Epialtidae | ***Hyastenus spinosus*** | Indo-west Pacific (Red Sea to Fiji) | Hawaii | Hull fouling | Carlton and Eldredge (2009) |
| M – Epialtidae | ***Libinia dubia*** | West Atlantic (from Massachusetts to Cuba) | Mediterranean | Ballast water | Enzenross et al. (1997) |
| M – Epialtidae | *Menaethius monoceros* | Indo-Pacific (Red Sea to Hawaii and Tahiti) | Mediterranean | Suez Canal and Shipping | Falciai (2003) |

| | | | | | |
|---|---|---|---|---|---|
| M – Inachoididae | ***Pyromaia tuberculata*** | Northeast Pacific (San Francisco Bay, Gulf of California to Panama Canal) | Southwest Atlantic (Brazil, Argentina), Northwest Pacific (Japan), Southwest Pacific (Australia, New Zealand) | Ballast water | Furota (1996a) |
| M – Majidae | ***Micippa thalia*** | Indo-west Pacific | Mediterranean | Suez Canal | Enzenross and Enzenross (1995) |
| M – Oregoniidae | ***Chionoecetes opilio*** | Sub-Arctic species found in North Pacific, Beaufort Sea, Arctic and Northwest Atlantic and west coast of Greenland | Barents Sea | Ballast water? | Alvsvag et al. (2009) |
| M – Oregoniidae | *Hyas araneus* | North Atlantic (from Iceland, Spitsbergen and European Russia to the English Channel) | Southern Ocean | Ballast water or ship fouling | Tavares and de Melo (2004) |
| M – Hymenosomatidae | ***Halicarcinus innominatus*** | New Zealand mainland and Stewart Island | Tasmania | Accidentally transported with oysters | McLay (1988) |
| M – Hymenosomatidae | ***Halicarcinus planatus*** | Circum-subantarctic: Chile, Falkland Is, Kerguelen, Macquarie, Campbell, Auckland Ids | Brazil | Transported with oysters | Tavares (2003) |
| M – Hymenosomatidae | *Neorhynchoplax kempi* | Confluence of Euphrates and Tigris Rivers, near Basra, Iraq | In freshwater from Pedro Miguel Locks, Panama Canal | Probably introduced along with an aquarium plant, *Hydrilla verticillata.* | Abele (1972) |

(continued)

**Table 1** (continued)

| Family | Species | Origin (Native range) | Alien range | Likely vector/ route | Recent reference |
|---|---|---|---|---|---|
| Pi – Galenidae | *Halimede tyche* | Indo-west Pacific (Persian Gulf to Australia) | Mediterranean | Suez Canal | Galil (2000) |
| Pi – Pilumnidae | *Actumnus globulus* | Red Sea, Western Indian Ocean | Mediterranean | Suez Canal & Shipping | Galil et al. (2006) |
| Pi – Pilumnidae | *Glabropilumnus laevis* | Indian Ocean | Mediterranean | Suez Canal | CIESM |
| Pi – Pilumnidae | ***Glabropilumnus seminudus*** | Indo-west Pacific | Hawaii | Ballast water fouling | Carlton and Eldredge (2009) |
| Pi – Pilumnidae | ***Pilumnopeus vauquelini*** | Red Sea, Persian Gulf | Mediterranean | Suez Canal | CIESM |
| Pi – Pilumnidae | *Pilumnus minutus* | Indo-west Pacific | Mediterranean | Suez Canal | CIESM |
| Pi – Pilumnidae | ***Pilumnus oahuensis*** | Unknown | Hawaii | Fouling or ballast water | Carlton and Eldredge (2009) |
| Pl – Pilumnoididae | *Pilumnoides inglei* | South America (perhaps Patagonia) | Northeast Atlantic (Plymouth) | Fouling on derelict ship? | Guinot and Macpherson (1987) |
| Po – Portunidae | *Callinectes danae* | West Atlantic (from North Carolina to Brazil) | Mediterranean | Ballast water | Mizzan (1993) |
| Po – Portunidae | ***Callinectes sapidus*** | North and Southwest Atlantic (from Nova Scotia to Uruguay) | Baltic, Black Sea, Mediterranean, North Sea, and Northeast Atlantic | Vessel fouling, ballast water, deliberate or accidental release | Carlton and Eldredge (2009); Galil (2007) |
| Po – Portunidae | ***Carcinus aestuarii*** | Mediterranean | Northwest Pacific (Japan), South Africa | Shipping, ballast water | Carlton and Cohen (2003) |

| | | | | | |
|---|---|---|---|---|---|
| Po – Portunidae | ***Carcinus maenas*** | East Atlantic, North Sea, Baltic Atlantic coast of Europe and northern Africa, from North Norway and Iceland to Mauritania | North and Southwest Atlantic (Argentina), South Africa, North Pacific, Australia, Tasmania | Ship hulls, ballast water | Klassen and Locke (2007) |
| Po – Portunidae | ***Carupa tenuipes*** | Indo-Pacific (from Red Sea to Japan, Australia, Polynesia and Hawaii) | Mediterranean | Suez Canal | Galil (2004) |
| Po – Portunidae | *Charybdis feriata* | Indo-Pacific (E and S Africa, from China and Japan to Australia) | Mediterranean | Escape from seafood holding tank on merchant ship | Abello and Hispano (2006) |
| Po – Portunidae | ***Charybdis hellerii*** | Indo-west Pacific (Red Sea to New Caledonia) | Mediterranean, North and Southwest Atlantic (Florida to Brazil) French Guiana | Suez Canal, ballast water and fouling | CIESM |
| Po – Portunidae | ***Charybdis japonica*** | China, Japan, Korea, Taiwan, Malaysia | Southwest Pacific (New Zealand), Mediterranean | Vessel fouling, ballast water | Smith et al. (2003) |
| Po – Portunidae | ***Charybdis longicollis*** | Indo-Pacific | Mediterranean | Suez Canal | Galil and Innocenti (1999) |
| Po – Portunidae | *Liocarcinus navigator* | East Atlantic, Mediterranean, Adriatic Sea, Black Sea | Southwest Atlantic | Fouling and/or ballast water? | De Melo and Crivelaro (2002) |
| Po – Portunidae | ***Portunus pelagicus*** | Indo-Pacific | Mediterranean & Turkey | Suez Canal | CIESM |

(continued)

**Table 1** (continued)

| Family | Species | Origin (Native range) | Alien range | Likely vector/ route | Recent reference |
|---|---|---|---|---|---|
| Po – Portunidae | ***Scylla serrata*** | Indo-Pacific, Red Sea to Tahiti, New Zealand occasionally | Hawaii, Southwest Atlantic (isolated record from Brazil) | Intentionally for fishery | Carlton and Eldredge (2009) |
| Po – Portunidae | *Thalamita gloriensis* | Indo-West Pacific | Mediterranean | Suez Canal, fouling and/or ballast water | Relini and Mori (1979) |
| Po – Portunidae | *Thalamita indistincta* | Indo-Pacific | Mediterranean | Suez Canal | Hasan and Noël (2008) |
| Po – Portunidae | ***Thalamita poissonii*** | Indo-West Pacific (Red Sea to Taiwan) | Mediterranean | Suez Canal | Holthuis (1956) |
| X – Panopeidae | ***Acantholobulus pacificus*** | Probably tropical Eastern Pacific | Hawaii | Hull fouling and/ or Ballast water | Carlton and Eldredge (2009) |
| X – Panopeidae | ***Dyspanopeus sayi*** | Northwest Atlantic | Mediterranean | Ballast water, accidental transfer with clam seed | Froglia and Speranza (1993) |
| X – Panopeidae | ***Panopeus lacustris*** | Northwest Atlantic – Bermuda and southern Florida through the Caribbean and south to Brazil | Hawaii | Ship Fouling | Carlton and Eldredge (2009) |
| X – Panopeidae | ***Rhithropanopeus harrisii*** | Northwest Atlantic New Brunswick (Canada) to Veracruz (Mexico) | Baltic, Black Sea, Mediterranean, North Sea, Northeast Pacific, Northeast Atlantic, Brazil, Panama Canal, Japan, Aral, Caspian Sea, Azov Sea | Ballast water, accidental transfer with clam/oyster seed, vessel fouling | Roche and Torchin (2007) |

| | | | | | |
|---|---|---|---|---|---|
| X – Xanthidae | ***Atergatis roseus*** | Indo-Pacific (Red Sea to Fiji) | Mediterranean | Suez Canal | Lewinsohn and Holthuis (1964) |
| Gr – Grapsidae | ***Platychirograpsus spectabilis*** | Mexico | Hillsborough River, Tampa Bay, Florida, Gulf of Mexico | Imported with cedar logs used to make cigar boxes | Marchand (1946) |
| Gr – Grapsidae | *Grapsus granulosus* | Red Sea | Mediterranean | Suez Canal, vessel fouling | Zaouali et al. (2007) |
| Gr – Grapsidae | ***Metopograpsus oceanicus*** | Indo-west Pacific | Hawaii, Guam | Fouling and ballast water | Carlton and Eldredge (2009) |
| Gr – Grapsidae | ***Pachygrapsus fakaravensis*** | West and Central Pacific | Hawaii | Fouling and ballast water | Carlton and Eldredge (2009) |
| Gr – Grapsidae | ***Pachygrapsus marmoratus*** | Northeast Atlantic (southern Europe: Portugal, Spain, France, Black Sea, Mediterranean, Moroccan Atlantic, Canary Islands, Madeira, Azores) | Southern and Southwest England | Fouling or ballast water? | Dauvin (2008) |
| Gr – Grapsidae | ***Pachygrapsus transversus*** | Tropical and warm-temperate western and eastern Atlantic and Eastern Pacific Oceans | Mediterranean | Hull fouling | Zaouali et al. (2007) |
| Gr – Plagusiidae | ***Percnon gibbesi*** | North and Southeast Pacific (California to Chile), North and Southwest Atlantic (Florida to Brazil), Madeira to Gulf of Guinea (North and Southeast Atlantic) | Mediterranean | Vessel transported; via Strait of Gibraltar; coastal larval transport | Cannicci et al. (2006) |

(continued)

**Table 1** (continued)

| Family | Species | Origin (Native range) | Alien range | Likely vector/ route | Recent reference |
|---|---|---|---|---|---|
| Gr – Plagusiidae | ***Plagusia squamosa*** | Indo-Pacific (Red Sea to eastern Pacific) | Mediterranean | Suez Canal, as fouling organism | Zaouali et al. (2007) |
| Gr – Sesarmidae | ***Nanosesarma minutum*** | Indo-west Pacific (East Africa to Thailand) | Northwest Pacific (Hawaii) | Ballast water? | Carlton and Eldredge (2009) |
| Gr – Varunidae | ***Eriocheir sinensis*** | Northwest Pacific (Southeast Asia; China, Korea) | Baltic, Black Sea, Mediterranean, most of Europe, U.K., Spain and Portugal, recently Iran and Iraq, San Francisco Bay, Chesapeake and Delaware Bays | Freshwater canals, and ballast water? | Dittel and Epifanio (2009) |
| Gr – Varunidae | ***Hemigrapsus sanguineus*** | Northwest Pacific (from Sakhalin to Hong Kong and Japan) | North Sea, Northeast Atlantic (France, Netherlands), Northwest Atlantic (Schoodic Peninsula, Maine south to New Jersey, Massachusetts to North Carolina), Mediterranean | Vessel fouling, ballast water | Schubart (2003) |
| Gr – Varunidae | ***Hemigrapsus takanoi*** | Northwest Pacific (Japan to China) | Northeast Atlantic, North Sea (Spain, France, Belgian, Netherlands) | Vessel fouling, ballast water | Asakura and Watanabe (2005) |
| O-Macrophthalmidae | ***Macrophthalmus graeffei*** | Western Indo-Pacific | Mediterranean | Suez Canal | Ksiunin and Galil (2004) |

| | | | | | |
|---|---|---|---|---|---|
| AnP – Porcellanidae (Anomura) | ***Petrolisthes armatus*** | Eastern Pacific (Gulf of California to Peru), the western Atlantic (Bermuda, Gulf of Mexico, Caribbean, and Brazil), and Western Africa | Northward from Florida to coasts of Georgia and South Carolina | Larvae in ballast water? and adults transported with oysters or spreading as a result of Global warming? | Hollebone and Hay (2007) |
| AnP – Porcellanidae (Anomura) | ***Petrolisthes elongatus*** | New Zealand | Tasmania, and Victoria & New South Wales, Australia | Accidental transport along with oysters imported for sale | McLay (1988) |
| AnL – Lithodidae (Anomura) | ***Paralithodes camtschaticus*** | Okhotsk and Japan Sea, Bering Sea and North Pacific Ocean | Barents Sea initially, now spreading southwards along Norwegian coast | Transplanted by Russian scientists to establish a new fishery | Jørgensen (2005) |

Taxonomic families listed in order following Ng et al. (2008) classification. Following superfamily names are abbreviated: Calappoidea (Cl), Cancroidea (Cc), Dairoidea (Da), Dorippoidea (Do), Eriphioidea (E), Goneplacoidea (Go), Grapsoidea (Gr), Leucosioidea (L), Majoidea (M), Ocypodoidea (O), Pilumnoidea (Pi), Pilumnoididae (Pl), Portunoidea (Po), Raninoidea (R), Xanthoidea (X), Anomura (An). At least one reference is provided for each alien species with additional references in the text for species treated in greater detail. Species in bold have become established somewhere outside their native range

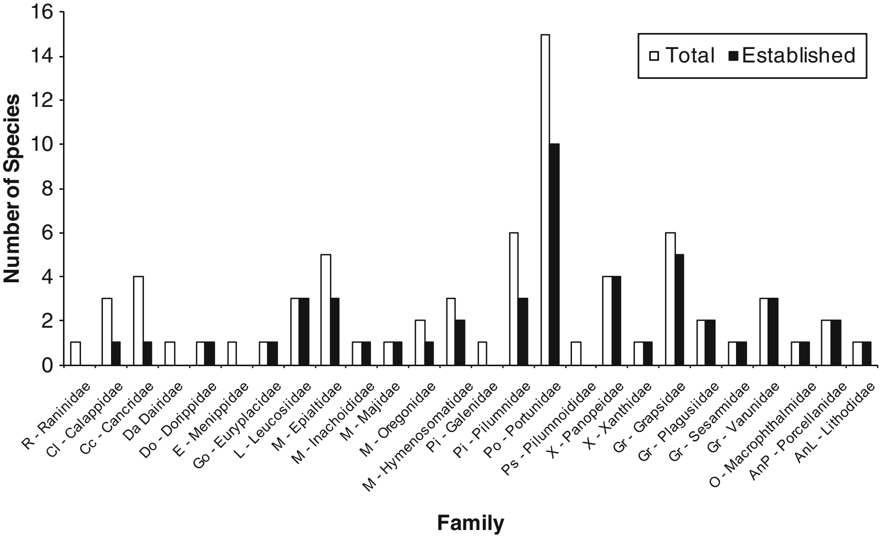

**Fig. 1** Number of established and non-established alien species recorded in each Family (*Note*: Taxonomic classification of the Brachyura follows Ng et al. 2008. Two anomuran families are also shown. Capital letters in front of family names indicate belonging into same superfamily, i.e. from *left to right R* Raninoidea, *Cl* Calappoidea, *Cc* Cancroidea, *Da* Dairoidea, *Do* Dorripoidea, *E* Eriphoidea, *Go* Goneplacoidea, *L* Leucosioidea, *M* Majoidea, *Pi* Pilumnoidea, *Po* Portunoidea, *Ps* Pseudozioidea, *X* Xanthoidea, *Gr* Grapsoidea, *O* Ocypodoidea, *An* Anomura)

only provide food, but may also provide refuge or concealment. Some, such as algae, shellfish and fouling may also directly or indirectly provide the means of transport to a new area. The proportion of established species is greater in the biogenic habitats than it is in sand, rock or mud (Fig. 5).

## 3 Regional Invasions (See Table 3, Fig. 6)

Here we present the alien species in different parts of the world's oceans. The regions are not precisely defined and mainly emphasize coastal rather then oceanic crab faunas.

### *3.1 The North Sea*

The North Sea area has become home to six alien crab species: *Rhithropanopeus harrisii*, *Eriocheir sinensis*, *Hemigrapsus sanguineus* and *Hemigrapsus takanoi*. *Callinectes sapidus* has been reported from the German North Sea, but has not yet established itself (Nehring et al. 2008). The Russian introduction of the anomuran

**Table 2** Overview of size, depth distribution and habitat in native range of alien marine brachyuran decapods worldwide

| Family | Species | Max size CW or CL mm | Depth distribution (m) | Habitat |
|---|---|---|---|---|
| R – Raninidae | *Notopus dorsipes* | CL 25 mm | 50–100 m | Sandy bottoms |
| Cl – Calappidae | *Calappa hepatica* | CL 51 mm | Intertidal to 100 m | Sandy, muddy or gravel bottoms |
| Cl – Calappidae | ***Calappa pelii*** | CL 59 mm | 20–400 m, mostly between 50 and 150 m | Muddy bottoms |
| Cl – Calappidae | *Cryptosoma cristatum* | CL 59 mm | Intertidal to 75 m | Sandy or coralligenous bottoms |
| Cl – Matutidae | *Ashtoret lunaris* | CL 55 mm | Surf zone | Sandy, muddy-sand |
| Cc – Cancridae | *Glebocarcinus amphioetus* | CW 41 mm | Intertidal to 65 m; also down to 260 m | Weedy or rocky beaches near the low tide mark |
| Cc – Cancridae | *Metacarcinus magister* | CW 200 mm | Intertidal to 107 m | Eelgrass, sandy shell bottoms |
| Cc – Cancridae | ***Metacarcinus novaezelandiae*** | CW 150 mm | Intertidal to 50 m | Under stones, among large seaweed in intertidal, on sandy bottom in deeper water |
| Cc – Cancridae | *Romaleon gibbosulum* | CW 42 mm | 33–238 m | Muddy-sandy or broken shell and sandy bottoms |
| Da – Dairidae | *Daira perlata* | CL 35 mm | 2–20 m | Sand, stones, coral reefs |
| Do – Dorippidae | ***Dorippe quadridens*** | CL 42 mm | Intertidal to 73 m, mostly to 30 m | Sandy, muddy or gravelly bottom, but also on coral reefs and oyster banks |
| E – Menippidae | *Sphaerozius nitidus* | CL 13 mm | Intertidal | Rock crevices, on oil platform |
| Go – Euryplacidae | ***Eucrate crenata*** | CL 35 mm | 10–100 m | Sandy-mud bottom. |
| L – Leucosiidae | ***Ixa monodi*** | CL 35 mm | 14–60 m | Sandy-mud bottom |
| L – Leucosiidae | ***Coleusia signata*** | CL 25 mm | Sub-tidal to 22 m | Muddy and sandy gravel bottoms, with *Halophila* |
| L – Leucosiidae | ***Myra subgranulata*** | CL 40 mm | 8–150 m | Sandy-mud bottom |

(continued)

**Table 2** (continued)

| Family | Species | Max size CW or CL mm | Depth distribution (m) | Habitat |
|---|---|---|---|---|
| M – Epialtidae | ***Herbstia nitida*** | CL 13 mm | Intertidal to 73 m | Rough bottom, on rock, coral, calcareous algae. Mediterranean record from a submarine cave |
| M – Epialtidae | *Hyastenus hilgendorfi* | CL 36 mm | 2–93 m | Coarse sand, shell gravel, clay |
| M – Epialtidae | ***Hyastenus spinosus*** | CL 54 mm | 10–120 m | Pilings, coarse shells and sand |
| M – Epialtidae | ***Libinia dubia*** | CL 100 mm | 5– to 25 m | Among algae and seaweed |
| M – Epialtidae | *Menaethius monoceros* | CL 27 mm | 5–30 m | Rocky or sandy sub-tidal, on reef, among seaweeds or *Sargassum* |
| M – Inachoididae | ***Pyromaia tuberculata*** | CW 18 mm | Intertidal to 650 m | Under rocks in bays, sub-littoral on protected wharf pilings, sandy or muddy bottoms |
| M – Majidae | ***Micippa thalia*** | CL 40 mm | 2–100 m | Sandy, muddy, gravel, shell grit bottoms, among stones |
| M – Oregoniidae | ***Chionoecetes opilio*** | CW 140 mm | 50–1,400 m | Soft bottoms |
| M – Oregoniidae | *Hyas araneus* | CL 105 mm | Lower intertidal to 50 m (up to 555 m) | Rocky, muddy and sandy bottoms |
| M – Hymenosomatidae | ***Halicarcinus innominatus*** | CW ~ 19 mm | Intertidal from high rock pools to low tide level | Rocky shores under stones, among seaweeds, fouling on wharf piles |
| M – Hymenosomatidae | ***Halicarcinus planatus*** | CW ~24 mm | Intertidal to 270 m | Sheltered shores, under stones, and among algae |
| M – Hymenosomatidae | *Neorhynchoplax kempi* | CL ~6 mm | Freshwater | In the aquarium weed *Hydrilla verticillata* |
| Pi – Galenidae | *Halimede tyche* | CL 22 mm | 2–60 m | Sandy bottoms |
| Pi – Pilumnidae | *Actumnus globulus* | CL 14 mm | 25–50 m | Rocky sand |
| Pi – Pilumnidae | *Glabropilumnus laevis* | CL 8 mm | 5–25 m | Sand and stones |

| | | | | |
|---|---|---|---|---|
| Pi – Pilumnidae | ***Glabropilumnus seminudus*** | CW 10 mm | 5–25 m | Sand and stones |
| Pi – Pilumnidae | ***Pilumnopeus vauquelini*** | CL 10 mm | 0–3 m | Sandy mud, mixed with gravel and stones, or among, *Halophila*, *Sargassum*, and rich vegetation |
| Pi – Pilumnidae | *Pilumnus minutus* | CL 10 mm | 20–33 m | Stony, *Caulerpa* and *Halimeda* bottom, shell, gravel |
| Pi – Pilumnidae | ***Pilumnus oahuensis*** | CW 25 mm | 0–5 m | Associated with sponges, tunicates and barnacles which are attached to buoys, floats, and piling |
| Pl – Pilumnoididae | *Pilumnoides inglei* | CW 18 mm | 0–25 m | Among algae |
| Po – Portunidae | *Callinectes danae* | CL 58 mm | Lower intertidal to 75 m | Muddy estuaries, mangroves, open coast, hypersaline lagoons |
| Po – Portunidae | ***Callinectes sapidus*** | CW 209 mm | Intertidal to 90 m | Estuaries and shallow coastal waters |
| Po – Portunidae | ***Carcinus aestuarii*** | CW 60 mm | Intertidal to 26 m | Estuarine and shallow coastal waters; muddy sand, among sea grass, under stones, typically in sheltered habitats |
| Po – Portunidae | ***Carcinus maenas*** | CW 100 mm | Intertidal to 60 m | Sandy to rocky bottoms, estuarine to marine habitats |
| Po – Portunidae | ***Carupa tenuipes*** | CL 42 mm | Intertidal – 80 m | Among coral reef, coral rubble, rocky bottoms |
| Po – Portunidae | *Charybdis feriata* | CW 200 mm | Usually sub-tidal, 10–60 m | Mostly on sandy or muddy areas, occasionally in rocky areas, or on coral reef flats |
| Po – Portunidae | ***Charybdis hellerii*** | CW 80 mm | Intertidal – 50 m | On soft bottom, but also among rocks and live corals |
| Po – Portunidae | ***Charybdis japonica*** | CW 120 mm | 5–50 m | Eelgrass, estuarine and marine |

(continued)

**Table 2** (continued)

| Family | Species | Max size CW or CL mm | Depth distribution (m) | Habitat |
|---|---|---|---|---|
| Po – Portunidae | ***Charybdis longicollis*** | CL 30 mm | 10–80 m | Sandy to muddy bottom |
| Po – Portunidae | ***Liocarcinus navigator*** | CW 40 mm | Lower intertidal to 108 m | Hard and soft bottoms |
| Po – Portunidae | ***Portunus pelagicus*** | CL 70 mm | Intertidal to 55 m | Sandy or muddy substrate |
| Po – Portunidae | ***Scylla serrata*** | CW 210 mm | Low tide to 5 m | Muddy bottoms in brackish water among mangroves and in estuaries |
| Po – Portunidae | *Thalamita gloriensis* | CW 17 mm | 0–40 m | Coral sands and seaweeds |
| Po – Portunidae | *Thalamita indistincta* | CW 16 mm | Intertidal to 76 m | Sandy to muddy bottom |
| Po – Portunidae | ***Thalamita poissonii*** | CL 18 mm | 0–80 m | Under stones, sandy and sandy-mud bottoms, with *Posidonia*, *Caulerpa* |
| X – Panopeidae | ***Acantholobulus pacificus*** | CW 30 mm | Intertidal to 10 m | Associated with sponges, barnacles, tunicates on buoys and floats |
| X – Panopeidae | ***Dyspanopeus sayi*** | CL 25 mm | Intertidal to 5 m | Shallow brackish waters, soft bottoms with sparse stones and mussel beds |
| X – Panopeidae | ***Panopeus lacustris*** | CW 50 mm | Intertidal to 5 m | Algal mats, sabellariid reefs, mudflats in seagrass beds, under coral debris, and on mangroves |
| X – Panopeidae | ***Rhithropanopeus harrisii*** | CL 20 mm | Lower intertidal to 36 m | Brackish waters (estuarine habitats) and lakes; sandy muddy bottoms with stones or oyster reefs |
| X – Xanthidae | ***Atergatis roseus*** | CL 60 mm | 0–12 m | Rock and rubble |
| Gr – Grapsidae | ***Platychirograpsus spectabilis*** | CW ~45 mm | Rivers | In burrows, amongst rocks & wooden debris |
| Gr – Grapsidae | ***Grapsus granulosus*** | CL 23 mm | Intertidal | Rocky intertidal |

| | | | | |
|---|---|---|---|---|
| Gr – Grapsidae | ***Metopograpsus oceanicus*** | CL 25 mm | Intertidal | Rocky shore |
| Gr – Grapsidae | ***Pachygrapsus fakaravensis*** | CW 20 mm | Intertidal | Among rubble, algae and rocks |
| Gr – Grapsidae | ***Pachygrapsus marmoratus*** | CW 40 mm | Supra-tidal to infra-tidal | On rocky shores. Also below stones on sandy mud in estuaries and lagoons |
| Gr – Grapsidae | ***Pachygrapsus transversus*** | CW 26 mm | Semi-terrestrial and intertidal | Among rubble, algae and rocks |
| Gr – Plagusiidae | ***Percnon gibbesi*** | CL 30 mm | Shallow sub-tidal (1–2 m) | In rocky crevices |
| Gr – Plagusiidae | ***Plagusia squamosa*** | CL M 45 mm | Intertidal | Among stones, corals, known to attach itself to floating timber and the hull of ships |
| Gr – Sesarmidae | ***Nanosesarma minutum*** | CW 10 mm | Intertidal to 5 m | Estuarine, associated with oyster bed |
| Gr – Varunidae | ***Eriocheir sinensis*** | CL 62 mm | Shallow waters | Rivers, estuaries, lagoons, coastal regions |
| Gr – Varunidae | ***Hemigrapsus sanguineus*** | CL 30 mm | Intertidal, sometimes sub-tidal | Rocky bottoms |
| Gr – Varunidae | ***Hemigrapsus takanoi*** | CW 25 mm | Mid to low intertidal, occasionally sub-tidal (to 20 m) | Among rocks, cobbles and soft sediment |
| O – Macrophthalmidae | ***Macrophthalmus graeffei*** | CL F 13 mm | 5–74 m | Fine sand with little mud |
| AnP – Porcellanidae (Anomura) | ***Petrolisthes armatus*** | CW ~14 mm | Shallow sub-tidal and inter-tidal habitats | Rocky rubble and oyster reefs at high densities |
| AnP – Porcellanidae (Anomura) | ***Petrolisthes elongatus*** | CL ~17 mm | Intertidal from high tide to just below low tide | Rocky shores, found in large numbers under stones and boulders. Also on wharf piles |
| AnL – Lithodidae (Anomura) | ***Paralithodes camtschaticus*** | CL ~220 mm | 3–370 m | Spawn in shallow rocky areas among seaweed but feed on soft bottoms in deeper water |

Taxonomic families listed in order following Ng et al. (2008) classification. Following superfamily names are abbreviated: Calappoidea (Cl), Cancroidea (Cc), Dairoidea (Da), Dorippoidea (Do), Eriphioidea (E), Goneplacoidea (Go), Grapsoidea (Gr), Leucosioidea (L), Majoidea (M), Ocypodoidea (O), Pilumnoidea (Pi), Pilumnoididae (Pl), Portunoidea (Po), Raninoidea (R), Xanthoidea (X), Anomura (An). References are provided in text. Species in bold have become established somewhere outside their native range

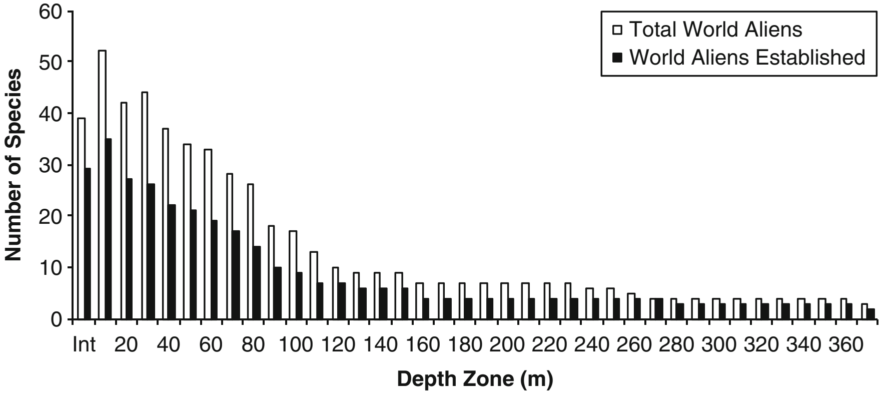

**Fig. 2** Depth distribution of non-established and established aliens in the world's oceans. All species were plotted on the same depth scale and their distribution from the minimum to the maximum depth was assumed to be continuous. The total number and number of established aliens are shown separately for each depth zone (*Note*: the final bars on the depth axis indicate the number of species who live at depths greater than 370+ m)

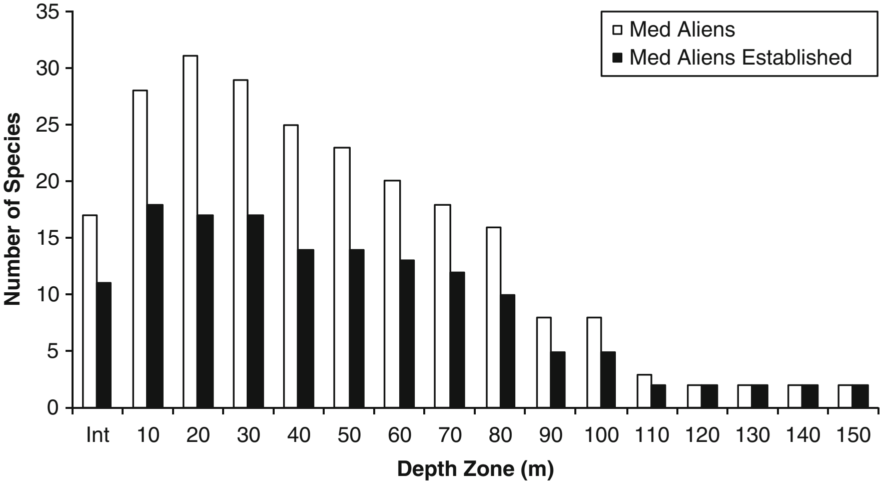

**Fig. 3** Depth distribution of non-established and established alien crabs in Mediterranean Sea (See caption of Fig. 2 for explanation)

crab *Paralithodes camtschaticus* from the Pacific into the Barents Sea to establish a new fishery has resulted in this crab spreading along the Norwegian coast (Jorgensen 2004, 2005). Larvae, juveniles and adults were transported from West Kamchatka to Kolafjord, east Barents Sea during 1961–1969. More recently *Chionoecetes opilio* has been introduced into the Barents Sea by ballast water (Alvsvag et al. 2009).

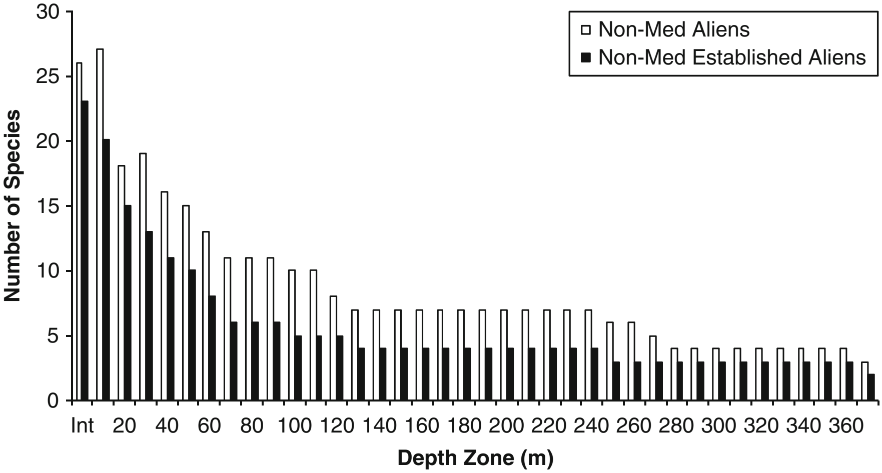

**Fig. 4** Depth distribution of non-established and established non-Mediterranean species (See caption of Fig. 2 for explanation)

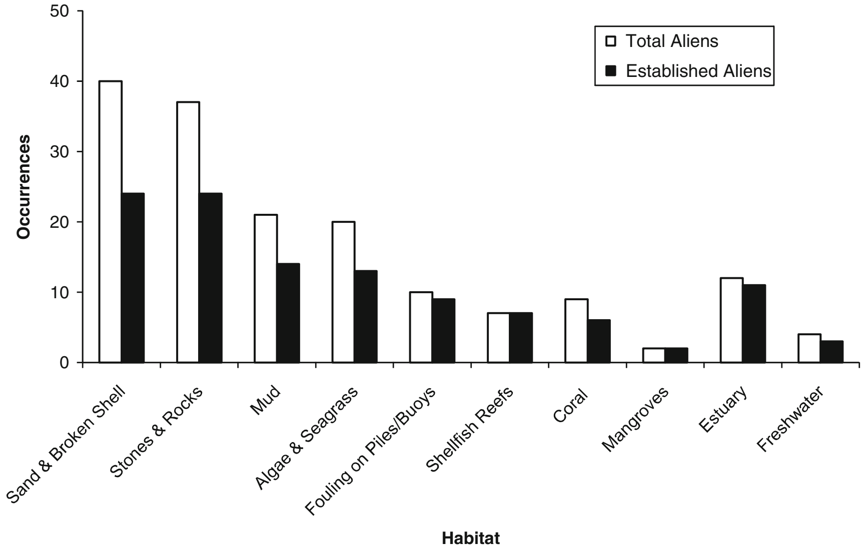

**Fig. 5** Comparison of frequency of occurrence of established and non-established aliens in different habitats (see Table 2 for details). Notes: each species can occur in more than one habitat; “shellfish reefs” include oysters and mussels; “fouling” includes sponges, hydroids, tunicates and stalked barnacles; “coral” includes both live and dead coral

**Table 3** Alien crab species in the main oceanic regions and rivers draining therein

| Oceanic region | No. established (non-established) species | Alien crab species |
|---|---|---|
| Arctic ocean | 2 (2) | ***Paralithodes camtschaticus***, ***Chionoecetes opilio*** |
| North Sea | 6 (2) | *Callinectes sapidus*, ***Eriocheir sinensis***, ***Hemigrapsus takanoi***, ***Hemigrapsus sanguineus***, *Pilumnoides inglei*, ***Rhithropanopeus harrisii***, ***Chionoecetes opilio***, ***Paralithodes camtschaticus*** |
| Baltic | 2 (1) | ***Callinectes sapidus***, ***Eriocheir sinensis***, *Rhithropanopeus harrisii* |
| Black Sea | 1 (2) | ***Callinectes sapidus***, *Eriocheir sinensis*, *Rhithropanopeus harrisii* |
| Mediterranean Sea | 25 (17) | *Notopus dorsipes*, *Calappa hepatica*, ***Calappa pelii***, *Cryptosoma cristatum*, *Ashtoret lunaris*, *Daira perlata*, ***Dorippe quadridens***, *Sphaerozius nitidus*, ***Eucrate crenata***, ***Ixa monodi***, ***Coleusia signata***, ***Myra subgranulata***, ***Herbstia nitida***, *Hyastenus hilgendorfi*, ***Libinia dubia***, *Menaethius monoceros*, ***Micippa thalia***, *Halimede tyche*, *Actumnus globulus, Glabropilumnus laevis*, ***Pilumnopeus vauquelini***, *Pilumnus minutus*, *Callinectes danae*, ***Callinectes sapidus***, ***Carupa tenuipes***, *Charybdis feriata*, ***Charybdis hellerii***, ***Charybdis longicollis***, ***Portunus pelagicus***, *Thalamita gloriensis*, *Thalamita indistincta*, ***Thalamita poissonii***, ***Dyspanopeus sayi***, ***Rhithropanopeus harrisii***, ***Atergatis roseus***, *Grapsus granulosus*, ***Pachygrapsus transversus, Hemigrapsus sanguineus***, ***Percnon gibbesi***, ***Plagusia squamosa***, ***Eriocheir sinensis***, ***Macrophthalmus graeffei*** |
| Northeast Atlantic | 5 (0) | ***Callinectes sapidus***, ***Eriocheir sinensis***, ***Hemigrapsus takanoi***, ***Hemigrapsus sanguineus***, ***Rhithropanopeus harrisii*** |
| Northwest Atlantic | 5 (1) | *Metacarcinus magister*, ***Carcinus maenas***, ***Charybdis hellerii***, ***Eriocheir sinensis***, ***Hemigrapsus sanguineus***, ***Petrolisthes armatus*** |
| South Africa | 1 (0) | ***Carcinus maenas*** |
| Southwest Atlantic | 5 (6) | *Cancer pagurus*, ***Pyromaia tuberculata***, *Taliepus dentatus*, ***Carcinus maenas***, ***Charybdis hellerii***, *Liocarcinus navigator*, *Scylla serrata*, *Pilumnoides perlatus*, *Bellia picta*, ***Rhithropanopeus harrisii***, ***Halicarcinus planatus*** |

(continued)

**Table 3** (continued)

| Oceanic region | No. established (non-established) species | Alien crab species |
|---|---|---|
| Northeast Pacific | 3 (0) | ***Carcinus maenas***, ***Rhithropanopeus harrisii***, ***Eriocheir sinensis*** |
| Hawaiian Islands | 9 (1) | ***Hyastenus spinosus***, *Callinectes sapidus*, ***Scylla serrata***, ***Glabropilumnus seminudus***, ***Pilumnus oahuensis***, ***Acantholobulus pacificus***, ***Panopeus lacustris***, ***Pachygrapsus fakaravensis***, ***Nanosesarma minutum***, ***Metopograpsus oceanicus*** |
| Panama/Caribbean | 3 (2) | *Neorhynchoplax kempi*, ***Rhithropanopeus harrisii***, *Charybdis hellerii*, ***Eriocheir sinensis***, ***Platychirograpsus spectabilis*** |
| Northwest Pacific | 4 (2) | *Metacarcinus magister*, ***Pyromaia tuberculata***, ***Carcinus aestuari***, ***Carcinus maenas***, *Callinectes sapidus*, ***Rhithropanopeus harrisii*** |
| Southeast Pacific | 0 | None |
| Southwest Pacific | 6 (2) | ***Pyromaia tuberculata***, ***Halicarcinus innominatus***, ***Carcinus maenas***, ***Charybdis japonica***, *Glebocarcinus amphioetus*, ***Metacarcinus novaezelandiae***, *Romaleon gibbosulum*, ***Petrolisthes elongatus*** |
| Indian Ocean | 0 | **None** |
| Southern Ocean | 1 (0) | *Hyas araneus* |

Species established in the region are in bold

## 3.2 North Atlantic

In the North Atlantic a total of nine mostly portunid and varunid alien species have been recorded. Along the North American coast *Carcinus maenas*, *Charybdis hellerii*, *Hemigrapsus sanguineus* and *Petrolisthes armatus*, can be found. *Eriocheir sinensis* has been recently recorded in Chesapeake and Delaware Bays, but is not yet established (Ruiz et al. 2006a). There is a single record of *Metacarcinus magister* from Massachusetts (Cohen 2006). On European coasts we find *Callinectes sapidus*, *Rhithropanopeus harrisii*, *Eriocheir sinensis*, *Hemigrapsus sanguineus* as well as *Hemigrapsus takanoi* (see Dauvin et al. 2009). Prior to 2005 "*Hemigrapsus penicillatus*" was reported from Northeast Spain, France and the Netherlands (Noël et al. 1997; Gollasch 1999; Breton et al. 2002), but these refer to the recently recognized species *H. takanoi* (see Asakura and Watanabe 2005). In addition *Pachygrapsus marmoratus* is spreading northwards into the English Channel and England (Ingle and Clark 2006).

**Fig. 6** World map showing the numbers of established alien crabs (from *left to right*) in Hawaiian Islands, Pacific coasts of North America and South America, Panama and Caribbean, South American East Coast, Southern Ocean, North Atlantic, North Sea, Barents Sea, Mediterranean, South Africa West Coast, South Africa, Indian Ocean, Pacific coast of Asia and finally Australasia. Distribution details are in Table 1

### 3.3 Mediterranean and Black Sea

In the Mediterranean and Black Sea we find the greatest number and diversity of alien crab species in the world. The established alien species (25) include: *Calappa pelii*, *Dorippe quadridens*, *Eucrate crenata*, *Ixa monodi*, *Coleusia signata*, *Myra subgranulata*, *Herbstia nitida*, *Libinia dubia*, *Micippa thalia*, *Pilumnopeus vauquelini*, *Callinectes sapidus*, *Carupa tenuipes*, *Charybdis hellerii*, *Charybdis longicollis*, *Portunus pelagicus*, *Thalamita poissonii*, *Dyspanopeus sayi*, *Rhithropanopeus harrisii*, *Atergatis roseus*, *Pachygrapsus transversus*, *Hemigrapsus sanguineus*, *Percnon gibbesi*, *Plagusia squamosa*, *Eriocheir sinensis*, and *Macrophthalmus graeffei*. Other alien crabs (17) have been occasionally recorded in the Mediterranean and these include: *Notopus dorsipes*, *Calappa hepatica*, *Cryptosoma cristatum*, *Ashtoret lunaris*, *Daira perlata*, *Sphaerozius nitidus, Hyastenus hilgendorfi*, *Menaethius monoceros*, *Halimede tyche*, *Actumnus globulus*, *Glabropilumnus laevis*, *Pilumnus minutus*, *Callinectes danae, Charybdis feriata*, *Charybdis japonica*, *Thalamita gloriensis*, *Thalamita indistincta*, and *Grapsus granulosus*. In the Mediterranean, the majority ($n=36$, 86%) of alien brachyurans are alien only there, with only a few ($n=6$, 14%) also alien in other seas. Many of these 36 species have become alien only because of the opportunity presented by the opening of the Suez Canal in 1869 (resulting in the Erythrean invasion) (Galil and Zenetos 2002). Without that route to the Red Sea the Mediterranean would probably only have an alien level similar to that of other seas. Of the 42 alien species recorded in the Mediterranean 25 (59.5%) have become established (Table 1).

Amongst the first alien crabs in the Mediterranean were *Pachygrapsus transversus* (as *P. advena*) and *Plagusia squamosa* found amongst ship fouling, in 1873 in the port of Marseilles (Catta 1876). *Percnon gibbesi*, which was first recorded in 1999, is spreading rapidly and it may be the most invasive decapod currently expanding its distribution in the Mediterranean Sea (Thessalou-Legaki et al. 2006) although its ultimate impact on the rest of the fauna has yet to be determined.

### 3.4 South Atlantic

In the South Atlantic the eastern coast of South America has only been colonized by five alien species: *Pyromaia tuberculata*, *Carcinus maenas*, *Charybdis hellerii*, and *Rhithropanopeus harrisii*. *Halicarcinus planatus* was introduced into Brazilian waters amongst oysters (*Crassostrea gigas*) transported from Chile for aquaculture (Tavares 2003). Another six species have only been rarely recorded: *Cancer pagurus*, *Liocarcinus navigator*, *Scylla serrata*, *Bellia picta*, *Taliepus dentatus* and *Pilumnoides perlatus*. On the other side of the Atlantic no alien decapod species are known on the Namibian coast of South Africa (see Macpherson 1991; Manning and Holthuis 1981). *Carcinus maenas* is established in South Africa, but remains limited to the west coast from Table Bay to Hout Bay (Griffiths et al. 2009). Orensanz et al. (2002) suggest that the list of aliens may also include the cryptogenic species *Panopeus meridionalis* (from Uruguay and Argentina) and *Pachygrapsus transversus* (from Uruguay).

### 3.5 Indian Ocean

No alien established species have been recorded from the Indian Ocean and there are no records of Mediterranean crabs that might have colonized the Red Sea via the Suez Canal counteracting the Erythrean fauna that has invaded the Mediterranean. Species' traffic through the canal is largely one-way because, even though shipping travels in both directions, the flow of sea water is northward from the Red Sea to the Mediterranean (Rilov and Galil 2009).

The lack of records of alien crabs from the northern Indian Ocean and south-east Asia is remarkable considering the substantial shipping traffic to the Indian subcontinent and especially the large amount of maritime traffic through Singapore: many of these ships have to wait offshore for long periods before they can enter port and be unloaded and it might be expected that they could "unload" both ballast water and hull fouling organisms into local waters while waiting. The port of Jurong is a shipping cross road and one might have expected similar levels of alien species to that found in the Mediterranean. The only records of aliens are from a semisubmersible oil platform, from the Timor and South China Seas, serviced in a dry dock in

Singapore: 25 crab species were recorded including *Glabropilumnus seminudus* and *Carupa tenuipes* that are invasive elsewhere (Yeo et al. 2009). More careful attention to port surveys would be expected to reveal many alien species in this region. Insufficient knowledge about natural faunas make it difficult to detect alien species: indeed it may already be too late distinguish alien from native species in this area.

## *3.6 North West Pacific*

In the North West Pacific (Japan and China) three alien crab species have established: *Pyromaia tuberculata* (Tokyo and Sagami Bays, Sakai 1976, as a result of post second world war naval shipping from California to Yokohama), *Carcinus maenas* and *Carcinus aestuarii* (Tokyo Bay, Furota et al. 1999). There are rare records of *Metacarcinus magister* and *Callinectes sapidus.* Given the booming Chinese economy and the resulting increase in maritime traffic we expect increasing numbers of arrivals (and departures for that matter) of species along this coastline.

## *3.7 South West Pacific*

In the South West Pacific (Australia and NZ) six species are established: two in New Zealand, *Pyromaia tuberculata* and *Charybdis* (*Charybdis*) *japonica*, while in Australian waters five alien species have been recorded, *Pyromaia tuberculata*, *Carcinus maenas*, *Metacarcinus novaezelandiae*, *Halicarcinus innominatus* and *Petrolisthes elongatus*. *Metacarcinus novaezelandiae* was accidentally transported to Tasmania in shipments of oysters from New Zealand in the early twentieth century, probably along with *H. innominatus* and *P. elongatus*. This is a very low number of species given the size of Australia and its range of climatic zones, but there are relatively few major shipping ports (Hewitt 2003). Sliwa et al. (2009) provides a list of other Australian aliens, many of which are cryptogenic, recorded during port surveys. In New Zealand a few juvenile *Glebocarcinus amphioetus* and *Romaleon gibbosulum* have been collected during port surveys (McLay 2004). We do not incorporate the records of crabs reported in Cranfield et al. (1998): a re-analysis suggests that these are likely to be rare native species rather than aliens.

## *3.8 North East Pacific*

The three established species recorded from the continental coastline of the North East Pacific (Canada/USA/Central America) are *Carcinus maenas*, *Rhithropanopeus harrisii*, and *Eriocheir sinensis* whose putative release point was San Francisco Bay (Cohen and Carlton 1997).

### 3.9 Hawaiian Islands

Nine alien species are found in Hawaiian waters including: *Hyastenus spinosus*, *Scylla serrata*, *Glabropilumnus seminudus*, *Pilumnus oahuensis*, *Acantholobulus pacificus*, *Panopeus lacustris*, *Pachygrapsus fakaravensis*, *Nanosesarma minutum*, *Metopograpsus oceanicus*. Many of these have been transported from the east Atlantic to Pearl Harbour, Hawaii, with naval vessels (see Carlton and Eldredge 2009). *Callinectes sapidus* has also been reported from Hawaii, but only six individuals were collected between 1985 and 1992 and none have been found for the past 17 years (J. Carlton, pers. comm. 2010).

### 3.10 South East Pacific

In the South East Pacific (South America: Ecuador, Peru, Chile) no alien crab species have been recorded (Castilla et al. 2005). The relatively low volume of maritime traffic and sparse scientific surveys may be the main reasons for that. Possibly more intensive efforts would reveal a different picture, as alien species belonging to other taxa have been recorded (Castilla and Neill 2009).

### 3.11 Southern Ocean

Few alien species are known from polar regions. In the Southern Ocean the only alien is the spider crab *Hyas araneus* (Tavares and de Melo 2004). In the arctic Barents Sea the deliberately transported *Paralithodes camtschaticus* (red king crab) and accidentally introduced *Chionoecetes opilio* (snow crab) occur. Herein we place them as part of the North Sea fauna because they are expanding their range southwards. These cases illustrate the fact that all seas are vulnerable to colonization, not just temperate seas. However, colonization of polar regions by crabs is limited by their inability to regulate $Mg^{2+}$ (Thatje et al. 2005).

## 4 Vectors and Routes (Fig. 7)

Crabs can be transported as larval stages (zoea and megalopae) or as adults (i.e., post-settlement). Often it is unclear as to what the agent of transfer was: for example it is difficult to separate hull fouling from ballast water. Under the circumstances unless the culprits are caught in the act we can only guess the most likely cause. The vector/route most responsible for colonization of areas outside the normal range of crabs has been the Suez Canal, which connected two major biogeographic areas and separate theatres of crab evolution. Since its opening in 1869, a total of 29 species

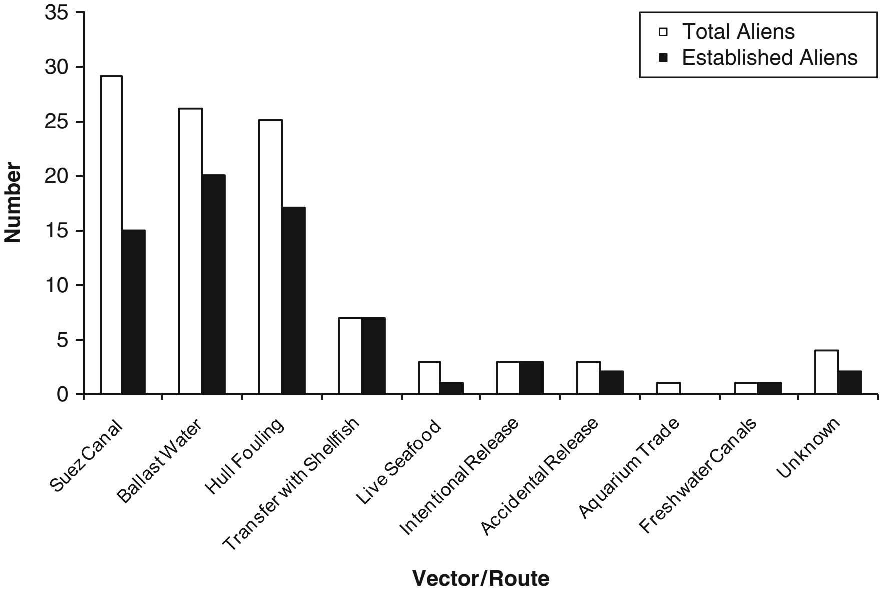

**Fig. 7** Summary of vectors and routes that have facilitated the spread of established and non-established alien crabs (*Note*: some species can be transported in more than one way so that the Y-axis does not refer to number of species (the data are in Table 1))

have gained access to the Mediterranean Sea, via the canal. Out of 73 alien crab species worldwide, the Suez Canal alone has been responsible for 40% of them. However, hull fouling and ballast water have resulted in transferring more species that successfully established (Fig. 7). While spread via the canal was the most common for the Mediterranean, we cannot rule out either fouling and/or ballast water contributing to the colonization. The Panama Canal is a major centre of shipping activity in the Americas, allowing transit of approximately 13,000–14,000 vessels per year from around the globe (Ruiz et al. 2006a, b). We should be eternally grateful to the architects of the Canal for choosing to cut costs by making the route pass through a freshwater lake rather than directly connecting the Pacific and Caribbean Oceans! In doing so they preserved the integrity of both the Caribbean and East Pacific faunas. Besides canals, shipping and aquaculture continue to be amongst the most important vectors facilitating transport of marine animals (Streftaris et al. 2005). Included as part of hull fouling are the so-called "sea chests" or intakes for seawater used to cool the engines (Coutts et al. 2003). These sheltered pockets are not subject to water shear and maybe free of antifouling paint.

The remaining vectors are only minor in relation to the big-three (Fig. 7). Amongst these six vectors, which mostly involve transport of adults rather than larvae, transport with shellfish ranks highest: the most common shellfish involved were oysters. Transport of three native New Zealand crabs to Tasmania probably happened when sacks of native oysters were carried by ship to Hobart to prop up the local supply of oysters after populations dwindled in the early 1900s (Dartnall 1969). All the alien porcelain crabs were transported outside their range by this means. These anomuran crabs are especially common in oyster reefs worldwide. The seafood live trade industry has been responsible for the transport of the adults of only three species: *Callinectes sapidus*, *Charybdis feriata* and *Scylla serrata* (all portunids). Intentional release to establish new fisheries has been successful for *C. sapidus* in the Mediterranean, *S. serrata* in Hawaii and for *Paralithodes camtschaticus* in the Barents Sea. Only three species have been accidentally released perhaps the most curious one being the bizarre river crab, *Ptychognathus spectabilis,* that was transported from Mexico to the Hillsborough River, Tampa Bay, Florida on cedar logs imported to make cigar boxes (Marchand 1946)! Sometimes what appear to be minor vectors can lead to major problems: *Carcinus maenas* was introduced to the American Pacific coast in seaweed wrapped with bait worms from the State of Maine (J. Carlton pers comm. 2010). The aquarium trade is responsible for transporting *Neorhynchoplax kempi* on water weed from Iraq to one of the freshwater locks on the Panama Canal. The final vector or route has been freshwater canals on continental Europe and in England which have provided conduits for the spread of the Chinese mitten crab, *Eriocheir sinensis*. The “unknowns” are all tropical East Atlantic species whose mode of transport into the Mediterranean is uncertain.

# 5 Most Significant Alien Crab Species Worldwide

A list of all the crabs that have been recorded outside their native range is provided in Table 1 and in Table 2 we summarize the features of their habitat and body size. Here we concentrate on the 18 species that have had the greatest impact or spread, alphabetically listed. For each species, information is provided on distribution (native and non-native as well as invasion history as far as it is known), habitat, biology, and impact. We include species of the same genus if they are also listed in Tables 1 and 2.

## *5.1 Callinectes sapidus Rathbun, 1896, Blue Crab*

### 5.1.1 Distribution

Native: North and South West Atlantic (from Nova Scotia to Uruguay); Alien: North-East Atlantic, Baltic, Black Sea, Mediterranean (from 1940s), North Sea (Netherlands, Germany) and Japan. *Callinectes sapidus* was reported from Hawaii (Eldredge 1995), but has not been collected during recent years (Carlton and Eldredge 2009). The first record of *C. sapidus* in European waters was from Rochefort, Atlantic coast of France, 1901 (Bouvier 1901; Wolff 2005; Nehring et al. 2008 for other European records). *Callinectes sapidus* has been recorded from

Japan a few times (Muraoka and Taguchi 1992). It was most likely introduced with ballast water and possibly also through hull fouling or live seafood and aquarium trade (Nehring et al. 2008). It has been reported from Danish waters, but has not become established yet (Jensen and Knudsen 2005). *Callinectes sapidus* was recently recorded from a power station on the Atlantic coast of Spain (Cabal et al. 2006). The case for accepting that *C. sapidus* is now established in German water is presented by Nehring et al. (2008).

### 5.1.2 Habitat

Intertidal to 90 m, estuaries and shallow coastal waters.

### 5.1.3 Biology

*Callinectes sapidus* is tolerant to a wide range of temperature and salinities. However, egg development usually requires water temperatures of at least 19°C so this could regulate local recruitment (Hill et al. 1989). It is highly fecund (1–2 million offspring per brood and up to 8 million per female) and omnivorous (e.g., clams, mussels and oysters). *Callinectes sapidus* is an important commercially fished species in its native range (Atlantic coast of North America south to Uruguay) and also some locations in its introduced range (e.g., Northern Sinai) (see Hayes and Sliwa 2003). The population in Greece may be declining due to over fishing (CIESM). The recent book by Kennedy and Cronin (2007) is valuable as it summarizes the wide-ranging research on this species and has become a standard reference for crab research in general.

### 5.1.4 Impact

*Callinectes sapidus* has been reported to feed on fish caught in traps and to damage nets (CIESM 2008) and readily feeds on clams, mussels and oysters. Potential impact may therefore include some loss of aquaculture, commercial, or recreational harvest. *Callinectes sapidus* is a successful invader because it is eurythermal and euryhaline, highly fecund, aggressive and a good swimmer.

## *5.2 Carcinus aestuarii Nardo, 1847, Mediterranean Green Crab*

### 5.2.1 Distribution

Native: Mediterranean; Alien: Japan (since 1984): Tokyo Bay, Osaka Bay, Katsuura River (Tokushima) (Kimura et al. 2004). Possibly hybrid of *C. maenas* and *C. aestuarii* in Japan and South Africa (Carlton and Cohen 2003). *C. aestuarii* was one of the first alien crab species whose cryptic invasion was detected using microsatellite DNA (Geller et al. 1997; Grosholz 2002).

### 5.2.2 Habitat

Intertidal to 10 m (up to 26 m), estuarine and shallow coastal waters; muddy sand, among seagrass, under stones, typically in sheltered habitats.

### 5.2.3 Biology

In Japan, *Carcinus aestuarii* occurs abundantly in the organically polluted water in Tokyo Bay and its seasonal migratory patterns allow the alien crab to avoid bottom hypoxia in summer by migrating to near shore areas and therefore to maintain high population densities (Furota et al. 1999; Furota and Kinoshita 2004).

### 5.2.4 Impact

May be similar to *C. maenas* but less is known about the ecology of *C. aestuarii* to estimate their impact (Carlton and Cohen 2003). *Carcinus aestuarii* appears to be able to tolerate slightly warmer regions than *C. maenas* but not enough is known about the physiological tolerance of the Mediterranean species to estimate their exact potential range (Carlton and Cohen 2003).

## *5.3 Carcinus maenas (Linnaeus, 1758), European Shore Crab, Green Crab*

### 5.3.1 Distribution

Native: East Atlantic (North-Western Europe and northern Africa), North Sea, Baltic; Alien: North and South West Atlantic (USA, Argentina), South Africa (Cape Town), North and South Pacific (USA, Australia). Invasion history: First recorded in 1817 Massachusetts; in the late nineteenth century southern Australia (Port Philip Bay); in 1983 South Africa; in 1989 San Francisco Bay, California; in 2003 Argentina (Klassen and Locke 2007) and Patagonia (Hidalgo et al. 2005). In recent years *C. maenas* has spread northwards up the west coast of North America and the establishment of this crab along the Oregon coast and west coast of Vancouver Island by the strong cohort of 1997/1998 is now being sustained by local reproduction and recruitment (Behrens Yamada and Gillespie 2008). Single records of *C. maenas* include Red Sea, Madagascar, Pakistan, Sri Lanka, Myanmar, and Bay of Panama (see Carlton and Cohen 2003), and the lack of subsequent records suggests that the species has not become established in those areas.

Many vectors have played a role in distributing *C. maenas* around the world. Fouling on ship hulls probably played a role, but ballast water was probably the main vector followed by secondary local dispersal through natural dispersal and water currents (Klassen and Locke 2007).

### 5.3.2 Habitat

Common intertidal to 6 m (i.e., upper intertidal to shallow sub-tidal), but to 62 m (Bouvier 1940: 235), sandy to rocky bottoms, estuarine to marine habitats (euryhaline).

### 5.3.3 Biology

*Carcinus maenas* is predominantly predatory, but feeds on a wide range of different organisms including plants, protists and animal phyla which encompass about 100 families and 158 genera. The most common prey items are mussels, clams, snails, polychaetes, crabs, isopods, barnacles and algae (Klassen and Locke 2007). *Carcinus maenas* is euryhaline and tolerates salinities from 4 to 53 psu. *Carcinus maenas* is also eurythermic and survives in temperatures ranging from 0ºC to 35ºC, but need temperatures between 18ºC and 26ºC to reproduce. Females lay up to 185,000 eggs per clutch. Larval stages include a protozoea, four zoeal stages and the megalopa. Green crab live up to 4–7 years, with females typically living for about 3 years and males about 5 years. *Carcinus maenas* appears to experience some biotic resistance by adult *M. magister* (Hunt and Behrens Yamada 2003), but juvenile *M. magister* may emigrate from refuge habitats as a result of competition and predation by adult *C. maenas* (McDonald et al. 2001). Therefore, *C. maenas* can potentially negatively influence juvenile *M. magister* survival, and subsequently, recruitment to the Dungeness crab fishery. The extent to which these two species overlap will determine the full impact of *C. maenas* on *M. magister* (McDonald et al. 2001). On the east coast native predators, *Callinectes sapidus* and *Homarus americanus* provide some biotic resistance, via predation, to the spread of *C. maenas* making the intertidal zone the safest place for the green crab (DeRivera et al. 2005; League-Pike and Shulman 2009 respectively). However, the green crab has now been established along the American Atlantic coast for almost 200 years so should be regarded as being acclimatized. On the Pacific coast a native nemertean egg predator, *Carcinonemertes epialti*, whose normal host is *Hemigrapsus oregonensis*, has been found on the green crab where it consumes the eggs of ovigerous females (Torchin et al. 1996) thus proving some biotic resistance.

### 5.3.4 Impact

Just the mention of the name *Carcinus maenas* is enough to instantly elevate the pulse rate of conservationists and marine biologists everywhere: it has a severe “image problem" despite coexisting with many species of crab, in both its native and alien range, worldwide. On North American shores *C. maenas* interacts with both native (*Hemigrapsus oregonensis*, Pacific coast) and alien (*H. sanguineus*, Atlantic coast) species in an east-meets-west situation (Jensen et al. 2002). Competition for food and habitat may cause decline of other crab and bivalve species including mussel farm species (Le Roux et al. 1990). *Carcinus maenas* also has effects on the phenotype and behavioural response of prey (Smith 2009). Impacts on prey populations seem to be greater in soft-bottom habitat and in sheltered habitats protected from strong wave actions. New Zealand biosecurity has maintained a high level of vigilance in order to prevent *Carcinus maenas* from crossing the Tasman Sea from Tasmania because it could be a major threat to the green lip mussel (*Perna canaliculus*) industry.

### 5.3.5 Management

Control efforts have included a range of methods including fencing, trapping and poisoning, however, with limited effect. The potential use of biological control has been investigated in the case of the parasitic barnacle *Sacculina carcini*, however, because of its low host specificity and its potential to infect native Australian and North American species it is not likely to be used in the future (Thresher et al. 2000; Goddard et al. 2005). Commercial fisheries for green crabs have occasionally reduced the number of crabs in parts of its native range.

## *5.4 Charybdis (Charybdis) hellerii (A. Milne Edwards, 1867)*

### 5.4.1 Distribution

Native: Indo Pacific (Japan, Philippines, New Caledonia, Australia, Hawaii, and throughout the Indian Ocean, including the Red Sea); Alien: Mediterranean, Northwest and Southwest Atlantic (Florida to Brazil); invasion history: In the Mediterranean, *C. hellerii* was first recorded from Palestine about mid-1920s and subsequently from Egypt (1936), Turkey (1981), Lebanon (1981), Syria (1993) and Cyprus (1999) (see CIESM 2008). In the West Atlantic, *C. hellerii* was first reported in 1987 and 1988 in the Gulf of Mexico and the Caribbean Sea; Cuba (Gómez and Martinez-Iglesias 1990); Venezuela (Hernández and Bolaňos 1995); and Colombia (Campos and Türkay 1989), and then in 1995 in Florida (Lemaitre 1995) and Brazil (Tavares and Mendonça 1996; Mantelatto and Dias 1999; Ferreira et al. 2006). *Charybdis hellerii* was found in the sea-chest of a fishing vessel in New Zealand (Dodgshun and Coutts 2003), but has so far not been detected in New Zealand waters. It is most likely that *C. hellerii* arrived in the Mediterranean via the Suez Canal (CIESM) and to the Western Atlantic originally via ballast water or as fouling organisms and possibly subsequently spread by larval transport with local currents (Campos and Türkay 1989; Gómez and Martinez-Iglesias 1990; Tavares and Mendonça 1996).

### 5.4.2 Habitat

Intertidal – 50 m; prefers soft bottom, but also among rocks and live corals. In its native range *C. hellerii* is reported to inhabit soft bottoms, but also to occur among rocks and live corals (Stephenson et al. 1957). In Florida, the alien populations are also common within structured habitats near inlets such as inter and sub-tidal coralline rock, ledges, rocks around jetties, concrete rubble and bulkheads (Dineen et al. 2001). In Columbia, *C. hellerii* was found among sea grass meadows and mangrove roots (Campos and Türkay 1989).

### 5.4.3 Biology

The maximum carapace width of males is about 8 cm in Malaysia (Wee and Ng 1995). Ovigerous females range in carapace width from the 4.7 cm plus in Australia (Stephenson et al. 1957) to a maximum of 5.4 cm in Florida (Lemaitre 1995), 5.6 cm in Colombia (Campos and Türkay 1989) to 5.7 cm in Brazil (Mantelatto and Garcia 2001). In Brazil, *C. hellerii* ovigerous females are present throughout most of the year, with peak spawning during the winter (Mantelatto and Dias 1999; Mantelatto and Garcia 2001). Fecundity of *C. hellerii* is high and ranges from 22,550 to 3,200,000 eggs per brood depending on female size (Sumpton 1990; Siddiqui and Ahmed 1992 as cited in Dineen et al. 2001; Lemaitre 1995). The larval period was 44 days for larvae reared in the laboratory at 24°C (Dineen et al. 2001). Sexual maturity was reached at 67 mm carapace width of a single female in the laboratory which subsequently laid six broods within a year (Dineen et al. 2001). It has been suggested that the geographic range of five species of *Charybdis* along the coast of east and west Australia is temperature regulated and that *C. hellerii* is most tolerant of lower temperatures (Stephenson et al. 1957). The epibiont barnacle *Chelonibia patula* was found on crabs from Pakistan (Javed and Mustaquim 1994) and a parasitic barnacle *Sacculina* sp. has been found in 1.3% of crabs in Australia (Stephenson et al. 1957).

### 5.4.4 Impact

Unknown. *Charybdis hellerii* could potentially compete for food and habitat with native brachyuran crabs, such as the blue crab *Callinectes sapidus*, and therefore negatively impact on the blue crab fishery in certain areas. Over all, *C. hellerii* is more a tropical species but can tolerate relatively low temperature in comparison to five other Australian *Charybdis* species (Stephenson et al. 1957). It has been suggested that *C. hellerii* is a successful marine invader because of its life and natural history traits such as (1) long larval life (44 days) facilitating dispersal, (2) maturation within a year which promotes rapid population growth, (3) sperm storage and production of multiple large broods allows rapid expansion of founder populations, (4) generalized, opportunistic carnivore, allows exploitation of a variety of food resources and (5) use of diverse habitats (Dineen et al. 2001). These are similar traits described for the invasive *Carcinus maenas* (Cohen et al. 1995; Grosholz and Ruiz 1996).

## 5.5 *Charybdis (Charybdis) japonica (A. Milne Edwards, 1861), Asian Paddle Crab, Lady Crab*

### 5.5.1 Distribution

Native: China, Japan, Korea, Taiwan, Malaysia (Wee and Ng 1995 in Smith et al. 2003); Alien: South-West Pacific (first in 2000 in New Zealand) (Gust and Inglis 2006). In New Zealand *C. japonica* is abundant in the Waitemata Harbour (Auckland) and occurs in two nearby estuaries, but have not spread to other shipping ports nationwide. However, since their arrival they have spread 120 km from the putative release point. It remains to be shown whether the *C. japonica* population in New Zealand is self-sustaining (Gust and Inglis 2006) in the long term. A single live, mature, male specimen of *C. japonica* was also discovered by a fisherman in the Port river in Adelaide in 2000 (Poore 2004), but none have subsequently been reported. The vector of introduction in this case is unknown but ballast-water or hull-fouling are likely candidates, along with the possibility of sea-chests.

### 5.5.2 Habitat

Sub-tidal, eelgrass, estuarine and marine habitats. In its native habitat in Korea, juvenile *C. japonica* are abundant in eelgrass (*Zostera marina*) meadows (Huh and An 1998, in Smith et al. 2003). In New Zealand it is found in estuarine habitats with fine, silty muddy bottom to coarse, shelly sand bottom (Gust and Inglis 2006).

### 5.5.3 Biology

*Charybdis japonica* is an opportunistic predator of bivalves, fish, cephalopods and other benthic invertebrates (Jiang et al. 1998, in Smith et al. 2003). In China spawning occurs in spring and autumn when sea temperatures are between 20°C and 28°C (Wang et al. 1996 as cited in Gust and Inglis 2006). Females lay an average of ca. 85,000 eggs per brood (Wang et al. 1996; Smith et al. 2003) and may produce multiple broods in a single year.

### 5.5.4 Uses

A commercially important species in its native range of central and South East Asia where it is trapped using pots and gill nets (Archdale et al. 2006).

### 5.5.5 Impact

*Charybdis japonica* is a host or carrier of the White Spot Syndrome Virus (WSSV) which can be a serious fisheries threat. WSSV infects a broad spectrum of crustaceans, and can cause cumulative mortalities of up to 100% within 3–10 days of the first signs of the disease. Some infected individuals do not die from the disease but are carriers that can spread the pathogen (Maeda et al. 1998). In New Zealand, the distribution of *C. japonica* overlaps with that of the native portunid crab *Ovalipes catharus*, but they seem to prefer slightly different habitats. *Charybdis japonica* occupied muddy sediments in which *O. catharus* was rare. If the *C. japonica* population in New Zealand is self-sustaining and continues to spread, it is likely to have significant impacts on native estuarine benthic flora and fauna (Gust and Inglis 2006). Southward expansion from Auckland is likely to be limited by colder water temperatures.

## *5.6 Chionoecetes opilio (Fabricius, 1788), Snow Crab*

### 5.6.1 Distribution

Native: sub-Arctic species found in North Pacific, Beaufort Sea, Arctic and Northwest Atlantic and west coast of Greenland; Alien: recently introduced into the Barents Sea, first record 1996, presumably by ballast water (Alvsvag et al. 2009; Puebla et al. 2008).

### 5.6.2 Habitat

Depth range 50–1,400 m, but most are found around 200 m.

### 5.6.3 Biology

*Chionoecetes opilio* has determinate growth and high fecundity 10,000–35,000 eggs per female. Males survive 7–8 years (Fonseca et al. 2008). Diet includes algae, fish, polychaetes, cannibalism and other crustaceans such as shrimps, shellfish, and echinoderms. This species is the basis of an important fishery in Canada and Greenland. Distribution of micro-satellite loci markers shows high connectivity in *C. opilio* with some suggestion of structuring within the Labrador Sea population, despite the long larval life of 3–5 months (Puebla et al. 2008). The *C. opilio* fishery in Japanese waters is one of the oldest commercial crab fisheries beginning in 1,724 (Kon 1996). The snow crab fishery is regulated by setting quota and a minimum size which means that males make up a large portion of the catch. This can result in limited sperm supply and males to guard primiparous females (Sainte-Marie et al. 2008).

### 5.6.4 Impact

Competition for food with other crabs and modification of the food web (Wieczorek and Hooper 1995).

## 5.7 *Eriocheir sinensis H. Milne Edwards, 1853, Chinese mitten crab*

### 5.7.1 Distribution

Native: North-West Pacific (China and North Korean Peninsula); Alien distribution: since 1912 in North-East Atlantic (first in Germany, now from Finland to Sweden, Russia, Poland, Germany (1927), Czech Republic, Netherlands (1931), Belgium, England, France (1943), Spain, Portugal), Black Sea, Baltic, North Sea, Mediterranean (via the Garonne canal system, but not a viable population); since 1992 in North-East Pacific (San Francisco Bay, Portland, Oregon, on the Columbia River) (Cohen and Carlton 1997); found in Detroit River 1965 and later some records from Great Lakes, but not established there; 2004 first records in St. Lawrence River (Veilleux and de Lafontaine 2007). *Eriocheir sinensis* must return to brackish waters to breed and release its larvae. Currently, it is not established in Danish Waters (Jensen and Knudsen 2005). Colonization of the Baltic Sea over the past 80 years by the mitten crab is detailed by Ojaveer et al. (2007). Reproduction in the Baltic is physiologically difficult because of the low salinity, so maintenance of the population is dependent upon migration from the North Sea (probably the Elbe River estuary) via the Kiel Canal. Chinese mitten crabs have persisted in Europe for almost 100 years. Several vectors have been identified for *E. sinensis* and include the illegal introduction for the live food trade, ballast water and ship hull fouling (Cohen and Carlton 1997). In addition, natural dispersal is likely after initial invasion. In the light of events in Europe, *E. sinensis* has the potential to establish itself in major UK estuaries (Herborg et al. 2005). The potential distribution in North America in major ports was estimated based on a model using environmental match and volume of ballast water received. Chesapeake Bay and Portland were highlighted as locations of high invasion risk and several other locations are also likely to be invaded (Herborg et al. 2005; Hanson and Sytsma 2008). The recent discovery of mitten crabs, including ovigerous females, in Chesapeake and Delaware Bays has borne out these predictions (Ruiz et al. 2006a, b; Dittel and Epifanio 2009). An analysis of genetic variation of *E. sinensis* shows that the European populations originated from multiple rivers in China on multiple occasions and that the San Francisco population originated from both the native Chinese populations and the alien European populations, probably the Thames population (Wang et al. 2009).

### 5.7.2 Habitat

*Eriocheir sinensis* is catadromous and spends most of its life in rivers, but must migrate to the sea to breed. It therefore occupies estuarine habitats, lakes, riparian zones, water courses and wetlands. It can also travel over dry land.

### 5.7.3 Biology

*Eriocheir sinensis* is catadromous (migrates between freshwater, estuarine and marine environments), tolerates a wide range of abiotic conditions (salinities and temperatures) and is found in temperate climates around the world. *Eriocheir sinensis* is an omnivore with juveniles primarily eating vegetation and adult crabs mainly eating small invertebrates such as worms and clams. Overall, it has an opportunistic diet including algae, detritus, and a variety of macro-invertebrates (Panning 1939; Hoestlandt 1948; Gollasch 1999; Rudnick et al. 2003). The time to maturity in the wild varies between 2 and 5 years and appears to depend on environmental factors (Herborg et al. 2005; Rudnick et al. 2005). *Eriocheir sinensis* is a semelparous ("big-bang") reproducer with adults in both native and alien populations making a single synchronized reproductive trip to the coast for one spawning season (Kobayashi and Matsuura 1995). Many females produce only one brood but some may produce a further smaller brood (Ng, N-K pers. com. 2010). The Japanese mitten crab, *E. japonica*, can produce up to three broods in a season (Kobayashi 2001). Once they complete the pubertal moult *E. sinensis* migrate to brackish waters of estuaries or the sea to mate and females typically lay between 100,000 and 1 million small (0.35–0.38 mm diameter) eggs (in the spring). Males die after the mating season and females after releasing the larvae. The extent of larval dispersal offshore remains enigmatic. After about 6–7 weeks in the estuarine or marine plankton larvae (5 (6) zoea+the megalopa stage) metamorphose into juvenile crabs, which then migrate back up the river into freshwater to complete the life cycle. The crabs form dense colonies and create burrows in the intertidal portions of streams. *Eriochier sinensis* is an aggressive space competitor (Dittel and Epifanio 2009). Crabs can colonize new rivers by larval transport and by adults walking overland from one river to another.

### 5.7.4 Impact

*Eriocheir sinensis* has many major impacts which include competing for resources with native freshwater invertebrates (Clark et al. 1998), modifying habitats and causing erosion through its intensive burrowing activity (Dutton and Conroy 1998 in Herborg et al. 2005), feeding on bait and trapped fish which cost fisheries and aquaculture industries (Ingle and Andrews 1976), and blocking water intakes in irrigation and water supply schemes (Cohen and Weinstein 2001; Dittel and Epifanio 2009). In Britain vulnerable freshwater decapod species may be eaten and out-competed (Owen 2003). Under laboratory conditions, native *Carcinus maenas* were excluded from shelters by *E. sinensis* (Gilbey et al. 2008). Stream banks in Europe and the USA are being eroded by the burrowing behaviour of the dense juvenile colonies (Peters 1933; Dutton and Conroy 1998; Rudnick et al. 2003). This crab spread very rapidly following its introduction into Europe (Wolff 2005). The mitten crab is the secondary intermediate host for the Oriental lung fluke, with mammals, including humans, being the final host (Cohen 2003). Humans can become infected by eating raw or poorly cooked mitten crabs. The Chinese mitten crab is a culinary delicacy in Asia and supports a $1.25 billion per annum aquaculture industry in China (Herborg et al. 2005). There is a small market for *E. sinensis* in Germany, but the revenue generated does not even approach the cost of their impact and its mitigation (Gollasch et al. 2009). Crabs have been used as bait for eel fishing, to produce fish meal, cosmetic products and as fertilizer in agriculture.

### 5.7.5 Management

Control of this species is difficult because of its abundance, ubiquity, high reproductive rate, and wide range of physiological tolerances (Rudnick et al. 2003). Intense trapping of crabs has not been sufficient to reduce the damage caused by crabs significantly. Electrical screens were installed in the 1930–1940s to prevent the migration of the crab up rivers in Germany but with little success (McEnnulty et al. 2001). Alternatively, it has been suggested to commercially harvest them in Britain and to export them to China (Owen 2003).

## *5.8 Hemigrapsus sanguineus (de Haan, 1853), Japanese, Asian Shore Crab*

### 5.8.1 Distribution

Native: North-West Pacific (from Sakhalin to Hong Kong and Japan); Alien: distribution: North-West Atlantic, Mediterranean Sea; history: In America, it was first reported in 1988 in New Jersey and has subsequently spread north to Massachusetts and south to North Carolina (McDermott 1991, 1998). A recent coastal survey by "citizen-scientists" established a new northern limit of the Scoodic Peninsula, Maine (Delaney et al. 2008). In Europe, it was first found in 1999 in the Netherlands (Wolff 2005) and France (Breton et al. 2002) and in 2002 in the Mediterranean (Schubart 2003). Both and *H. sanguineus* and *H. takanoi* are spreading along the Channel Coast of France (Dauvin et al. 2009).

### 5.8.2 Habitat

*Hemigrapsus sanguineus* occupies estuarine and marine habitats and occurs there predominantly in the middle and lower intertidal and occasionally in the sub-tidal and preferring structurally complex habitats (Lohrer et al. 2000a, b). In Japan, *H. sanguineus* is commonly found among boulders on rocky intertidal shores (Fukui 1988). It prefers rocky hard-bottom habitats or other hard structures such as mussel beds or oyster reefs where it can shelter easily. It can also be found on tidal flats hiding under rocks or shells. The distribution and population density often increases with the availability of shelter (Lohrer et al. 2000a, b). In the North-West Atlantic it occupies the same habitat as several mud crabs (Xanthidae) and juvenile green crabs *Carcinus maenas* (Kopin et al. 2001; McDermott 1998) and in the North-East Atlantic in the same habitat as the two other alien crabs, *Carcinus maenas* and *Hemigrapsus takanoi* (formerly presumed to be *H. penicillatus*) (Breton et al. 2002). On the Channel Coast of France *H. sanguineus* occupies more exposed shores than *H. takanoi*, thereby not competing for the same habitat (Dauvin et al. 2009).

### 5.8.3 Biology

*Hemigrapsus sanguineus* can tolerate a wide range of salinities and temperature, as well as damp conditions in the upper intertidal regions (Benson 2005). It is an opportunistic omnivore and will feed on a range of marine invertebrates including crustaceans, commercially important bivalves such as the blue mussels *Mytilus edulis*, soft-shell clams *Mya arenaria*, and oysters *Crassostrea virginica*, and algae (McDermott 1998; Brousseau et al. 2001). When given the choice *Hemigrapsus sanguineus* showed a strong preference of animal food over algae (Brousseau and Baglivo 2005). *Hemigrapsus sanguineus* can be an important predator of juvenile blue mussels *Mytilus edulis*, especially when it occurs in high population densities and compared to the other predator *Carcinus maenas* (Lohrer and Whitlach 2002). *Hemigrapsus sanguineus* is a carrier of the White Spotted S Virus (WSSV) (Maeda et al. 1998). Larval development takes about 1 month (depending on temperature) and this long development has the potential for long distance transport depending on the local currents (Epifanio et al. 1998). Settlement of megalopa larvae and metamorphosis to the juvenile stage appears to be highly species specific and induced by exposure to water-soluble exudates produced by conspecific adults (Kopin et al. 2001; Steinberg et al. 2007, but see O'Connor 2007). *Hemigrapsus sanguineus* has a high reproductive output with a relatively long breeding season over several months (5 in New Jersey) and includes two or more broods annually with up to 44,000 eggs (McDermott 1998). In addition growth and maturation are rapid and crabs are mature within a few months. McDermott (1998) suggested that the length of the reproductive period of *H. sanguineus* is related to latitude and therefore water temperature as in the warm southern Japan the breeding season is 8 months long whereas in colder northern Japan it lasts 3 months. A total of 13 ecto-symbionts have been identified from *H. sanguineus* along the US Atlantic coast, but no gill or internal parasites have been found (McDermott 2007).

### 5.8.4 Impact

*Hemigrapsus sanguineus* has the potential to cause significant changes in the inshore marine and estuarine communities of southern New England and mid-Atlantic coast because of its predation and possible habitat displacement of several important native species (Gerard et al. 1999). *Hemigrapsus sanguineus* has been observed to occupy in parts, the same habitat as another alien crab *Hemigrapsus takanoi* and the native *Carcinus maenas* in France (Breton et al. 2002) and other regions (Lohrer and Whitlach 2002). *Hemigrapsus sanguineus* has now replaced *Carcinus maenas* from their intertidal habitat at some locations, and has also been shown to be a strong competitor for food and space in the laboratory (Brousseau et al. 2001). In addition, it competes for habitat and possibly displaces several native crabs, such as xanthid and mud crabs, of the mid-Atlantic coast of North America (McDermott 1991; Gerard et al. 1999). In comparative feeding and behaviour trials involving 3 crab species, the native blue crab *Callinectes sapidus* and the two aliens, *Hemigrapsus sanguineus* and *Carcinus maenas*, it was shown that *H. sanguineus* is equally successful when it comes to competing for food with juvenile *C. sapidus*, but less so compared to *Carcinus maenas* (McDonald et al. 2007). Furthermore, it has been shown that *H. sanguineus* can, like *Carcinus maenas*, induce shell thickening in mussels as a predator defence mechanism. Freeman and Byers (2006) showed that in southern New England (where the crab occurs) mussels express inducible shell thickening when exposed to waterborne cues from *Hemigrapsus*, whereas naïve northern mussel populations (where the crab does not yet occur) do not show any changes. Griffen and Byers (2009) report the results of intriguing field experiments involving two alien predatory crabs, *H. sanguineus* (the new-comer, arrived 20 years ago) and *Carcinus maenas* (arrived nearly 200 years ago), one from Asia and the other from Europe, respectively, that show how they affect each other when neither is native. They show that determination of whether the impact of these two invaders is novel or redundant needs to be measured in the actual communities rather than on isolated captive individuals. Lohrer et al. (2000a, b) compared habitat use by *H. sanguineus* in its native habitat with that found on the New England coast. The work done on this species, in its new range, is undoubtedly the best research to date done on an alien crab and it illustrates the kind of investigations that need to be made when impacts are being assessed.

### 5.8.5 Management

Ballast water management will help to reduce new introductions from occurring. No parasites have been found in *H. sanguineus* in its introduced range along the US Atlantic coast that might control the population (McDermott 2007).

## 5.9 *Hemigrapsus takanoi* Asakura and Watanabe, 2005

This species has only been recently described by Asakura and Watanabe (2005) and recognized as distinct from *Hemigrapsus penicillatus*. Previous records of *H. penicillatus* in Europe were actually *H. takanoi* (see Asakura and Watanabe 2005).

### 5.9.1 Distribution

Native: North-West Pacific (Japan to China, Taiwan); Alien: North–East Atlantic, North Sea. History: It was first documented in 1993 from France and is now present in several other European countries (Spain, Netherlands, Belgium, Germany) (Noël et al. 1997 and references therein; Wolff 2005, as *H. penicillatus*). Both *H. takanoi* and *H. sanguineus* are spreading along the Channel Coast of France (Dauvin et al. 2009).

### 5.9.2 Habitat

In Japan, *H. takanoi* can be commonly found in bays and estuaries and includes areas where salinities and temperatures fluctuate highly (7–35‰ S and 12.5–20°C, respectively) (Mingkid et al. 2006a). In France, *H. takanoi* is mostly found in sheltered areas of the mid-littoral zone and is locally abundant with up to 50–60 individuals per $m^2$ (Dauvin et al. 2009).

### 5.9.3 Biology

The salinity tolerance of larvae of *Hemigrapsus takanoi* from hatching to the first juvenile stage was investigated by Mingkid et al. (2006b) in the laboratory at an average water temperature of about 24°C. Successful development occurred only at higher salinities (at 25‰, 30‰ and 35‰ S), no larvae developed further than the megalopa stage in lower salinities (10‰, 15‰ and 20‰ S), and only a few larvae metamorphosed to the second zoeal stage at very low salinity (5‰ S) and died shortly after. This shows that although juveniles and adults can be found in a range of salinities, higher salinities are required for successful larval development (Mingkid et al. 2006b). Adults have a wide tolerance range to abrupt and substantial changes in water salinity thereby enhancing their ability to colonize coastal habitats where salinities may fluctuate (Shinji et al. 2009).

### 5.9.4 Impact

This species is likely to compete for food and shelter with native shore crabs on the rocky shore habitat in particular where it occurs in high densities (Noël et al. 1997; Gollasch 1999). This might also include competition with *Carcinus maenas* in Europe.

## 5.10 *Metacarcinus novaezelandiae (Hombron and Jacquinot, 1846), Pie-Crust Crab*

### 5.10.1 Distribution

Native: New Zealand (South West Pacific); Alien: Australia (Tasmania, Victoria, New South Wales) (Poore 2004). Invasion history: First recorded in about 1930 from Hobart harbour (and around eastern Tasmania) and Port Phillip Bay (where it has not been found since). In 1991, a single specimen was collected by a fisherman in the Gippsland Lakes, Victoria. Since at least 1995, a local population has resided on Flinders Reef, Victoria. There are also a few records from other locations in Victoria such as Bass Strait and Eden, New South Wales (Poore 2004). This crab probably arrived in Tasmania accidentally amongst shipments of oysters from New Zealand. Larval colonization from New Zealand is not possible because of the strong eastward flowing Tasman Current. As early as 1885 and up to 1930 sacks of oysters (*Ostrea chilensis*) from Bluff, New Zealand were imported to prop up a failing local supply in Hobart. They were sold on the Hobart docks and while awaiting sale they were kept alive in wooden crates hung from the wharf. The oysters were carried as deck cargo, and sometimes chucked along the way with refuse sometimes dumped over the side entering the Derwent Estuary (Dartnall 1969). Other molluscs were also accidentally transported and several of these have become nuisance species.

### 5.10.2 Habitat

Low intertidal to sub-tidal; sand bottom, under stones and among large seaweeds.

### 5.10.3 Biology

*M. novaezelandiae* is a benthic crab which burrows amongst sand to hide itself. The diet comprises of predominantly sessile and slow-moving macro-invertebrates such as bivalves and gastropod molluscs, followed by crustaceans, and also includes fish, sponges, coelenterates, and plant matter (Cresswell and Marsden 1990). *M. novaezelandiae* can easily open cockle and oyster shells.

### 5.10.4 Impact

In Australia, potential impacts may include economic (loss of aquaculture, commercial or recreational harvest) and environmental (dominates or out competes and limits resources of native species or predation of native species) impacts (Hayes et al. 2005).

*Note*: *Metacarcinus magister* (Dana, 1852) Dungeness crab, a native of the Northeast Pacific, has been found in Japan, where it probably arrived in ballast water (Abe 1981), and Massachusetts (Northwest Atlantic) (Cohen 2006).

## *5.11 Pachygrapsus marmoratus (Fabricius, 1787), Marbled Crab*

### 5.11.1 Distribution

Native: Black Sea, Mediterranean, Moroccan Atlantic, Canary Islands, Madeira and Azores as well as the Atlantic coast of Portugal, Spain and France (Udekem d'Acoz 1999); Alien: now recorded from two sites in the British Isles, Southampton Water and Teignmouth region the species perhaps being transported by shipping (Ingle and Clark 2006). Human agency also seems to be responsible for spread along the European coast of the English Channel. New records from Blainville-sur-mer and Gonneville on the Cotentin coast, Normandy, indicate a northward spread that could reflect the effects of global warming and natural dispersal (Dauvin 2008).

### 5.11.2 Habitat

Semi-terrestrial, upper and middle levels of rocky shores, and often present at high densities (Ingle and Clark 2006). Found in crevices, pilings, mussel beds and rock pools (Silva et al. 2009). Once the most common crab in this habitat it now has to contend with increasing numbers of alien *Hemigrapsus takanoi* on Spanish, French, Belgian and Dutch coasts.

### 5.11.3 Biology

Diet of *P. marmoratus* includes limpets and mussels as well as filamentous and macroalgae in equal amounts (Cannicci et al. 2002). It grows quickly, reaching maturity in less than a year. Recruited in September-October, crabs were able to reproduce the following May (Flores and Paula 2002). Larval period lasts for ~4 weeks (Silva et al. 2009). This is a crab able to respond quickly to favourable environmental changes.

### 5.11.4 Impact

Unknown but could result in increased competition among intertidal crabs on rocky shores of the English Channel.

*Note*: Another *Pachygrapsus* species, *P. transversus*, an inhabitant of rocky and sandy shores, and mangroves in warmer waters, may also become established outside its native range. However, at present the exact identity of the "*P. transversus*" records, which include eastern Pacific to the eastern Atlantic and the Mediterranean, are complicated by the fact that several cryptic species are probably involved. Morphological and molecular variation between Pacific and Atlantic indicate that several new species are warranted (Cuesta and Schubart 1998; Poupin et al. 2005). Another crab from the same kind of habitat, *Metopograpsus oceanicus*, has been recorded from Hawaii (Paulay 2007) (see Table 1). *Pachygrapsus* is similar to *Planes* which has a peripatetic pelagic life style travelling around the oceans associated with weeds and other floating objects and at the mercy of currents (Poupin et al. 2005).

## *5.12 Paralithodes camtschaticus (Tilesius, 1815), Red King Crab*

### 5.12.1 Distribution

Native: Okhotsk and Japan Sea (as far south as Korea), Bering Sea and North Pacific Ocean (as far south as Vancouver Island, Canada); Alien: as a result of intentional transfer, by Russians, red king crab are now established in the

Barents Sea and northern Norway (Jorgensen 2004). They are spreading southwards towards Sweden and Denmark.

### 5.12.2 Habitat

Found on soft bottoms over a range from 3 to ~370 m with size tending to increase with depth.

### 5.12.3 Biology

*Paralithodes camtschaticus* is among the world's largest arthropods with CL > 22 cm and weighs over 10 kg. Fecundity varies between 15,000 to nearly 500,000 eggs per female, depending on size (Jewett and Onuf 1988). There are 4 planktonic stages plus a megalopa lasting about 2 months. Larvae settle at shallow depths (<20 m) and adults are found as deep as ~400 m on soft bottoms. Red king crabs perform seasonal migrations between shallow (spawning and mating areas in spring/summer) and deep waters (feeding areas in autumn/winter). Tagged adults are fairly sedentary and feed on molluscs, echinoderms and polychaetes. They also filter organic particles with maxillipeds. *Paralithodes camtschaticus* is now the subject of major fisheries in northern Russia and Norway. The red king crab has become abundant along the coast of northern Norway, with an estimated population of larger crabs (>70 mm CL) of 2.9 million individuals in 2001, and 4 million in 2004 in depths below 100 m (Jorgensen and Primicerio 2007). Fishing in the Barents Sea has an effect on limb loss especially in immature crabs (Dvoretsky and Dvoretsky 2009).

### 5.12.4 Impact

During the early stages of colonization polychaetes, bivalves and echinoderms made up most of the stomach contents, but as these were reduced fish residues assumed greater importance (Sundet and Berenboim 2008). It is the slow moving benthic animals such as echinoderms and shellfish that bear the impact of king crab predation and they probably compete with the native stone crab, *Lithodes maja*, for food (Kuzmin et al. 1996; Jørgensen 2005). Growth in the red king crab numbers may well endanger commercial scallop (*Chlamys islandica*) populations (Jørgensen and Primicerio 2007).

## *5.13 Percnon gibbesi (H. Milne Edwards, 1853), Sally Lightfoot*

### 5.13.1 Distribution

Native: this crab has a very large native range: in the Pacific from California to Chile, in the Atlantic from Florida to Brazil and Madeira to Gulf of Guinea (Manning and Holthuis 1981); Alien: Mediterranean Sea. First recorded from Italy in 1999 (Relini et al. 2000 as cited in CIESM), then rapidly from other locations in the Mediterranean such as the Libyan coast (Elkrwe et al. 2008). In many parts of the Mediterranean *P. gibbesi* is established and locally common (Crocetta and Colamonaco 2008).

### 5.13.2 Habitat

Shallow subtidal, mostly 1–2 m depth; between rocks and boulders (Deudero et al. 2005; Thessalou-Legaki et al. 2006; Yokes and Galil 2006). Fast moving, when disturbed it quickly scampers to hide in crevices and under stones.

### 5.13.3 Biology

*Percnon gibbesi* is herbivorous, feeding primarily on algae and the animals living thereon. One reason for its successful establishment may be that this kind of diet is not shared by any other comparable Mediterranean crab with which it might have to compete (Puccio et al. 2006). The native *Pachygrapsus marmoratus* is also herbivorous, but lives in the intertidal rather than sub-tidal zone so is unlikely to be displaced by *P. gibbesi,* which is also the loser in behavioural interactions (Sciberras and Schembri 2008). However there may be other infra-littoral grazers such as sea urchins with which it might have to compete. *Percnon* species tend to have exceptionally large megalopae which is probably the result of having 6–7 zoeal instars and may result in precocious sexual maturity in only the third crab instar (Hartnoll 1992). These life history features and a long larval lifespan of 6 weeks (Puccio et al. 2003; Yokes and Galil 2006) probably enhance their dispersal potential.

### 5.13.4 Impact

It is uncertain what impact *P. gibbesi* has in the Mediterranean.

## *5.14 Petrolisthes armatus (Gibbes, 1850), Green Porcelain Crab*

### 5.14.1 Distribution

Native: widely distributed in Eastern Pacific (Gulf of California to Peru), the western Atlantic (Bermuda, Gulf of Mexico, West Indies, Caribbean, and Brazil), and tropical Western Africa; Alien: East coast USA Georgia-South Carolina.

### 5.14.2 Habitat

Rocky rubble, oyster reefs and other shallow sub-tidal and inter-tidal habitats.

### 5.14.3 Biology

During summer *P. armatus* densities of 11,000 $m^2$ have been recorded in the low intertidal. Maximum body size is CW ~14 mm, but females mature at only 3–4 mm. Population fecundity on shores of Georgia are an order of magnitude higher than in its native range. This species is euryhaline, tolerant of salinities 6.7–31.5‰ (Hollebone and Hay 2007). In Brazil the population of *P. armatus* carries a high load of the bopyrid gill parasite *Aporobopyrus curtatus* (Oliveira and Masunari 2006).

### 5.14.4 Impact

Has been spreading northwards along the east Coast since 1994–1995 probably by larval dispersal, but its spread may be enhanced by transport amongst shellfish. Warming of the sea may have extended its northern limit, but minimum winter temperatures could be the limitating factor. At high density *P. armatus* may have detrimental effects on oyster harvesting by inhibiting recruitment and competing for planktonic food (Hollebone and Hay 2007). However, presence of *P. armatus* may provide more prey for fish, thereby making available energy harvested by a filter feeder (the crab) that would not normally be available (from the oyster). The impact of this porcelain crab could be to alter several interactions (both as competitor and prey) between species in the marine community (Hollebone and Hay 2008).

*Note*: Another porcelain crab, *Petrolisthes elongatus*, was probably accidentally introduced into Tasmania amongst oysters from Bluff, New Zealand (see *Metacarcinus novaezelandiae*, above and Table 1).

## *5.15 Portunus (Portunus) pelagicus (Linnaeus, 1758), Blue Swimming Crab*

### 5.15.1 Distribution

Native: Indo Pacific; Alien: Mediterranean Sea. In the Mediterranean Sea it was first recorded from Egypt in 1898 (Fox 1924), and then from Palestine (Fox 1924), Turkey (Gruvel 1928), Lebanon (Steinitz 1929), Syria, Cyprus, and Italy (as cited in CIESM). Established in Mediterranean Sea.

### 5.15.2 Habitat

Intertidal to 55 m; sandy or muddy substrate.

### 5.15.3 Biology

Benthic carnivore eating hermit crabs, gastropods, bivalves and ophiuroids. *P. pelagicus* is a widespread species that grows to a large size, 185 mm, and is fished in many areas. Has been fished commercially in the Mediterranean.

### 5.15.4 Impact

Could modify food webs and compete with other benthic carnivores.

## *5.16 Pyromaia tuberculata (Lockington, 1877), Spider Crab*

### 5.16.1 Distribution

Native: San Franisco Bay and Gulf of California to Panama (Northeast Pacific); Alien: Brazil, Argentina, Japan (Sakai 1971; Asakura 1992), Australia, New Zealand; invasion history: in Japan, *Pyromaia tuberculata* was first recorded in 1970 in Tokyo Bay and is now distributed along the Pacific coast of central Japan, eastern part of Seto Inland Sea, and the Sea of Japan off Honshu (Furota and Furuse 1988). In Australia *Pyromaia tuberculata* was first collected in Western Australia in 1978 and has since been recorded from southern (Port Phillip Bay) and eastern (New South Wales) Australia (Ahyong 2005). In New Zealand it was first recorded in 1978 in Firth of Thames (Auckland) (Webber and Wear 1981) and since become more common in Waitemata Harbour and spread northwards to Whangarei (McLay 2009).

### 5.16.2 Habitat

Under rocks, among sponges and sea weed on wharf piles, on sand and mud, intertidal to 650 m.

### 5.16.3 Biology

In Japan, *P. tuberculata* is abundant in organically polluted, large shallow bays such as Tokyo Bay, Osaka Bay, Sagami Bay and Ise Bay from the intertidal down to 80 m (Furota and Furuse 1988; Sakai 1976). In Tokyo Bay *P. tuberculata* is abundant and sustains significant population densities in the Bay despite large scale bottom hypoxia in summer. Adult crabs perish due to oxygen deficiency in late summer in the inner harbour, but fast re-colonisation of the oxygen recovered bottom in autumn, from crabs from the outer half of the bay, maintains the inner harbour population (Furota 1990, 1996a, b; Furota and Kinoshita 2004).

In New Zealand ovigerous crabs have been collected in the winter months from April to August, whereas in Southern California ovigerous females occur over most the year with a peak in the summer months (McLay 1988).

### 5.16.4 Impact

Although it has become widely established its impact is probably not significant. Since it hides amongst fouling organisms its long distance transport is likely to be by shipping.

## *5.17 Rhithropanopeus harrisii (Gould, 1841), Dwarf Crab, Harris Mud Crab*

### 5.17.1 Distribution

Native: North West Atlantic (from Gulf of St. Lawrence, Canada to Vera Cruz, Mexico; Alien: Black Sea, Mediterranean, North Sea, North-East Pacific, North East Atlantic, Southwest Atlantic; Invasion history: First in Netherlands (<1874, see Wolff 2005), later in the North-East Pacific (Lake Merritt, Oakland and San Francisco Bay, 1937; Coos Bay, Oregon, 1950; Netarts Bay, 1976; Yaquina Bay and Umpqua River, 1978), Panama canal (1969), and at various locations throughout Europe (Baltic coast of Poland, 1951; Copenhagen, 1953; Azov, Black and Caspian Seas, 1958; southern Spain 1980s). Iseda et al. (2007) recently reported it from Japan. Although found in many locations, it is not established in some, such as the Danish Waters: (Jensen and Knudsen 2005). *Rhithropanopeus harrisii* is one of those species to have become established after not being detected for years after initial records were taken. It was rediscovered in the Panama Canal 40 years after initial findings with an established reproductive population (Roche and Torchin 2007; Roche et al. 2009). Likely vectors include ballast water, hull fouling and accidental introduction with oyster and seed clams (Roche and Torchin 2007; Rodriguez and Suarez 2001).

### 5.17.2 Habitat

*Rhithropanopeus harrisii* occurs in estuarine habitats (brackish water) and lakes. It is typically found in shallow waters with muddy or sandy substrates, and hiding in shelter such as oyster reefs, vegetation, or debris.

### 5.17.3 Biology

*Rhithropanopeus harrisii* is known to feed on bivalve molluscs, oligochaetes and dead fish. It was originally transported to San Francisco Bay with Atlantic oysters

(Roche and Torchin 2007). Mating is independent of female moulting and usually occurs during the summer months. Typically, females spawn between 1,200 and 4,800 eggs per clutch depending on its size, but can lay up to 16,000 eggs (Turoboyski 1973). Ovigerous females tend to hide among debris, shells, or sediment. *Rhithropanopeus harrisii* has four zoeal larval forms and the megalopa post larval stage. Larval development is fast and takes about 16 days and sexual maturity is occurs within 9–12 months at the size of about 8 mm (Turoboyski 1973; Forward and Lohman 1983; Cripe et al. 2003).

### 5.17.4 Impact

*Rhithropanopeus harrisii* is known to compete with native species and spread the white spot baculovirus. It is an especially aggressive predator and is known to compete with and displace native crabs, crayfish, and bentho-phagous fishes, as well as, alter food webs. In Texas they are known to foul PVC intakes in lakeside homes (Roche and Torchin 2007; Grabowski et al. 2005). The deadly white spot baculovirus also causes disease in penaeid shrimp and blue crab. Hayes and Sliwa (2003) list *R. harrisii* as a potential next pest species and possible impacts could include loss of aquaculture/commercial/recreational harvest as it may feed on newly settled mussels and oysters (spat). In its native range, *Rhithropanopeus harrisii* is host to the parasitic barnacle *Loxothylacus panopaei*, which causes growth reduction and castration of its host (Alvarez et al. 1995).

### 5.17.5 Management

As ballast water is assumed to be the main vector, the reduction and prevention of contaminated ballast water is the best preventative method. The chemical Diflunezuron, an active chemical in pesticide Dimilin, has been tried out on hatching larvae of *R. harrisii* and found to be lethal in concentrations of 7–10 ppb because it inhibits chitin synthesis. However, Diflunezuron is not species specific and therefore eliminates a range of arthropods in the aquatic environment (McEnnulty et al. 2001).

## *5.18 Scylla serrata (Forskål, 1775), Mangrove Crab*

### 5.18.1 Distribution

Native: Indo Pacific (Red Sea to Tahiti); From South Africa to Tahiti, north to Japan, and south to Port Hacking, Australia and the Bay of Islands, New Zealand; including China, Philippines, Indonesia East. Alien: Hawaii, and single record from South West Atlantic (Brazil) (Melo 1983). In Hawaii it can be found around all of the islands (Coles et al. 1999; DeFelice et al. 2001).

### 5.18.2 Invasion History

*Scylla serrata* has been introduced intentionally in Hawaii and throughout the Indo-Pacific to start commercial crab fisheries. In Hawaii, *Scylla serrata* was first introduced into Kaneohe Bay in 1926 to start a commercial crab fishery. A total of 98 crabs were released on Oahu, Hawaii, and Molokai between 1926 and 1935 (Brock 1960). Edmondson and Wilson (1940) reported that the mangrove crab was already an established species by that time. A study undertaken in 1981 in Kahana Estuary, Oahu, Hawaii found that *Scylla serrata* was the most abundant species of crab even though they were highly fished (Maciolek and Timbol 1981). Mangrove crabs are native to the island of Guam but in 1975 the population was increased by crabs imported from Taiwan and the Philippine Islands. They were cultured at the University of Guam Marine Lab until the facility was destroyed by a typhoon (Eldredge 1994). Recently *Scylla serrata* has colonized Southwest Australia, more than 1,000 km south of its normal range, but genetic studies suggest that this can be accounted for by natural larval dispersal from northern Australia, resulting from an unusually strong coastal current pattern in 1999/2000, rather than human assisted larval transport (Gopurenko et al. 2003).

### 5.18.3 Habitat

Muddy bottoms in brackish water among mangroves and in estuaries (Edmondson 1954; DeFelice et al. 2001).

### 5.18.4 Biology

Large, aggressive omnivorous crab that matures at a carapace width of about 9–11 cm. The male and female begin the mating process when a female is in pre-moult condition. The crabs remain paired for 3–4 days until the female moults, and then they copulate (Knuckey 1996). The female then migrates offshore with the fertilized eggs, where they hatch in a couple of weeks (Hill 1994).

### 5.18.5 Impact

*Scylla serrata* is the largest and most aggressive swimming crab occurring commonly around all of the Hawaiian Islands. This species is not considered invasive in Hawaii because it has been introduced there intentionally for fisheries, but *S. serrata* would likely become invasive if not commercially fished (DeFelice et al. 2001). *Scylla serrata* is an important source of income for many people and the ecological impacts of this crab have not been studied in Hawaii.

## 6 Life History Trends and Body Size of Alien Crabs

There are several life history traits that appear to facilitate marine invasions in brachyuran crabs. Those that have become established are mostly intertidal to shallow sub-tidal species and are capable of tolerating a wide range of temperatures and salinities. They tend to be omnivores or generalist predators and are often highly aggressive and competitive in regards to food and shelter. They are often widespread and common in their native range thereby giving them a greater chance of being transported by ships. Their reproductive output is typically high which can be achieved by, for example, maturing early (within a couple of years), producing several thousand eggs per clutch and/or several clutches per year. Migratory behaviour allows the use of a range of habitats and depths and breeding offshore can increase successful reproduction by avoiding hypoxia/organic pollution of shallow bays, ports or harbours.

We have chosen to analyse the life history features of alien species by looking at egg-size. This character is useful because it integrates several important features into a single measure and it is a property of a species rather than an individual whose size varies. Typically egg size and egg number are negatively correlated as are egg size and larval duration. There is a trade off between egg size and egg numbers because of energetic and female morphological constraints (Hines 1982, 1992). At the extremes are small eggs with little yolk meaning that larvae must feed on plankton to reach megalopa (indirect development or planktotrophy) through to large eggs adequately provisioned to produce juvenile crabs (direct development). In between are many combinations of hatching size and number of zoeal stages, which may be feeding or non-feeding, all equally fit for the particular environment (lecithotrophy). One might predict that species with small eggs (longer larval life and greater numbers) would be more likely to become alien than species with large eggs (short larval life and small numbers).

A comment is necessary here about data analysis and which of the recorded alien species should be included in that analysis. The species listed in Table 1 are divided into two groups: species that have become established outside their native range and species that have been recorded outside their native range but have yet to establish self-sustaining populations. The first group includes all the successes while the second group includes all the failures. While there is a high probability of detecting the successes the probability of detecting failures is much lower because individual crabs are rare and many species that arrive may not be detected at all. Therefore in our life history analysis we only include the successful species. There could be several reasons why species failed: environmental mismatch (e.g., unsuitable salinity or temperature), a high level of biotic resistance (e.g., predation, parasites or competition) and low post-transport viability (e.g., arrivals were only of one sex, females lack sperm storage ability so that reproduction was impossible). Thus egg size of these species is not relevant to their failure, but for successful species egg size may well have some explanatory power and predictive value because they've overcome the impediments to colonization, and with the life history strategy that they have, begun to produce recruits. We are using egg size as an indicator of that strategy. We have not included any of the Anomura because only three species are involved.

We gathered together available data on egg size of established aliens and compared it with a matched sample of native species from the same families as a control. Within the native Brachyura included in our data set egg size varies by 3 orders of magnitude ($2.57\times10^{-3}$ $mm^3$ {*Metopograpsus messor*} to $2144.8\times10^{-3}$ $mm^3$ {*Elamena panglao*}) (see Fig. 8) and differs between the major groups of crabs (Table 4): portunoids (mean = 20.1, range $9.2\times10^{-3}$ to $47.7\times10^{-3}$ $mm^3$) have the smallest eggs followed by, grapsoids (mean = 27.2, range $2.57\times10^{-3}$ to 114.95 $mm^3$), pilumnoides + xanthoids combined (mean = 30.7, range $16.4\times10^{-3}$ to $2144.7\times10^{-3}$ $mm^3$), and majoids (mean = 129.5, range $12.7\times10^{-3}$ to $860.33\times10^{-3}$ $mm^3$) who have the largest eggs. Just as van Dover and Williams (1991) found for squat lobsters (Galatheoidea) there is much greater variation in crab egg size amongst species known to or presumed to have lecithotrophic development (range $10\times10^{-3}$ $mm^3$ {*Munida tenella* Benedict} to $11{,}260\times10^{-3}$ $mm^3$ {*Munidopsis verrucosus* Khodkina}). They argue that when brood size is maximized then egg size must be minimized and tightly controlled (as in the planktotrophic strategy) whereas if brood size does not need to be maximized there can be much wider variation in egg size (as in the lecithotrophic strategy). Crabs have a similar range of egg size and the same constraints on the production of viable larvae probably apply to them as well.

Overall, alien species of crabs tend to have smaller eggs (~1/4th) than the control group of native species (Fig. 8) ~$30\times10^{-3}$ $mm^3$ vs 117.7 $10^{-3}$ $mm^3$ (Table 4) however the difference is not significant ($p > .05$) given the wide variation in egg size.

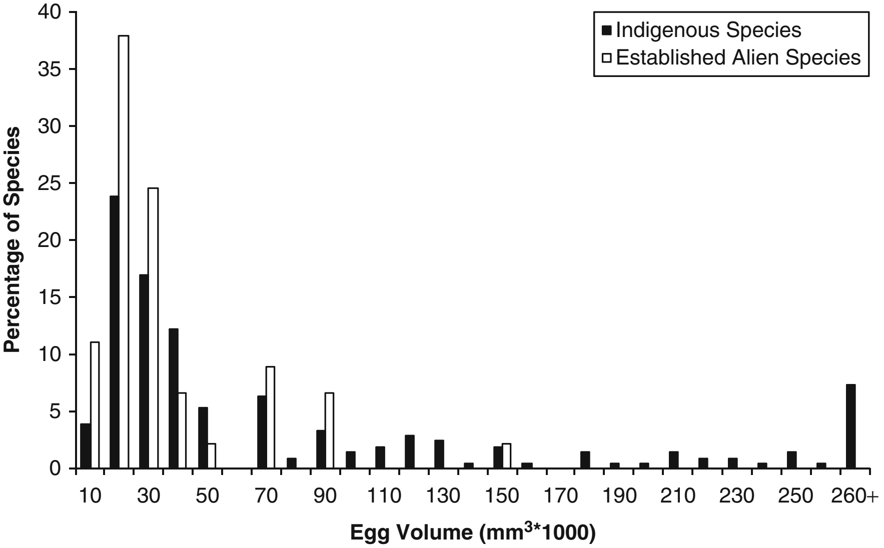

**Fig. 8** Comparison of the variation in egg size in established alien and a set of native species of Brachyura ($n = 206$) from the same families

**Table 4** Comparison of mean egg volume (SE, n) between established alien and native species of crabs broken down by group

| | Egg volume ($mm^3$*1,000) | | |
|---|---|---|---|
| | Established aliens | | |
| Group | Mediterranean | Rest of world | Native species |
| Majoidea | 74.0 (6.6, $n=3$) | 81.8 (20.0, $n=5$) | 129.5 (16.6, $n=74$) |
| Pilumnoidea + Xanthoidea | 28.4 (5.6, $n=4$) | 19.6 (1.4, $n=5$) | 30.7 (5.1, $n=14$) |
| Portunoidea | 14.4 (1.8, $n=6$) | 15.9 (3.1, $n=6$) | 20.1 (1.4, $n=40$) |
| Grapsoidea | 25.1 (4.4, $n=5$) | 17.5 (2.9, $n=8$) | 27.2 (2.7, $n=53$) |
| Mean for all species | 29.5 (4.2, $n=25$) | 31.0 (6.5, $n=25$) | 117.7 (20.4, $n=199$) |

*Note*: The anomuran crabs are not included

**Table 5** Comparison of alien composition of Mediterranean Invaders and the rest of the world at the Suerfamily level

| Superfamily group | Erythrean invaders | Rest of the world |
|---|---|---|
| Calappoidea | 1 (4%) | 0 |
| Cancroidea | 0 | 1 (4%) |
| Dorippoidea | 1 (4%) | 0 |
| Goneplacoidea | 1 (4%) | 0 |
| Leucosidea | 3 (12%) | 0 |
| Majoidea | 3 (12%) | 5 (20%) |
| Pilumnoidea | 1 (4%) | 2 (8%) |
| Portunoidea | 6 (24%) | 6 (24%) |
| Xanthoidea | 3 (12%) | 3 (12%) |
| Grapsoidea | 5 (20%) | 8 (32%) |
| Ocypodoidea | 1 (4%) | 0 |
| Totals | 25 (100%) | 25 (100%) |

Numbers of established species (and percentage) are shown. Note that there is a small overlap in the groups of species with three species in common

The same is true when egg sizes of alien species and natives are broken down into the major groups: in each group the mean egg size for aliens is smaller (Table 4), but these differences are not significant ($p > .05$) partially because of egg size variation but also because the sample sizes of aliens are small (there are only 47 established aliens). Egg size may be a useful indicator of the likelihood of being spread outside the native range, but it is not a sufficient indicator by itself.

We take this opportunity to compare the species which colonized the Mediterranean via the Suez Canal with alien species established elsewhere (see Table 4). At the same time we compare, at the family level, the Erythrean invaders with invaders elsewhere (Table 5). If we use egg size as a guide to life history then there are no significant differences in the egg size of Erythrean invaders and crabs elsewhere, and thus no difference in their degree of planktotrophy/lecithotrophy. Most of the Erythrean species probably arrived by dispersing as adults or being carried as larvae by the northward flow of sea water, but the non-Erythrean species have dispersed to various parts of the world by shipping rather than currents. Some groups are represented by species that have only spread by the Suez Canal but are not aliens elsewhere: these are in the Calappoidea, Dorippoidea, Goneplacoidea, Leucosoidea and Ocypodoidea (7 species in total). Conversely the Cancroidea (1 species) is the only group to have spread elsewhere, but not into the Mediterranean. The other 5 groups are represented by similar numbers of species in the Mediterranean (18 species) as elsewhere (24 species). Overall there is no significant difference between the number of species in each group ($\chi^2=15.1$, $p>0.13$). There are no anomuran aliens amongst the Erythrean invaders so these are not included. We conclude that the species that have colonized the Mediterranean are more diverse (10 vs 6 superfamilies), but are a similar suite of species as those colonizing other seas.

Amongst the commonly encountered aliens that have become established we mostly find portunoids (e.g., *Carcinus* spp., *Charybdis* spp., *Callinectes sapidus*, *Portunus pelagicus* and *Scylla serrata*) and grapsoids (e.g., *Eriocheir sinensis*, *Hemigrapsus* spp., *Pachygrapsus* spp. and *Percnon gibbesi*). *Rhithropanopeus harrisii* has a similar egg size to *Percnon gibbesi* and smaller eggs than *Eriocheir sinensis*. Thus egg size should be a good predictor of the potential of a crab to spread and be spread by anthropogenic means, but at the same time other factors must be involved as there is considerable overlap in egg size between alien and native species. Carlton and Geller (1993) may well be correct in calling the process leading to the spread of aliens an example of "ecological roulette". Miller and Ruiz (2009) present an analysis for some other groups of organisms, of the biological attributes of successful and failed invaders, incorporating consideration of the source and recipient regions as well as the nature of the vector and pathway.

The range of maximum body size of alien species is shown in Fig. 9. They range in size from CW=6 mm for *Neorhynchoplax kempi* (Hymenosomatidae) to CW 220 mm for *Paralithodes camtschaticus* (Lithodidae) (see Table 2). The mean maximum size of species that became established was 53.1 mm compared to species not yet established that was 46.7 mm, a difference that is not significant.

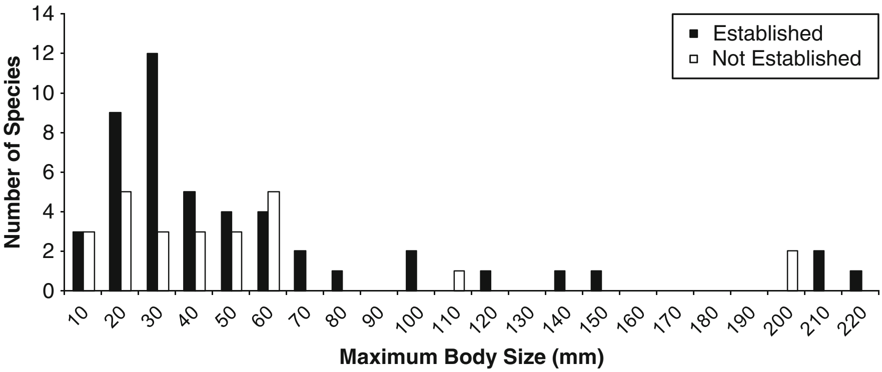

**Fig. 9** Comparison of distribution of maximum body size (CW or CL) of established and non-established alien crabs

# 7 Discussion

The success of a marine invader is a product of many factors, such as surviving transport, becoming established in the new location and reproducing under the new abiotic and biotic conditions (Carlton 1996; Ruiz et al. 2000). In addition, high propagule supply (density, frequency, duration) will allow easier establishment (Carlton and Geller 1993; Kolar and Lodge 2001; Colautti et al. 2006). The probability of arrival and exact impact of the invasive species are not always easy to predict (Strauss et al. 2006; Strayer et al. 2006; White et al. 2006). However, benthic animals have been shown to be the dominant alien group in the European "seas" (which includes the Mediterranean, Atlantic, North Sea, Baltic Sea, Black Sea and Arctic) accounting for 57% of alien species (Streftaris et al. 2005). Of the 737 alien multicellular marine species recorded from the seas bordering Europe by 2009, the largest number were molluscs, followed by crustaceans and bony fish (DAISIE 2009). By comparison, in San Francisco Bay crustaceans are the richest alien taxon (53 species), followed by molluscs (30) and fish (28) (Cohen and Carlton 1995). In Pearl Harbour, Hawaii molluscs (38) and crustaceans (35) comprise the two richest introduced groups (Coles et al. 1999). Carlton and Eldredge (2009) provide a more complete and up to date lists of species for all the Hawaiian Islands. In Port Philip Bay (Australia) crustaceans were the fourth richest invasive taxon (after bryozoans, cnidarians, and chordates) and molluscs ranked seventh (Hewitt et al. 2004). It is important to note the caveat that sampling and the availability of taxonomic expertise differs among regions.

## *7.1 Regional Observations*

The ability of a species to invade a new area will depend on its genetic fitness, the biophysical similarity of the new area compared to its native range, as well as the level of predation and competition for food and shelter it will encounter (Hutchings et al. 2002).

Of all the oceans of the world, the Mediterranean is of particular interest because it has had a chequered history and because it represents the only surviving part of the Tethys Sea, the cradle for so many groups of marine animals that survive today. It once connected the Indo-West Pacific, tropical Atlantic and eastern Pacific Oceans, but has been isolated since the Miocene. The opening of the Suez Canal in 1869 restored the connection with the Indo-West Pacific, via the Red Sea, which had been blocked for 10 m years. Tectonic changes and sea level decline resulted in the size of the Mediterranean sea being greatly reduced, connection with the Atlantic also lost, and the extinction of many Tethyian species. Subsequent colonizations of the basin came from the Atlantic, transforming what was a tropical fauna into a more temperate one, Atlantic-derived biota (Rilov and Galil 2009). Tropicalization of the Mediterranean Sea, coupled with anthropogenic effects, will determine the extent of faunal change (Bianchi 2003).

Fifty-eight percent (42 of 73) of the alien crabs recorded worldwide can be found in the Mediterranean Sea of which about 60% (25 species) have become established, perhaps because of the impoverished fauna left resources unutilized. For both established and non-established species most have entered the Mediterranean via the Suez Canal (the so-called Erythrean invasion) (60% and 88% respectively) while the balance have entered from the Atlantic direction (40% and 12% respectively) (see Table 1). A total of 116 species of native marine crabs are known from the Mediterranean (Števčić and Galil 1994) so that the combined crab fauna is 141 species (116+25) of which 18% are aliens. As a measure of the effect of the Suez Canal we can eliminate the Erythrean fauna leaving the Atlantic aliens, which would be 8% (10 of 126). By comparison the level of established aliens in more remote regions like New Zealand is only 2% (2 of 90) and in Australia <1% (5 of 950) (see below). There is no other region in the world that has such a high level of alien crabs, but this is not unexpected because the Mediterranean Sea has long been a cross road of shipping from all parts of the world. It is ironic that this remnant of the once rich and diverse Tethys Sea harbours a fauna drawn worldwide: perhaps the Mediterranean Sea is a symbol of the human era and its impact on the world.

Two other regions have been colonized by significant numbers of aliens: these are the North Atlantic and Hawaiian Islands where 9 aliens have been recorded (see map Fig. 6). The North Atlantic is, by comparison, a vast area where large scale ocean currents and shipping dominate faunal change. Like the Mediterranean, the Hawaiian Seas (Islands) are a cross road for shipping from several directions as well as a place where alien species were deliberately introduced to establish fisheries (Carlton and Eldredge 2009). Many species derive from the Atlantic, and were probably introduced into Pearl Harbour by naval vessels, but others remain cryptogenic. Because they are oceanic islands "rafting", whether it be by natural or human-mediated processes (including Polynesian migration), is always going to be a significant factor in their faunal dynamics and loom much larger than in the Mediterranean, which is an enclosed Sea.

Many alien species are first picked up in port surveys and in most cases their occurrence, port by port, is all that we know about their new distribution. Often the fauna in these places is somewhat less than pristine and the ability of aliens to invade ports maybe quite different to their ability to invade unmodified habitats, which is what we try to protect. For example, Coles and Eldredge (2002) highlight the need for better information about coral reefs and whether or not alien species are present.

All the aliens (5 species) in the South Atlantic are found along the eastern coastline of South America rather than West Africa, probably due to lack of investigation of the latter region. Reports of *Scylla serrata* here are based on an isolated record off Brazil and there is no evidence of viable populations (Davie 2002). A similar number of aliens (6) have been recorded in the south Pacific, although some of these are "local" movements, between New Zealand and Australia. These trans-Tasman transfers from New Zealand were unintentional and associated with transportation of oysters to Hobart. The others came from Japan and Europe and were shipping-related. Given the size of continental Australia it is remarkable that so few alien crabs have been recorded (see Sect. 3.7). New Zealand too has few alien brachyuran species. New Zealand has a relatively low brachyuran diversity of around 90 species (McLay 1988) compared to more than 950 species in Australia (Davie 2002).

In the north Pacific there have been surprisingly few species (four on the Asian and three on Pacific coasts) introduced, given the high level of maritime activity, but this may be related to the fact that large distances are involved and so transit times are long. *Rhithropanopeus harrisii* probably arrived on the Pacific coast from the east amongst oyster imports in the 1930s and/or via shipping through the Panama Canal while the other two got there by various means. *Carcinus maenas* arrived after a stop-over on the Atlantic coast of the USA and *Eriocheir sinensis* probably arrived directly from China as well as indirectly from the UK population (Wang et al. 2009).

Two significant biogeographic regions, the Indian Ocean and Eastern Pacific effectively have no records whatsoever of alien crabs. There are several single records of *Carcinus maenas* from the Indian Ocean, but no permanent populations are known (Carlton and Cohen 2003). The apparent absence of alien crabs from the Indian Ocean (and Southeast Asia) may well be an artefact because we do not know the native range of many tropical species. No alien crabs are known from the west coast of South America (Castilla et al. 2005). In maritime terms this is a remote and sparsely frequented part of the world's oceans: its remoteness means that any species spreading from a new colony have a long way to travel. Given the current patterns in temperate climes they would have to cross the entire South Pacific from Australasia or via the circum-subantarctic current further south. Only *Hyas araneus* has been found in Antarctic waters. For various physiological reasons crabs are not able to thrive in these cold waters so that temperature limits their invasibility (Thatje et al. 2005; Aronson et al. 2007). While the Eastern Pacific is apparently pristine many species have been introduced as part of the aquaculture programs of Chile and Peru. Castilla and Neill (2009) list 51 marine alien species of plants and animals, including around 20 invertebrates, but no crabs. About one-third of these species probably arrived via the shipping vector while others escaped from aquaculture.

When thinking about alien species we automatically think of coastlines. All known aliens are coastal and tied to each countries coastline and thus regarded as a problem to be solved nationally. However, coastlines and the littoral zone are only a minute fraction of the marine realm. The high seas constitute more than 70% of the earth's surface and little attention is paid to which species might be off-loaded there far from home. Countries monitor their own waters and coasts, but no one takes responsibility internationally. In fact at the moment many countries have ballast water exchange rules that see larval stages dumped off-shore on the assumption that they will not survive there. But do we know whether this assumption is valid? A safer option would be to insist that shipping only release sterilized (perhaps heated) ballast water. In fact if all ships treated their ballast water we would not need any restrictions on dumping.

## *7.2 Dominant Alien Brachyuran Groups (Fig. 10)*

Three brachyuran super-families stand out for their high number of recorded alien species: namely the Portunoidea (swimming crabs, 15 aliens), Grapsoidea (shore crabs, 12 aliens) and Majioidea (spider crabs, 12 aliens) (Fig. 10). Collectively 29 out

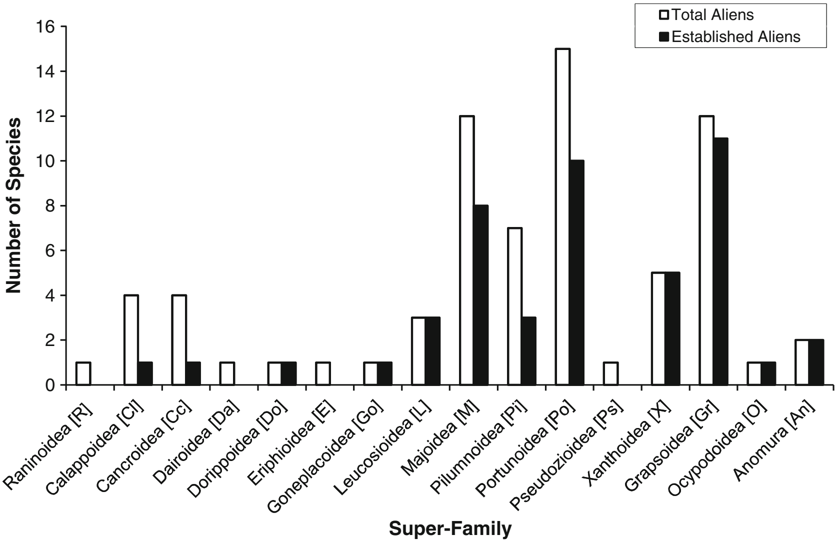

**Fig. 10** Comparison of numbers of established and non-established alien in brachyuran super families and in crab-like Anomura

of the 39 species became established. These crabs have life styles that make them more prone to transport: having numerous long lived larval stages, occupying shallow waters where they are likely to encounter ships or by being part of the fouling community that colonizes such temporary surfaces as hulls of ships and wharf piles. Grapsoid shore crabs have evolved semi-terrestrial air-breathing species as well as nektonic species like *Planes* spp. which spend their entire lives clinging to floating objects that are carried over long distances by ocean currents. Both of these strategies ensure wide dispersal by natural means. Out of the total of 73 species 47 species have become established outside their native range. With only three and five alien species respectively, the Leucosioidea and Xanthoidea are remarkable as all have become established. Similarly with the crab-like anomurans but in this case two of them were spread by human transplant, one intentional the other accidental. The Cancroidea include four species which have been recorded outside their native range. The New Zealand crab *Metacarcinus novaezelandiae* which was accidentally transferred with oysters to southern Australia and Tasmania, has become established there (Poore 2004). One cancrid crab that does not appear in Table 1 is the edible European crab *Cancer pagurus* that was deliberately introduced to New Zealand by early settlers between 1907 and 1913 for commercial fisheries (Thomson and Anderton 1921). Another cancrid crab that might appear on our list in the future is *Cancer irroratus*: larvae of this north-west Atlantic crab travelled and survived 17 days in ballast water from New York to England (Hamer et al. 1998). The megalopa larvae were transferred to the laboratory and grew to 58 mm CW in 5 months. Overall, the water temperature and salinity range of the southern North Sea would probably allow this species to survive there (Hamer et al. 1998), but none have yet been reported outside their native range.

At the other extreme representatives of the primitive crabs, sometimes known collectively as podotremes, are conspicuous by their absence except for one burrowing Indo-west Pacific raninid, *Notopus dorsipes*. This crab probably entered the Mediterranean via the Suez Canal. Many of these crabs have life styles that do not lend themselves to being transported: many live in deepwater while others have close associations with other invertebrate hosts or they rely on other organisms (or pieces thereof) for concealment, for example the dromiid sponge crabs which carry sponge umbrellas above their body. Such reliance on others is somewhat parallel to the case of parasites that cannot be transported without their intermediate hosts. None of these podotreme crabs have any means of trans-moult sperm storage so successful colonisation demands at least one male as well as one female. Also many of them have comparatively large eggs (McLay unpubl.) that make them less likely to be transported (see egg size analysis above).

## 7.3 Invasion Dynamics of Alien Brachyurans

Grosholz and Ruiz (1996) reviewed the spread rate of ten alien species. Large year-to-year variation in the geographic expansion rate of the ten marine alien species were found, which were possibly due to the variation in the ocean surface currents. In this study, no link between the mean annual rate of range expansion and planktonic duration was found. In addition, it appeared that the spread rate in one location was not a good indicator of spread for other locations in the case of *Carcinus maenas* (Grosholz and Ruiz 1996). Similarly, it was suggested for *Carcinus maenas* in Australia that recruitment is chiefly localised despite long planktonic durations and off-shore development of larvae and only occasionally punctuated wide scale dispersal (Thresher et al. 2003). In addition, global distribution patterns of alien *Carcinus maenas* and *C. aestuarii* seem to have been episodic and primarily regulated by temperature (Carlton and Cohen 2003). While *C. maenas* was first recorded outside Europe on the Atlantic coast of North America (and perhaps the Red Sea) in the early 1800s, *C. aestuarii* did not begin to spread until the 1980–1990s. They have become established in Atlantic North America, Australia, South Africa, Japan and Pacific North America (*C. maenas*); Japan and South Africa (*C. aestuartii*), but not in the tropical regions where one-off collections of *Carcinus* sp. were made (e.g., Red Sea, Madagascar, Pakistan, Sri Lanka, Myanmar, Bay of Panama) (Carlton and Cohen 2003).

Interestingly, it has been observed that invasions are linked to an increase in size in some marine and estuarine invertebrates in the new location (phenotypic change). Grosholz and Ruiz (2003) found that 12 out of 19 species were significantly larger in the introduced range compared with the native range. They also noted that this invasion-driven increase in body size contrasts with the pattern observed in many other taxa including plants, mammals and lizards. Brachyuran species showing this trend of larger size are *Rhithropanopeus harrisii*, *Eriocheir sinensis* and *Carcinus maenas*, but not *Hemigrapsus sanguineus*. Possible explanations for increased size could be the greater resources in the introduced range relative to the native range, which could translate into faster growth and larger body size and the absence of predators or parasites (particularly those which take control of host growth) in the introduced range (Grosholz and Ruiz 2003). Findings from modern invasions support the idea that size increase may often follow range expansions of marine invertebrates and can result from rapid phenotypic change during the early stages of colonization.

## 7.4 Alien Crab Fisheries

Several alien crab species have not only managed to establish large populations, but they also sustain locally important fisheries (Streftaris et al. 2005). Of these species only *Paralithodes camtschaticus* has begun to be managed for sustainability. These species are “invasive”, though some were deliberately introduced, and are likely to have a substantial impact on the host environment.

### 7.4.1 *Cancer pagurus*

Not all introductions of alien species, accidental or intentional, result in established and sustainable populations. Despite the availability of native *Metacarcinus novaezelandiae* there was an attempt early last century to transport the edible crab, *Cancer pagurus*, from Britain to New Zealand so as to provide acceptable and familiar crustacean food to the European colonists. Between 1907 and 1913, 56 adult *C. pagurus* were brought to New Zealand and kept at the Portobello Fish Hatchery (now Portobello Marine Laboratory, Otago University, Dunedin) and from there 19 were released into the harbour, along with ~20 million larvae from captive females, none of which were ever seen again (Thomson and Anderton 1921; McLay 1988)! This was part of the “Europeanization” of the land and the sea (known as the “Acclimatization Movement”): fortunately none of the transported marine animals, which also included several species of commonly eaten British fish, were successful. The failure of *C. pagurus* to establish was probably the result of the animals not being released at the optimal time and place, thereby not copying the natural depth migratory cycle. Meanwhile during the 1920–1930s an unknown number of *Metacarcinus novaezelandiae* was accidentally transported along with flat oysters from southern New Zealand to Hobart, Tasmania. This species became established, although never reached plague levels, and remains to this day around Tasmania in low numbers (R. Gurney, pers. comm. 2010). It has also been recorded on the Australian mainland in Victoria and New South Wales (Poore 2004). Other species probably accidently transported at the same time, include *Petrolisthes elongatus* (Porcellanidae), *Halicarcinus innominatus* (Hymenosomatidae) (see Tables 1 and 2), *Patiriella regularis* (Asteroidea) and several molluscs (Dartnall 1969). Last century no one paid much attention transporting biodiversity across the Tasman Sea, probably because it was assumed that the fauna was the same as in NZ.

### 7.4.2 *Chionoecetes opilio*

Beginning in 1996, occasional snow crabs were collected as by-catch in the Barents Sea (Eastern Atlantic), outside their native range that includes the North Pacific, Beaufort Sea, Arctic and Northwest Atlantic and west coast of Greenland. Larvae are presumed to have been transported there in ballast water (Alvsvag et al. 2009). Bottom trawl surveys 2004–2006 recovered a significant number of crabs (from ~5% of trawls), including ovigerous females, and up to 75% of the catch were juveniles <50 mm CW suggesting that there is now a high level of recruitment and that the population is self-sustaining. The *C. opilio* fishery is very important to fishermen in the Northwest Atlantic with a catch of >100,000 tons worth > $400 million in 2002. The fishery is based on males and regulated by a minimum legal size. If a population becomes established in the Barents Sea then it could become a valuable fishery, alongside the red king crab introduced some 30 years earlier (see below).

### 7.4.3 *Eriocheir sinensis*

The mitten crab is a delicacy in China and Southeast Asia where it is harvested in large quantities. Overfishing and habitat loss have lead to a decline in catches from wild populations resulting in a large Chinese aquaculture industry which produces a harvest valued at around $1.25 b for consumption annually (Herborg et al. 2005; Dittel and Epifanio 2009) to meet demand. Mature ovaries are a delicacy that commands a high price. *Eriocheir sinensis* is now widely established in Europe and beginning to expand its range in the UK. Gilbey et al. (2008) suggest that spread in the UK may have been hastened by attempts to establish fisheries for this species. Small scale fisheries already exist in California, where crabs are sold on local Chinatown black markets in Oakland and San Francisco, and in the U.K. where they are sold in London, but these crabs come from the Netherlands. Investigations by staff at the NHM show that mitten crabs from the Thames River are safe to eat so they could be harvested in the heart of London (Clark et al. 2009). It has been suggested that mitten crabs, free of lung flukes, could be sent back from whence they came by harvesting them commercially in Britain and exporting to China thereby turning a tidy profit (Owen 2003)!

### 7.4.4 *Paralithodes camtschaticus*

During 1961–1969 Russian scientists transplanted 1.5 million larvae, ~10,000 juveniles and ~2,600 adults of this species from western Kamchatka peninsula to the southern Russian Barents Sea and by the 1970s a reproductive population of Red King Crabs had become established (Orlov and Ivanov 1978). Estimated king crab trophic carrying capacity for the Barents Sea is $15 \times 10^6$ crabs and by 2005 the population had reached $13–20 \times 10^6$ (Sundet and Berenboim 2008). By 1992 the crab became abundant in Norwegian waters. As of 2007 it has been proposed that the northern part of the Norwegian stock is to be managed as a sustainable fishery, with quotas, while further south the aim is to limit its spread by having no limits to the catch (Sundet and Berenboim 2008). However, the effectiveness of this strategy is probably limited because only males are taken. It has not yet reached Sweden or Denmark. The value of the Norwegian catch increased from 1.3 million Nkr in 1994 to 75 million Nkr in 2004 (Jørgensen 2006). Crabs are caught in traps or trawled. No commercially exploited crab is native to the Barents Sea. The stone crab *Lithodes maja* is native to the area, but is not exploited.

### 7.4.5 *Portunus pelagicus*

First recorded in the Mediterranean during 1898 and was abundant enough to be of commercial interest in the 1920s. It first appeared in the Haifa fish markets in the early 1900s and continues to be sold in substantial numbers (Galil 2007). It is now caught in Augusta Bay Sicily and huge quantities are sold in the market (Crocetta 2006). Recently it has been collected in the Tyrrhenian Sea and in the Aegean Sea, Turkey (Crocetta 2006; Yokes et al. 2007). Global warming is expected to favour this tropical species (Galil 2007).

### 7.4.6 *Scylla serrata*

During the period 1926–1935 98 mangrove crabs were intentionally introduced from Samoa into Oahu and Molokai, Hawaii. By 1940 *S. serrata* was well established, migrating in and out of the larger rivers (Edmondson and Wilson 1940). By 1992 it was commonly collected on the island of Hawaii and sold in local markets (Eldredge 1994; Carlton and Eldredge 2009). *Scylla serrata* is native to the island of Guam but in 1975 the Government imported 270 specimens from Taiwan, some of which were experimentally cultured at the University of Guam Marine Laboratory until the facility was destroyed in 1976 by a typhoon. The aim was to increase local recruitment. Fish farmers on Guam, who occasionally found native crabs in their fish ponds, also imported mangrove crab juveniles from the Philippines in an attempt to farm the crabs (Eldredge 1994).

## 7.5 *Role of Live Exports and the Aquarium Trade in the Spread of Alien Crabs*

While a great deal of effort is devoted to deterring accidental introductions via ballast water and hull fouling, the same level of attention is not necessarily applied to live imports for the aquarium and restaurant trade. Live crabs chosen by the customer from a tank in a seafood restaurant command a much higher price than their frozen counterparts. Species from far-flung corners of the Pacific and Indian Oceans are transported by air in cooled containers to upscale consumer markets. The species frequently encountered in markets and seafood restaurants are mitten crabs (*Eriocheir sinensis*, *E. hepuensis*, *E. japonicus*), Tasmanian giant crabs (*Pseudocarcinus gigas*), snow crab (*Chionoecetes opilio*, *C. japonicus*), blue crabs (*Callinectes sapidus*), queen crabs (*Erimacrus isenbeckii*), Alaskan red king crab (*Paralithodes camtschaticus*) and mud crabs (*Scylla serrata*) (Ng 1998). Some, but not all, of these species are unlikely to become established if they escaped due to temperature differences, but the main reason why this is not more likely is the very high cost of importing them. At table large individuals fetch more than $100 per crab. The same cannot be said about those at the cheaper end of the spectrum, such as mitten crabs, which may only cost $10–20, and do not have to escape directly to the sea as they spend part of their life in rivers. Escape or release of live mitten crabs from ethnic markets and the ornamental aquarium industry is a hazard highlighted by Dittel and Epifanio (2009). The seafood trade may well have been responsible for the introduction of mitten crabs to the Pacific coast of North America (Chapman et al. 2003). Another example is *Scylla serrata* which are trussed up and transported widely throughout Southeast Asia so there are many of opportunities for them to escape. Eldredge (1994) suggested that live imports for consumption of blue crab (*Callinectes sapidus*) from Louisiana may well have lead to their release in Kaneohe Bay, Hawaii. Similar imports to Germany may also be a source of colonists (Nehring et al. 2008). On the web one can order a live lobster air-freighted to one's house anywhere in the USA (including Hawaii) for US$74 from "The Lobster Man", Maine http://www.thelobsterguy.com/. As the web page says – "If you wanted them any fresher you'd need your own boat!"

Probably an even larger problem is crabs imported and sold in the aquarium trade as pets. Sold for only a few dollars, and likely to be kept under circumstances much less secure than in restaurants, these animals can easily escape or be discarded live into a new environment. Many of these species are sesarmids and coenobitids who can easily survive in warm moist terrestrial habitats. A small selection that can easily be found on the WWW includes: *Stenorhynchus seticornis* (arrow crab), *Xenocarcinus* spp. (decorator crabs), *Mithrax sculptus* (emerald crab), *Sesarma bidens* (red claw crab), *Percnon planissimum* (nimble spray crab), *Grapsus grapsus* (sally-light foot crab), *Trapezia* spp. (calico crabs), *Cardisoma armatum* (rainbow crab), *Uca* spp. (red and gold fiddler crabs), *Coenobita clypeatus* (hermit crab) and *Neopetrolisthes ohshimai* (anemone crab). The scientific names and common names used in the aquarium trade are often unreliable: for example, if we assume that the photo on the web page does actually depict what one's purchasing, either or both the scientific and common names may well be erroneous (see http://www.aquacon.com/crabs.html or http://en.microcosmaquariumexplorer.com/wiki/Sally_Lightfoot_Crab or http://www.aquaticsworlduk.com/). There are many incarnations of the "sally light-foot" crab! We should also include live crabs used for educational purposes: for example, biological supply houses sell live *Carcinus maenas* often used for biology experiments in schools and universities (Carlton and Cohen 2003). While it is compassionate to have kids care about the animals they study and "return them to the sea" when they are finished with them, this is not a good idea when the crabs came from afar. Escape or release of these live imports at the wholesale level is probably more of a threat than at the domestic level. While some countries have very strict rules (e.g., Australia and New Zealand) about the import of live crustaceans, others (e.g., Singapore) have few if any rules at all (Hewitt et al. 2009).

## *7.6 Pest Management Options for Alien Brachyuran Crabs*

The main options for managing invasive marine species range from the more classical methods of physical removal or use of chemicals (biocides) to biocontrol, genetic technology, environmental remediation, commercial exploitation and intensification of native species (such as predators, herbivores, parasites or diseases) (Thresher and Kuris 2004). The acceptability of control methods depend on their feasibility/effectiveness and their side effects. Physical removal and biocides are efficient control methods for small scale incursions but there are no acceptable control methods for large-scale marine incursions at present (Thresher and Kuris 2004). Biological control in the marine environment has been viewed as too risky by some scientists (Secord 2003). We are not aware of a program that has been successful in eradicating an invasive marine crab.

However, in the past various methods have been tried to reduce the population size of alien brachyurans in their new range. For example, physical removal by setting nets and trapping has been tried for *Eriocheir sinensis* in Germany, but with no substantial or long-term effect. Similarly, fencing, trapping and poisoning have been tried for *Carcinus maenas* with limited success (see Klassen and Locke 2007). New lines of enquiry focussing on pheromone attractants to trap crabs may prove useful (G. Inglis pers. comm. 2009), although they may well be less efficient than baited pots because of their limited spatial range of effectiveness and they only attract sexually mature crabs. The advantage could be that they are species specific and the "bait" may have a longer shelf life. As noted above, harvesting alien species is another alternative, but as long as there is a profit to be made there is no incentive to reduce the crab population to zero.

The enemy release hypothesis holds that one reason why some alien species become more numerous is because, while they have been transported to a new environment, their natural enemies have not (Torchin et al. 2002, 2003). Amongst these enemies are parasites with complex life cycles that no longer attack the crab host: even though adult crabs may be transported with their parasites, the latter do not become established because the intermediate hosts are lacking. We expect native parasites in the new environment will not immediately attack the new host so its numbers can explode in the absence of any restraints. Ballast water maybe one of the most successful vectors for aliens because larval stages cannot carry adult crab parasites (Torchin and Lafferty 2009). However, native predators have a much greater potential to control the populations of alien species because they are less specific. Torchin et al. (2001) compared native *Carcinus maenas* populations with those from introduced regions and found that parasite loads were substantially less in alien populations and body size was larger. Interestingly, limb loss (an indicator for predation) was not significantly lower in these populations. The parasitic barnacle *Sacculina carcini* has been investigated in the laboratory as a potential biological control agent for *Carcinus maenas*, but was found to be not host-specific enough because it also infected, and often killed, native species in Australia (Thresher et al. 2000; Goddard et al. 2005). Rhizocephalan cirripede parasites emasculate their hosts and cause cessation of growth (Høeg et al. 2005). Entoniscid isopod parasites can castrate female hosts while not harming males (Brockerhoff 2004). In general, parasites used in biological control have the potential to reduce crab densities, but do not eradicate them: it is never in the interest of a parasite to eliminate its host (Torchin et al. 2002). The case of *Heterosaccus dollfusi* attacking the swimming crab, *Charybdis longicollis*, in the Eastern Mediterranean illustrates this point: both species are Erythrean invaders, but they arrived at different times. *Charybdis longicollis* was reported from the Levantine coast in the early 1950s, but the parasite was not detected until the early 1990s. A decade later, in the early 2000s, the crab was as abundant as ever despite the levels of the parasite being as high as 60–65%. The only affect of the parasite was to reduce the frequency of large crabs. The crab population had a head start, but the parasite has been unable to reduce the population of the invader. The effectiveness of the parasite as a control agent is limited by high host fecundity and the recruitment/infection dynamics of host and parasite. In an open system, where some hosts can escape infection, parasites may not be the answer (Innocenti and Galil 2007).

## 8 Summary

A total of 73 alien crabs (both Brachyura and Anomura) have been recorded with 48 (65.8%) becoming established. They have been most commonly transported by way of shipping and by access provided by canals. Alien species have a suite of life history characters that facilitate their transport, and compared to a control group they tend to have smaller eggs, but the difference is not significant because of high variation of egg size. Some of these crabs constitute a significant environmental and economic problem in many parts of the world (even those that are commercially harvested) as they often establish high population densities and compete with local fauna for food and shelter. Although the total number of alien brachyuran crabs is small compared to other major taxa (e.g., Mollusca) their impact can be substantial and glaringly obvious in places like waterways, but usually their effects are at best subversive and at worst subtle and insidious. Experimental measurement of impacts is in its infancy. Consequently, preventative measures are important as well as developing better control techniques to limit their impacts. A high level of biosecurity is preferable to having to try and eradicate species after they arrive. The current focus of attention on coastal alien species has resulted in the unfortunate agreement, at the international level, for untreated ballast water to be dumped with impunity on the high seas, without any knowledge of its impact.

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# The Global Spread of the Chinese Mitten Crab *Eriocheir sinensis*

## Matt G. Bentley

**Abstract** Chinese mitten crabs are one of the World's most notorious aquatic invasive species. Their catadromous life history, in which they spend most of their lives growing to maturity in freshwater, and their extreme euryhalinity, has made it relatively easy for the species to gain a foothold in the World's river systems. Ballast water introductions are thought to have brought them to continental Europe in the early twentieth century. These will have probably been as larvae, which will then have settled in the estuaries subsequently moving upstream as juveniles. The capacity of these crabs to move upstream (and over land) is staggering and individuals in their native range in the Far East have been found more than 1,000 km from the sea, where they must return to breed.

A number of successful separate introductions of mitten crabs have taken place in Europe, including the UK and America. Europe (Northern Germany) saw initial introductions in 1912, followed by others into both the North Sea coasts and English Channel coasts of France. The extensive network of Northern European waterways facilitated the spread in river systems. After a lag phase, which is typical of many invasive species following introduction, numbers of mitten crabs increased dramatically such that by 1936 attempts at removing the animals from rivers in Germany were abandoned; some 220 metric tonnes were removed from the River Weser alone in that year. Introductions into the UK (River Thames) followed in the mid-1930s but initial introductions appear not to have founded a population. It was not until 1970s that mitten crabs numbers increased and the Thames population became established, and it has subsequently increased and spread. The crab had spread rapidly both around UK coasts and up river systems by the end of the twentieth century and into the 1st decade of the 21st. Evidence suggests that there have been several separate introductions in France; the first in Northern France and then subsequently into western France.

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Whilst the most likely and common route of introduction is via discharge of ships' ballast water, it is possible that there may have already been and may also be future deliberate introductions. The mitten crab has considerable economic value and is farmed in the Far East. Introductions into San Francisco Bay area of the USA later in the twentieth century may have been a deliberate attempt to create a fishery for the species. In its native range, the mitten crab carries a lung fluke trematode parasite *Paragonimus westermani* that infects humans. The intermediate host for *P. westermani* is a snail of the genus *Semisulcospira*, which is not present in the USA and Northern Europe. This means that mitten crabs in these areas are likely to remain parasite free. Whatever the route of entry, the crab has become a major problem in the San Francisco Bay area as it interferes with other fishery activities and causes significant habitat modification. The large crab is a burrowing species creating long burrows in soft river banks causing siltation of the waterways, bank erosion and increasing the risk of flooding. These habitat effects are likely to be apparent wherever the crab is well established. The global spread of *Eriocheir sinensis* continues. In the UK, for example, it has extended its range to the river systems of South-West England, the Welsh River Dee and the River Mersey (North-West England) and has reached as far north as the River Tyne in northeast England. The crab has not yet been reported from further north in England and is so far absent in Scotland. In the USA, it has recently been found along the Atlantic seaboard around Chesapeake Bay, and it appears almost inevitable that many more estuaries and river systems around the globe will become host to the Chinese mitten crab.

## 1 Introduction

Mitten crabs are a large brachyuran species assigned to the Varunidae (see Ng et al. 2008), and are so called because of a covering of fine velvet-like setae on their chelae as adults; the males having a complete covering around the chela, the females having a strip lacking setae on the ventral side of the chela. The presence of the setal mat gives the crabs a distinctive and easily identifiable appearance (Fig. 1).

*Eriocheir sinensis* H. Milne Edwards, 1853 is one of a number of species of mitten crab indigenous to South East Asia. The native range of *Eriocheir sinensis* is in the Far East where it covers a range between Hong Kong (ca. 20°N) and North Korea (ca. 40°N) (Hymanson et al. 1999). The distributions of other mitten crab species overlap and include *E. japonica*, found in Japan, Eastern Korea and Taiwan, and *E. formosa* in Taiwan. Of these species, only *E. sinensis* has become invasive (Dittel and Epifanio 2009), and it is now found across the globe, although there has been a single record of *E. japonica* from the USA West coast (Jensen and Armstrong 2004).

Three related genera are recognised:-

*Eriocheir* De Haan, 1835
*Eriocheir hepuensis* Dai, 1991

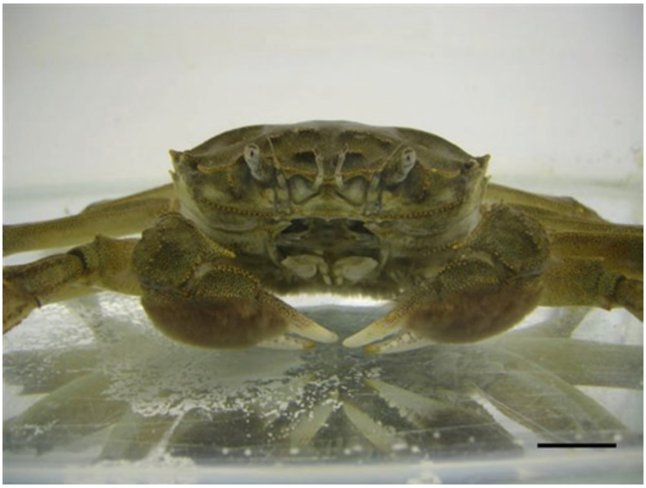

**Fig. 1** Adult Chinese mitten crab, showing clearly the presence of the velvety setae covering the chelae giving the crab its 'mitten' appearance. Scale bar = 2 cm

*Eriocheir japonica* (De Haan, 1835)
*Eriocheir ogasawaraensis* Komai, in Komai, Yamasaki, Kobayashi, Yamamoto and Watanabe, 2006
*Eriocheir sinensis* H. Milne Edwards, 1853
*Neoeriocheir* Sakai, 1983
*Neoeriocheir leptognathus* (Rathbun, 1913)
*Platyeriocheir* N. K. Ng, Guo and Ng, 1999
*Platyeriocheir formosa* (Chan, Hung and Yu, 1995)

*Eriocheir sinensis* is of interest for a number of reasons: it is a commercially important species as a high value delicacy (Cohen and Carlton 1997), and is important in aquaculture (Ying et al. 2006), it carries a lung fluke human parasite (Ingle 1985), and is destructive through its burrowing habit in freshwaters (Peters 1933).

*Eriocheir sinensis* spends part if its life in freshwater but breeds in outer estuaries. Following mating, fertilised eggs give rise to a series of usually five but occasionally six zoeal stages (Anger 1991; Montu et al. 1996), followed by a megalopa that then moults to the juvenile crab. The larval morphology and development have been described recently in a review by Dittel and Epifanio (2009) and so will not be considered here. The requirement to reproduce in a saline environment because of low tolerance to reduced salinity in the zoeal stages can be regarded as a key attribute to the success of *E. sinensis* as an invasive species and has facilitated its global spread. This, coupled with its ability to exploit the freshwater environment during its growth to maturity, makes the Chinese mitten crab one of the World's most formidable invasive species. It is recognised by the IUCN as being amongst the top 100 worst bioinvasives (Lowe et al. 2000; Hanson and Sytsma 2008).

## 2 Life History and Physiology

The Chinese mitten crab is a catadromous species with a life history similar to that of the European eel *Anguilla anguilla* in which most of its life is spent in freshwater, growing from juvenile to adult but must returns to the sea to reproduce. Being a ‘hard-shell’ mater, it does not have to coordinate copulation with the timing of the moult of the female, as happens in many brachyuran species. Breeding in the marine environment where the early life stages also take place is followed by it later ascending freshwater river systems, where growth to the adult takes place over several years, before returning ultimately to the marine environment to reproduce. Unlike eels, however, the extent of the seaward breeding migration of the Chinese mitten crab is only as far as the estuary (Fig. 2).

As these varunid crabs are hard shell maters (Peters 1938b; Herborg et al. 2006), they have no requirement for a moult of the female prior to insemination as is the case in many brachyuran crabs, for example the green or shore crab *Carcinus maenas* (Hartnoll 1969). Breeding is seasonal and takes place in estuaries in early winter. Maturing adults aggregate in large numbers in estuaries at this time and there is some evidence that lunar cues may be important in coordinating mating activity (Herborg et al. 2006). Mating is followed by extrusion of the fertilised eggs by the female, which are then carried for a period of several weeks to several months (Peters 1933; Herborg et al. 2006). There is some suggestion that multiple broods may also be carried by a

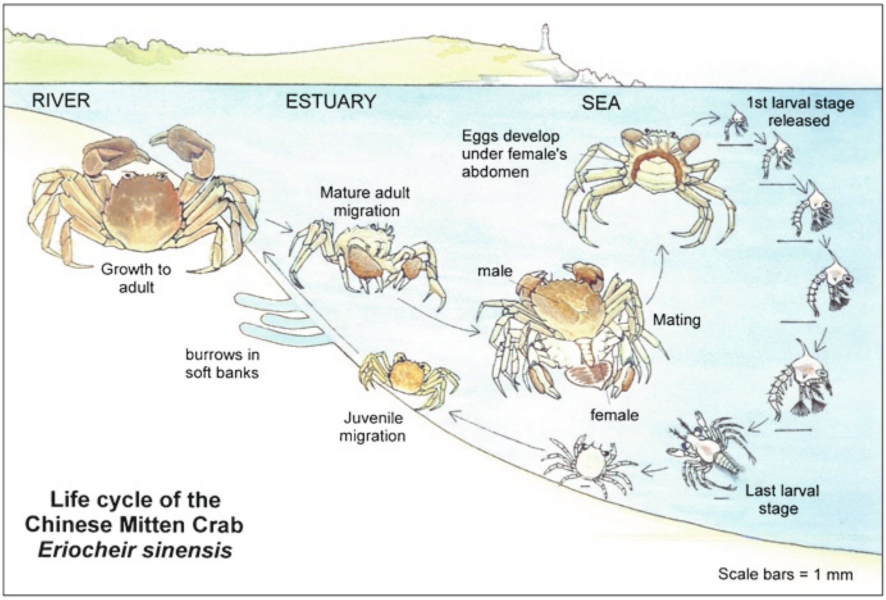

**Fig. 2** A schematic drawing of the life cycle of the Chinese mitten crab, zoea larval stages and megalopa are located in the estuary, the juvenile begins the upstream migration where burrowing activity and growth to adult takes place. Scale bar = 1 mm (From Bentley and Clare 2002; reproduced by permission of Philip Allan Updates)

female (Clark pers. comm.). The crabs though are essentially semelparous, breeding only once at the end of their life (Peters 1938a, b), although it is possible that some individuals may return to freshwater and subsequently breed again. Whilst adult mitten crabs are extremely euryhaline, larvae are stenohaline able to tolerate only sea and brackish waters. Release and subsequent development of early zoeal stages in the estuary (Anger 1991) overcomes the problems of salt loss and water gain that are faced by crustaceans when in freshwater and removes the requirement for a fully developed osmoregulatory system during early life stages (Cieluch et al. 2007). The ability to cope with reduced salinity is acquired from the late zoeal to megalopa larval stages, as osmoregulatory mechanisms are developed at the cellular level and only juvenile crab stages are able to osmoregulate fully in freshwater (Cieluch et al. 2007). The free-swimming zoeal stages of *E. sinensis* last ca. 6 weeks, although is variable being temperature dependent (Anger 1991; Montu et al. 1996). This is of major adaptive significance in facilitating the invasive capacity of *Eriocheir sinensis*.

## 3 Routes of Introduction and Capacity to Spread

As with most aquatic invasive species, there are a number of possible vectors for the spread and introduction of Chinese mitten crabs to previously un-colonised locations. Shipping accounts for the majority of aquatic introductions by one or more of several means. Transmission as part of the external hull fouling community is one of these and includes translocation of motile species such as crabs amongst the attached barnacles, bivalves and algae (Alcock 1900; Cohen and Carlton 1997). Introduction through ships' ballast water discharge (Carlton 1985; Carlton and Geller 1993), and from sea chests (Peters 1933), are also means of introduction and probably contribute most globally to invasive species' transport. Ballast water discharges have probably been responsible for the introduction of *E. sinensis* to most ports and river systems in Europe and North America from Asia (Peters 1933; Cohen and Carlton 1997), through the release of zoeal larvae that have been taken up in ballast water in the previous port. The case of *E. sinensis*, being one of the first species described from ballast water, highlights the importance of ships' ballast water as a vector for invasive species' transport (Carlton 1985). Measures to reduce the risk of introduction of aquatic invasive species and human pathogens via ballast water discharge have been introduced in recent years but these were not in place when *E. sinensis* was introduced into Europe during the first half of the twentieth century. The International Convention for the Control and Management of Ships' Ballast Water and Sediments (2004) was put in place to prevent transport of invasive species through ballast water transport. Vessels are required to have a ballast water management plan and to keep logs of ballast water exchange in the form of a Ballast Water Record Book. These measures include an important preventative measure, the exchange of ballast water at sea away from ports, although there are still problems with the policing of such ballast water exchange practice (Murphy et al. 2008), and small scale inter-coastal shipping is not similarly regulated (Simkanin et al. 2009). The tolerance of brackish water and euryhaline ability of the later larval stages of *E. sinensis*, as discussed above and in Cieluch et al. (2007) make survival in port environments a real likelihood.

Once introduced into estuarine environments, where the larvae complete their development, they settle as juvenile crabs into the benthos. At the same time they acquire the full osmoregulatory ability of the adult crab, and there is then the potential to move upstream and colonise the river system to which they have been introduced. Recently, juvenile mitten crabs (*E. japonicus*) have been shown to exhibit rheotaxis to assist them in navigating upstream (Tatsuo et al. 2002). It may take a number of introduction events before a population becomes established, and almost certainly most introductions of larvae into a new environment do not lead to the establishment of the invasive species (Dittel and Epifanio 2009). Factors, which influence the possibility of successful establishment of the invasive include the time of year of introduction, water flow and hydrographical regime (which vary seasonally), suitability of habitat, food availability, and the presence of competitors and predators. Once settled as juveniles, the crabs begin an upstream migration that takes them into all reaches of the river systems with their progress only being hindered by man-made obstacles such as weirs and screens (Panning 1939). They have been shown to cover considerable distances inland and in their native range have been found more than a 1,000 km from the sea (Peters 1933). They are thought to have the potential to travel upstream at a rate of about 500 km per year (Herborg et al. 2005). The spread of mitten crabs between river systems may take place via coastal movement of breeding adults or larvae (see Sect. 7), inland via canals connecting different rivers (Peters 1938a), and possibly also overland over short distances during damp weather conditions.

## 4 The Chinese Mitten Crab in Continental Europe

The Chinese mitten crab *Eriocheir sinensis* was first recorded in Europe, in the River Aller, a tributary to the River Weser system, Northern Germany in 1912 (Peters 1933), and in 1914 it was reported from the neighbouring river, the Elbe. Its introduction was almost certainly via the discharge of ships' ballast water and Gollasch et al. (2002) found evidence for larvae of *E. sinensis* in sediment collected from ship ballast tanks. The adoption of water as a ballast material in cargo ships, replacing previously used solid ballast, took place from the latter part of the nineteenth century into the first half of the twentieth century (Carlton 2008). In Europe, clay roof tiles known as pantiles were used as solid ballast from continental Europe by ships transporting coal, and the use of these tiles is now characteristic of many buildings in coastal former coal mining areas of England and East Scotland. Once this solid ballast was replaced by water, the transport of mitten crabs to and between European ports became a real possibility.

The spread of *E. sinensis* across continental Europe has been examined recently by Herborg et al. (2003) who examined an historical data set and used this not only to describe the incidence of *E. sinensis* in European river systems but also to determine the rate at which they had spread upstream in Northern and later in Southern Europe (Fig. 3).

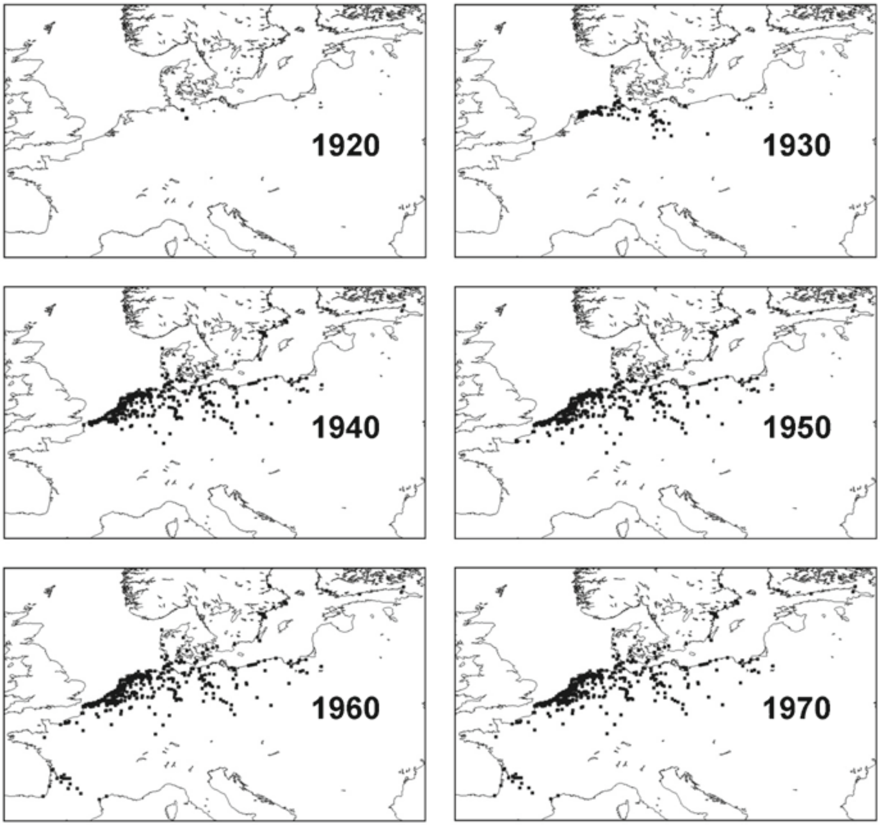

**Fig. 3** Map showing the spread of *Eriocheir sinensis* across continental Europe from 1920 to 1970 (From Herborg et al. 2003)

Reports of Chinese mitten crabs in continental Europe show that the species had spread eastwards via the Kiel Canal to the Baltic Sea by 1927 and then was reported to be further East, in Russia and Finland by 1933 (Peters 1938a). Westwards, the spread to Belgium the Netherlands and to Denmark (Herborg et al. 2003 and references therein) was reported during a similar period (1927–1945). Later during the twentieth century the range had extended eastwards to Le Havre along the English Channel (La Manche) (Hoestlandt 1959; Vincent 1996). It is likely that the spread of *E. sinensis* in along the river systems of Northern Europe occurred as a result of a single introduction or a few separate ballast water introductions into ports that plied frequent trade with China, and the subsequent spread was facilitated by the network of canals connecting the major river systems of the Elbe and Weser to other European river systems.

*Eriocheir sinensis* is also reported from southern continental Europe, where it became established between 1954 and 1960 following a separate introduction into the Gironde river system in Southern France. The subsequent coastal spread northwards in France is likely to have been facilitated once again by ship transport

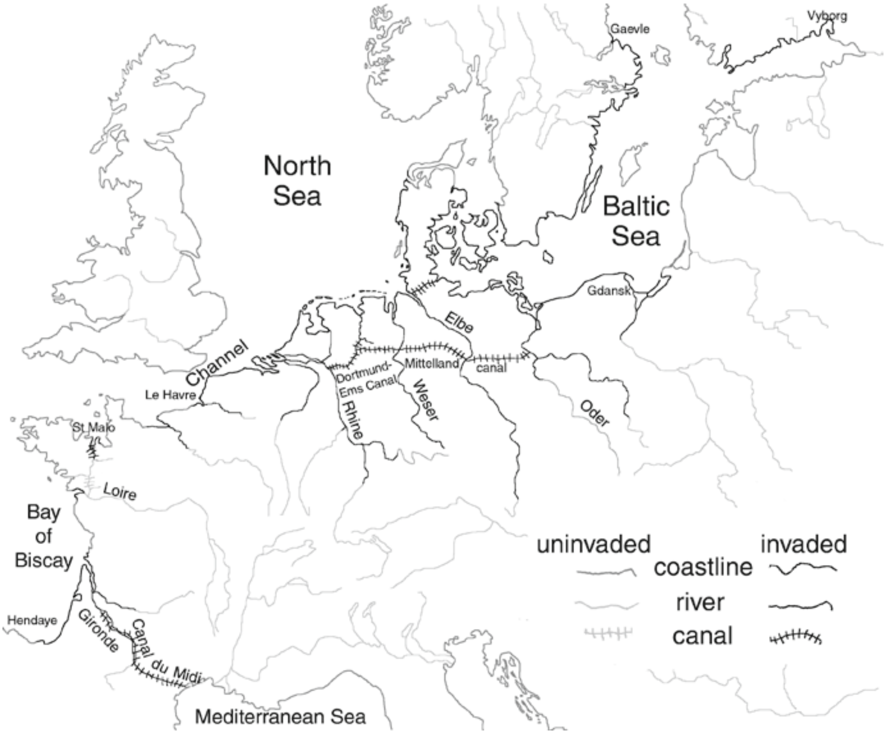

**Fig. 4** Map showing the spread of *Eriocheir sinensis* across continental Europe by 1970, indicating where it has become invasive along the coast, rivers and canals (From Herborg et al. 2005)

between neighbouring ports or possible association with movement of bivalve aquaculture species (Herborg et al. 2003).

Characteristic of many invasive species is an establishment phase, following initial introduction and subsequent spread. In most cases of mitten crab introduction, such as in northern continental Europe and the UK, this has also been the case, where a period of 10–15 years elapsed before rapid spread inland. This delay appears, however, not to have taken place in the introduction to Southern France where movement inland was observed in the years immediately following introduction (Herborg 2003). This initial establishment of the species is followed by an exponential increase in population size and, in the case of *E. sinensis*, movement up river and away from the coast. The spread away from the coast has been described by Herborg et al. (2003) and the rate of spread upstream in European rivers was quite startling. In the Rivers Elbe (Peters 1933), Rhine and Oder (Herborg 2003) it was found 700, 512 and 464 km upstream respectively by the early 1930s. The Rhine has recently been described as a major corridor for invasive aquatic species (Leuven et al. 2009). Similar rates of spread were reported to the Mediterranean coast via the Gironde system (Petit and Mizoule 1974) (Fig. 4).

The Chinese mitten crab has continued its range extension eastwards along the coast of the Baltic States. It has been reported in fairly low numbers in the Gulf of Gdansk, Poland (Normant et al. 2002). Further East, it has been reported from Lithuania (Bacevièius and Gasiûnaitë 2008), Latvia and farther into the Baltic basin (see Ojaveer et al. 2007, for example). It is found in Russia (Losovsky 2005; Panov 2006; Shakirova et al. 2007) and eastwards from Europe into Iraq (Clark et al. 2006) and Iran (Robbins et al. 2006). It is equally possible that the introductions into Iraq and Iran have resulted from shipping movements from China. Whichever is the case is strongly suggests that *E. sinensis* is becoming circum-global at these latitudes. Whilst most of the above examples are observations of first sightings, it suggests that *E. sinensis* is extending its global range eastwards, southwards to Portugal, where it occurs in the Tagus estuary (Cabral and Costa 1999), and northwards into Sweden (Lundin et al. 2007), and Norway (Christiansen 1977, 1988; Wergeland et al. 2008) from its initial introductions into continental Europe.

The extreme euryhaline nature of *E. sinensis* as a juvenile and adult suggests perhaps that it is these stages rather than larvae that may have been responsible for the species' spread in the inner Baltic region. Mitten crabs have been reported in Swedish waters since the 1930s but have recently become much more abundant (Lundin et al. 2007). It is not at present clear whether these Swedish populations have arisen from separate ships' ballast water introductions or via migration along the Baltic Coast from Baltic populations.

## 5 Introduction to the UK

The first record of a Chinese mitten crab in the UK was made by Harold (1935) who found an individual trapped on the intake screen of a major coal fired power station along the River Thames at Chelsea Creek, Lots Road, London, which had been built to generate power for the London Underground rail system. This discovery represents a significant milestone in the invasion ecology of *E. sinensis* and the Chinese mitten crab in the River Thames (see Clark 2011). For this reason the River Thames population of Chinese mitten crabs will not be discussed in detail here. Recently Gilbey et al. (2008) have undertaken a useful study on the distribution of juvenile crabs in the Thames estuary, which may help us understand the invasion ecology of this species. In essence, these juvenile crabs are found most frequently during the warmer months of the year and larger individuals (sub-adults) are found furthest upstream from the mouth of the estuary. The crabs' behaviour suggested a strong endogenous rhythmicity, entrained by both diurnal and tidal cycles, with activity being greatest during nighttime high tides. This may facilitate the upstream migration of juveniles that have settled in the estuary. Similar endogenous rhythmicity in reproductive adults has also been shown during the mating season (Herborg et al. 2006). From initial introductions into the River Thames estuary during the early twentieth century and the population becoming established following the species' reappearance in the 1970s (Ingle and Andrews 1976), the crab has extended its range in the UK northwards. Yorkshire records include reports from the tributaries of the River Humber catchment and in the South Field Reservoir, a reservoir connected to the Humber estuary

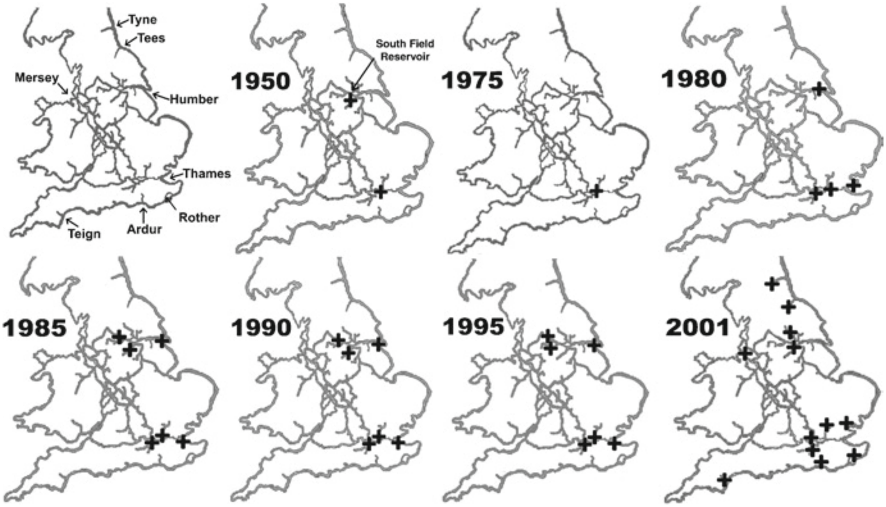

**Fig. 5** Map showing the spread of *Eriocheir sinensis* across the UK from first reports outside the River Thames catchment to the present day (From Herborg et al. 2005)

(a major estuary on the NE coast of England) via the New Junction Canal (Wall and Limbert 1983). More recently, it has been reported along the South coast to the River Teign, one of the Devon rivers in the South-West of mainland Britain (Robbins pers. comm. to LM Herborg). In a manner similar to the lag phase that often follows introduction of the mitten crab into an estuary and its spread though that river system, there has been a considerable lag between the establishment of the Thames and subsequently Humber populations, and reports from other river systems feeding the North Sea (Rivers Tees and Tyne) (Herborg et al. 2005). Almost 20 years passed before reports were obtained from the River Tees (Dutton pers. comm.) and the Tyne (Herborg et al. 2002). In 1999, *E. sinensis* was recorded from the Manchester ship canal which is linked to the Mersey estuary and which flows into the Irish Sea. Although there is an extensive canal network in the UK, it may be that this report arose from an introduction separate from that into east coast rivers (Fig. 5).

Confirmed sightings were made for the first time in the Welsh Dee estuary in November 2006 (Dave Thorpe, Environment Agency pers. comm.). This is perhaps not surprising given the proximity of the estuary to the Mersey estuary some 10 km to the east just across the Wirral peninsular. The Dee estuary has considerable mud and salt marsh and some of the lower reaches are canalised. This might facilitate the establishment of mitten crabs in at least the lower part of the River Dee system.

## 6 Introduction to West Coast USA

Concerns about the potential impacts, both to the physical environment and human health, of the introduction of *Eriocheir sinensis* into the USA were expressed in the early 1980s to the extent that pre-emptive legislation was introduced in an effort to minimise the risk. These measures included a ban in California in 1987 (Section 671(h)(2) Title 14 CCR) prohibiting import of the species and subsequently legislation across the USA in 1989 (50 CFR 16.13) banning possession, handling or import, which was put in place by the US Fish and Wildlife Service (Horwath 1989). The measures, however, proved ineffective and the first specimens were recorded in San Francisco Bay in the early 1990s (Cohen and Carlton 1995, 1997; Rudnick et al. 2003). Today, the San Francisco Bay area has a well established population of mitten crabs. By 2001 the species had covered several thousand square kilometres of the Bay area (Rudnick et al. 2003). It is generally accepted that the transport of *E. sinensis* across the globe from its native range and from later introductions in Europe has been by means of larval transport in ballast water tanks of ocean going vessels. It remains perhaps, most likely that this was the route of introduction into California (Cohen and Carlton 1997). Despite the legislation in place to ban the import of live mitten crabs, there is evidence that this trade continues, and indeed there is pressure for the ban to be lifted now that this species has become so well established (Cohen and Carlton 1997). It remains, therefore, a distinct possibility that the introduction of the crabs into San Francisco Bay resulted from intentional release of live imported crabs (see Cohen and Carlton 1997). The foothold in the US that the mitten crab has gained makes its spread along the Pacific coast likely, either by larval transport (peaks of late larval (megalopae) abundance have been observed in San Francisco Bay in May (Gonzales and Tsukimura 2009)), or possible by movement of adults along the coastal fringe. Long distance transport as larvae or as adults associated with marine debris are recognised as unlikely means of transport (Cohen and Carlton 1997) but movement of newly settled juveniles or even pre-reproductive adults remains a possibility. Recently, (Hanson and Sytsma 2008) have undertaken an analysis of the potential for continued range extension of *E. sinensis* to the Northwestern Pacific. They suggest that physical factors (temperature and flushing rates of estuaries) will limit the crab's spread to the Pacific North-West, with only Puget Sound (Washington) potentially at risk.

Apart from the well established population in the San Francisco Bay area of California, there are relatively few reports of *E. sinensis* from other parts of the USA and Canada. Most of these have been of isolated individuals or relatively few specimens, which would be regarded, therefore, currently as non-established populations (Dittel and Epifanio 2009). The species' presence has been reported from the Great Lakes since the 1970s (Nepszy and Leach 1973), and more recently from the Mississippi (Cohen and Carlton 1995), and East coast. (Ruiz et al. 2006). Of these, perhaps only the latter example has resulted from ballast water introduction with the former being escapees (Dittel and Epifanio 2009).

## 7 Recent Introductions and Rate of Spread

The recent appearance of *Eriocheir sinensis* in the Chesapeake Bay area of the East coast of the US (Ruiz et al. 2006), is perhaps some cause for concern. It seems likely that the physical conditions of salinity in the Bay area and the annual temperature regime would enable the mitten crabs to become established and become a breeding population and is therefore at risk (Herborg et al. 2007b). No reproductive individuals have been found to date.

In Europe, the mitten crab has been reported once from Ireland (Minchin 2006), and the first specimen has been recorded from the Venetian Lagoon, Italy (Mizzan 2005). Such sporadic sightings are likely to continue around Europe. From isolated sightings, it is difficult to make any predictions on the rate of coastal spread of the species. Examination by Herborg et al. (2005), however, has compared the spread of *E. sinensis* in both the UK and in continental Europe and it has become apparent that the rate of spread in both is considerable. The expansion along the UK coast has taken place over the past decade or so with the extent of distribution being fixed until 1997. Since then the crabs have extended their range northwards to the Tees and Tyne, (Herborg et al. 2002), a distance of 230 km from their previous northern boundary, the River Humber. Their westwards extent has increased by 340 km from the Thames estuary to the River Teign (Devon) and they have been reported from Shoreham on the South England coast between the two. Recent individual sightings from new locations in the UK demonstrate the continued spread. These reports include additional locations along the Sussex coast, South East England in 2008; the River Torridge (2004), North Devon, South West England; the River Ouse in North Yorkshire, North East England (2009) and most recently the River Conwy (2010), North Wales (data kindly provided by Stu Higgs DASHH from www.marlin.ac.uk). We must recognise that the range expansion may occur as a result of juvenile spread as well as accidental transport by coastal shipping, etc. (Herborg et al. 2005). Recent rates of coastal spread in the UK may be as high as 448 km per year. These rates are not dissimilar to those recorded for the expansion into the Baltic Sea from Germany earlier in the twentieth century. The rates of coastal spread are greater than up-river spread which typically occurs at a rate of about 50 km per year. On the basis of the current UK distribution and recent rate of spread it is likely that the mitten crab will become established in other major UK estuaries such as the Severn (Herborg et al. 2005) (Fig. 6).

Recently, Herborg et al. (2007a) examined the potential spread of mitten crabs in Europe based on modelling the characteristics of mitten crab habitats within their ‘normal’ range using ecological niche modelling. The model developed by Herborg et al. (2007a) predicts that much of Europe has the potential to be invaded by *E. sinensis* with only the eastern Baltic Sea, and mountainous areas proving unsuitable. Low coastal salinity may not be suitable for successful larval development and this might limit spread eastwards in the Baltic.

Potentially, the spread of invasive aquatic species may be limited by competition and predation. In the case of *E. sinensis* there are few competitors. In freshwaters, crayfish species occupy a similar ecological niche but are unlikely to out-compete mitten crabs. There are few avian and mammalian predators, but these might include herons, cormorant, inland sea gulls and otter. Weber (2008) has examined spraints from otters (*Lutra lutra*) in the Drömling Nature Reserve (Germany), through which the Midland Canal that connects the Rivers Weser and Elbe run. She found that mitten crabs form a significant part of the diet of otters in the reserve but

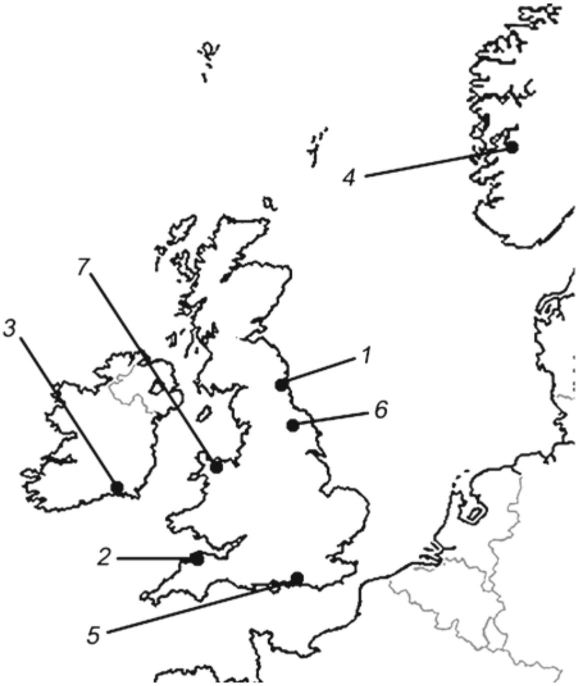

**Fig. 6** Map showing recently recorded mitten crab sightings in N Europe: *1* Rivers Tyne & Tees (NE England) 2002, *2* R Torridge (SW England) 2004, *3* Waterford (Ireland) 2006, *4* Eiddefjord (Norway) 2007, *5* Littlehampton (S England), *6* Selby (NE England) 2009, *7* R Conwy (N Wales) 2010

suggests that relatively few otters have adopted mitten crab as preferred diet. There is some suggestion that otters (along with foxes, *Vulpes vulpes*, when crabs are found out of water) may have contributed to some extent in a recent observed decline in *E. sinensis* numbers.

## 8 Economic Importance and Transmission of Human Pathogens

The Chinese mitten crab is of considerable economic importance. In one respect, this is because of damage and inconvenience caused to gear of commercial (e.g., eel, shrimp) fishermen (Veldhuizen and Hieb 1998), and also to recreational anglers (Peters 1933). There is also a cost incurred in removing crabs that are clogging the intake screens of power plants (Siegfried 1999; Veldhuizen and Hieb 1998), although this is much less than similar problems caused by the invasive zebra mussel *Dreissena polymorpha* in the Great Lakes system of North America which has been estimated at more than 1 billion US$ over the past 20 years (Josefsson and Andersson 2001). By far the greatest economic importance of *E. sinensis,* however, is through aquaculture. Over the past decade there have been enormous efforts, principally in China, towards the aquaculture of mitten crabs in order to meet demand for the species as a delicacy in SE Asia (Yang and Zhang 2005; Wu et al. 2009). Although popular as an aquaculture species, this industry has been particularly challenging because of the crab's catadromous lifestyle with the early life stages being marine. Although much of the literature is relatively inaccessible, being in Chinese, it is clear that much of the research effort has been concentrated on the hatchery and larval rearing with over 500,000 kg of megalopa being produced in China in 2004 (Sui et al. 2008), and considerable effort has been focused on the development of feeding strategies for larval rearing (Wu et al. 2009). Whilst the early life stage are intensive, grow on to harvestable adults is carried out extensively in rice paddies and ponds. The presence of juveniles for grow-on in rice paddies does not cause a significant reduction in vegetation (Li et al. 2007), but after the 1st year, growth to adults is carried out in ponds to prevent impact on the rice plants (Jin et al. 2001). At present aquaculture of *Eriochier sinensis* is restricted to the Far East. Any attempt to transfer this technology to other parts of the World would necessitate a similar intensive-extensive approach, which could lead to a decline in submerged macrophytes.

When aquaculture of the American signal crayfish, *Pacifastacus leniusculus*, was developed in Europe, escapees were quick to establish breeding populations and in many areas of the UK have since displaced the native white clawed crayfish, *Austropotamobius pallipes* (Gheraardi and Holdich 1999). If aquaculture of *E. sinensis* were to become established in a similar way, there would be less risk of populations becoming established, as adults would need to be able to find their way to an estuary to breed. Physical damage to the habitat and decline of aquatic vegetation would, however, be a likely result.

In addition to the above economic impacts of invasive Chinese mitten crab, there is potentially also a risk to human health. In its native range *E. sinensis* carries a trematode lung fluke *Paragonimus westermani* (Ingle 1985; Clark et al. 1998; Veldhuizen 2001). This causes a condition known as paragonomiasis, a tuberculosis-like condition of the upper lung. Humans become infected after eating poorly cooked or raw crabs that carry the parasite. The life cycle of the trematode requires a first intermediate host, a genus of snail called *Semisulcospira*, which is restricted to China, Japan, Taipei, Korea and Vietnam (Global *Biodiversity Information Facility* (Accessed through GBIF Data Portal, data.gbif.org, 2010-04-26)) in order to be able to complete its life cycle. The snail is penetrated by miracidia larvae and cercaria stages later emerge and infect the crab. For the lung fluke to become a potential problem in its invasive range there would have to be an unlikely combination of circumstances. There would be a requirement for the invasive individuals to have been introduced as parasite-infested adults, as larvae that might be brought via a ballast water discharge do not carry the parasite. Also there would have to be an intermediate host present and *Semisulcospira* is not found in Europe or North America. The risk of parasitism in invasive mitten crabs therefore remains extremely small. The very low likelihood of mitten crabs being host to *Paragonimus* outside their native range would make crabs farmed or fished from these areas especially desirable and they would be likely to command a premium in the marketplace. Exploitation of Chinese mitten crab by establishing a fishery where invasive populations would sustain this are a distinct possibility and this aspect is discussed by Clark (this volume) and it has already been demonstrated that from a microbiological and toxicological perspective, mitten crabs from the River Thames would be fit for human consumption (Clark et al. 2009).

## 9 Riparian Degradation

Whilst juvenile crabs tend to shelter under stones on river banks, the adult Chinese mitten crab in freshwater has a burrowing habit, creating burrows into soft river banks (Panning 1933; see also Dittel and Epifanio 2009), preferring a sand or silt substratum (Rudnick et al. 2005). Where these borrows become extensive, the appearance of the banks has been likened to “Swiss Cheese” (Herborg, Carlton Television 2002). The effects of the burrows are to cause degradation and erosion of the riparian habitat and cause siltation of the water channels, potentially increasing flood risk. An individual burrow may have up to 2 l volume of sediment removed in its creation by a single crab (Rudnick et al. 2005), so it is not difficult to appreciate the amount of sediment that can be removed from a river bank when large numbers of adult crabs are present.

## 10 The Future

Chinese mitten crabs have gained a considerable foothold in the Northern hemisphere in both Europe and America. Whilst in Europe large populations have spread across the continent, and new reports suggest that the spread eastwards is continuing, in North America only the San Francisco population could be considered to be an established population at the present time. The sightings in the Great Lakes, Mississippi and inland from the East coast, coupled with the extent of the waterways would suggest that further populations may become established in the near future. Modelling the spread of mitten crabs to make even conservative predictions suggest that the entire region inland form the coast from the Gulf of Mexico to north of Boston along the Atlantic Coast (Herborg et al. 2007b). Recently there has been considerable attention focused on genetic analysis of Chinese mitten crabs from populations in Europe (Hänfling et al. 2002; Herborg et al. 2007a, c), and the USA and its native range in China (Hänfling et al. 2002). As might be expected, these studies revealed that genetic diversity is lower in the invasive populations that in crabs that in China that gave rise to these. Interestingly, the Continental European populations arose from multiple introductions but there has been movement of crabs between Continental European populations and the UK in recent years (Herborg et al. 2007c). Data also suggest that it is possible that the San Francisco

Bay population may have arisen through the introduction of *Eriocheir* from Europe.

Mitten crabs have not yet reached sub-Saharan Africa, or Australasia. It is likely that lessons can be learned from the invasive European green (shore) crab, *Carcinus maenas*, that is present in the USA and Australia and has more recently been introduced to South Africa (Carlton and Cohen 2003), to help us in generating management approaches for Chinese mitten crab. Although present in Australasia *C. maenas*, it is not yet found in New Zealand. Both *Eriocheir sinensis* and *Carcinus maenas* have an overlap in habitats in the outer areas of ports, harbours and estuaries, and are both euryhaline species (although obviously *E. sinensis* is more so). For this reason they may be spread in the same way. After introduction, their spread differs in that *Carcinus maenas* has the potential for greater coastal spread but will not move inland whereas *E. sinensis* can exploit both routes, especially the latter. *Carcinus maenas* along the Pacific coast of the USA has spread rapidly covering a range of more than 1,000 km in a decade. This large range expansion appears to have arisen from a single introduction (Tepolt et al. 2009). *Carcinus maenas* has been present in Australia for more than a century where it was found in Port Philip Bay in Victoria but has recently shown range extension northwards into New South Wales and it is likely that is will continue to spread (Ahyong 2005). The shore crab has been shown to have difficulty in becoming established along some coasts (Hampton and Griffiths 2007), but where it does gain a foothold, it is a serious invasive. There is considerable concern from New Zealand that this invader might soon appear there. The global spread of *Eriocheir* appears to be following a pattern similar to that of *C. maenas* so it is reasonable to suppose that South Africa, Australia and New Zealand are all at risk.

To prevent the introduction of mitten crabs, as with other invasive species, preventative measures are the most effective means of ensuring that invasion does not take place. New Zealand has strict bio-security measures in place maintained by the Ministry of Agriculture and Forestry, but which also covers aquatic invasive species (http://www.biosecurity.govt.nz/). Vigilance is of paramount importance and the early detection of the presence of an invasive species offers really the only hope of its eradication (Park 2004). The fact that populations can become established and spread from a single introduction reinforces this (Tepolt et al. 2009). The importance of having a management plan in place that does not delay action to limit the spread and remove and invasive species has been recognised though the precautionary principle becoming part of the 1992 Convention on Biodiversity (Park 2004). One of the obstacles to effective management plans for the control of invasive species being developed and implemented is the often apparent conflict between stakeholder interests. This becomes further complicated by legislation designed to protect biodiversity and ensure effective conservation measures and that which protects the commercial interests of those engaged in trade, or interested in developing such markets for invasive species (Stokes et al. 2006).

Bioinvasions and climate change are considered separately to be immense threats to biodiversity. Climate change though will also exert an impact on the geographical range of native species and on the invasion potential and spread of invasive species (Walther et al. 2009), thereby compounding the possible effects of the both climate change and introductions of non-native species. It in some respects, one of the outcomes is that there is likely to be an increased tolerance to invasive species, with them becoming increasingly accepted as part of a region’s biota. The Chinese mitten crab across the globe is one species that is likely to become a more familiar sight as its geographic spread increases, perhaps aided by climate change.

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# The Japanese Skeleton Shrimp *Caprella mutica* (Crustacea, Amphipoda): A Global Invader of Coastal Waters

**Karin Boos, Gail V. Ashton, and Elizabeth J. Cook**

**Abstract** Successful invasion must be viewed as the result of a unique sequence of events, with the established species overcoming a number of previously prohibitive obstacles, for example lack of dispersal vectors, habitat characteristics and environmental conditions of the new area, and the ability to persist in interspecific interactions in the new community. The Japanese skeleton shrimp, *Caprella mutica*, is proving to be a highly successful non-native crustacean in coastal waters outside its native range having overcome these obstacles. In the past 40 years, *C. mutica* has spread from its native sub-boreal waters of north-east Asia to numerous locations in both the northern and southern hemisphere, where it has successfully established self-sustaining and thriving populations. After its first European record from the Netherlands in 1995, *C. mutica* spread rapidly within the North Sea and later to the west coast of Scotland and to Ireland in less than 15 years. *Caprella mutica* is generally associated with man-made structures and can be found in abundance on boat hulls, floating pontoons and aquaculture infrastructure clinging to fouling organisms.

Species-specific traits which enable *C. mutica* to perform superiorly in its introduced ranges include: rapid growth, short maturation time, high reproductive activity, broad tolerance towards prevailing environmental conditions, omnivorous feeding behaviour and efficient dispersal and distribution. These traits provide excellent prerequisites for any species to colonise a variety of different microhabitats. The availability of suitable structures, however, is of paramount importance to the invasion success of *C. mutica* in European coastal waters and most likely elsewhere. On artificial structures directed away from the seabed, *C. mutica* is able to avoid

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benthic predation pressure and thus, to develop massive population densities. These high abundances in disturbed habitats may also reflect the species' ability to inhabit fluctuating systems better than other species. *Caprella mutica* was found to be competitively superior over native congeners and to show aggressive behaviour towards conspecifics. The characteristics described here are surely not unique to *C. mutica* and, therefore, cannot explain its success relative to other potential non-native species. They do, however, provide insight into why *C. mutica* has been so successful and consequently in determining whether another species may also be successful. When making these assessments, it is of particular importance to consider potential risks of the species and how important prevention or eradication may be. Although *C. mutica* can be assigned a potentially harmful invader, detailed knowledge on community or ecosystem level impacts are still lacking. Recommendations on management and control actions, therefore, remain insufficient.

**Keywords** Life history • Population dynamics • Interspecific interactions • Competition • Dispersal • Distribution • Vectors • Anthropogenic transport

## 1 Introduction

The arrival of a non-native species in a new habitat and its initial settlement depends on a variety of factors including association with dispersal mechanism(s), propagule pressure, environmental match between source and donor regions and the physiological tolerance of the species (Carlton 1996; Vermeij 1996; Colautti and MacIsaac 2004; Colautti et al. 2006). The successful establishment and integration into native ecosystems are long-term events and depend on the species' ability to sustain itself successfully through reproduction and/or recruitment and to persist in interactions with other species (Vermeij 1996; Holway and Suarez 1999; Sakai et al. 2001).

Elton (1958), in his seminal volume 'The ecology of invasions by animals and plants' addresses two major concepts which are fundamental for research in invasion ecology: (i) the characteristics of invading species which make them more successful than other species (invasiveness) and (ii) the susceptibility of ecosystems towards invasions (invasibility). The scientific approach of understanding 'invasiveness' and 'invasibility' has been to derive general patterns applicable to potential invaders and thus, to predict their dispersal and distribution (Alpert et al. 2000; MacIsaac et al. 2001). While the concepts of invasiveness and invasibility are often met through providing theoretical or empirical evidence, the numbers of exceptions from these patterns are high and often generalizations have not been tested statistically (Lodge 1993). Hence, attempts to categorize certain life history traits of non-native species as characteristically invasive turned out to be inconsistent and not generally applicable (Sher and Hyatt 1999). Traits that might be advantageous to a certain species invading one habitat may be irrelevant when invading another. Some traits may be more pronounced in certain invaders than in others, or may even be absent (Heger and Trepl 2003). In addition, introductions occur in habitats that differ widely in native species composition and richness, environmental conditions and geography. Not all invaders are capable of exploiting all habitats and not all habitats are equally vulnerable to invasion (Sher and Hyatt 1999; MacIsaac et al. 2001). Species that are abundant and widely distributed in their introduced ranges may have undergone a series of failed introductions before becoming successfully established (Clarke 1971).

According to the above, detailed case-by-case studies of non-native species introduced to new habitats which provide information on life history traits, population biology and relative performance to other species are essential. Only in this way, can the underlying mechanisms of successful invasions be defined and potential impacts and further range expansion of the species' under study be assessed.

*Caprella mutica* Schurin, 1935 is a marine amphipod crustacean indigenous to north-east Asia, where it was first described from Peter the Great Bay, Vladivostok. In its native range (Fig. 1) it is distributed along the Russian coasts of the Sea of Japan and the Japanese archipelago (Schurin 1935; Arimoto 1976; Fedotov 1991; Vassilenko 2006). However, in the past 40 years, *C. mutica* has become successfully established along many coastlines outside its native range. Its apparent success as a non-native species in these habitats has sparked a number of studies investigating the invasion process as well as the species' biology, ecology and the reasons for the invasion success of *C. mutica*.

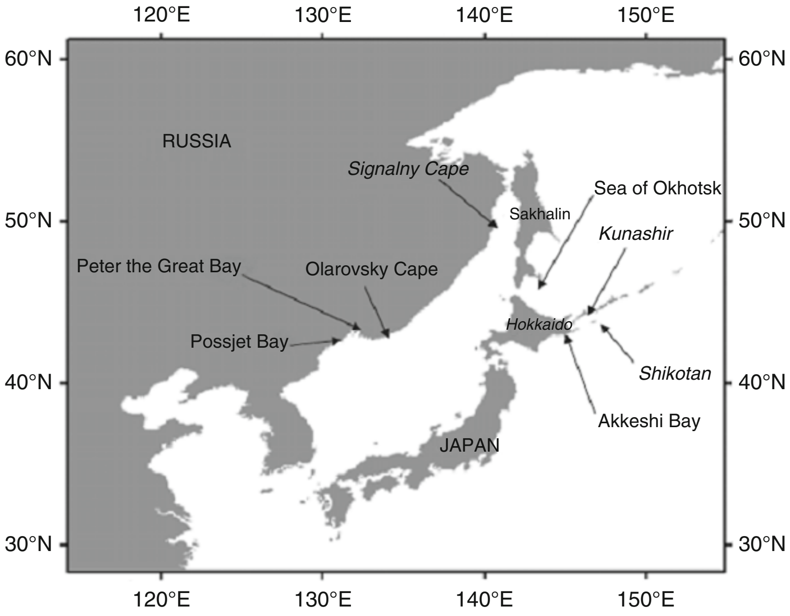

**Fig. 1** Native range of *Caprella mutica* (from Ashton 2006). Labels in *capitals* refer to countries, those in *italics* refer to islands, *arrows* indicate locations where *Caprella mutica* has been found (Schurin 1935; Arimoto 1976; Fedotov 1991; Vassilenko 2006)

Along with a number of other species, such as the green crab *Carcinus maenas* (Le Roux et al. 1990) and the Asian shore crab *Hemigrapsus sanguineus* (Breton et al. 2002), *C. mutica* has achieved a very widespread distribution in a relatively short timeframe. Other caprellid species have also been introduced outside their native range, including *C. simia*, *C. drepanochir* and *C. scaura* (Watling and Carlton 2007; Martínez and Adarraga 2008). However, none of these have yet achieved the global distribution of *C. mutica*.

*Caprella mutica* was first described in Europe 15 years ago and new records continue to be reported. Reproductive populations are established throughout the North Sea, Irish Sea, English Channel and Atlantic coastlines of Ireland and Scotland. A number of recent European studies have included those of distribution and dispersal, population dynamics, life history traits, habitat associations and interspecific interactions, both in field and laboratory studies. The present work is the first to provide a comprehensive review of these studies. Hereby, we particularly focus on the characteristics that have contributed to the successful establishment of *C. mutica* outside its native range and, consequently, on the attempts to identify the species' future range expansion and its environmental and economic impacts.

## 2 Biology and Ecology of *Caprella mutica*

### *2.1 Morphology*

Strongly diverged from the typical gammarid amphipod morphology, caprellid amphipods are recognized by their elongated bodies and a reduction in the number and type of appendages (Hayward and Ryland 1996). Because of their slender and stick insect-like appearance they are commonly referred to as 'skeleton' or 'ghost' shrimps (Fig. 2a, b).

In *C. mutica,* males are typically larger than females and can reach a body length of up to 50 mm (Nishimura 1995). Generally, however, males are about 25–30 mm and females about 15–20 mm in length (Ashton 2006; Boos 2009). Protrusions of the exoskeleton can vary between *C. mutica* individuals, but the extreme and most clearly identified are described here. In males, the first two pereonites as well as the second gnathopods are covered with dense setation (Fig. 2b). On the dorsal and lateral surfaces of the third to seventh pereonites (first to seventh in females), *C. mutica* is heavily armoured with spiny projections (Fig. 2a, b). In particular, paired spines dorsally, antero- and postero-laterally and several spines at the anterior side of the insertion of each gill. Spination is less in pereonites VI–VII (one to two pairs of spines on each).

### *2.2 Life History and Seasonal Population Dynamics*

Like all peracarid crustaceans, caprellids lack a larval stage and brood their young until they hatch from their mother's pouch into their first instar (stage) as small

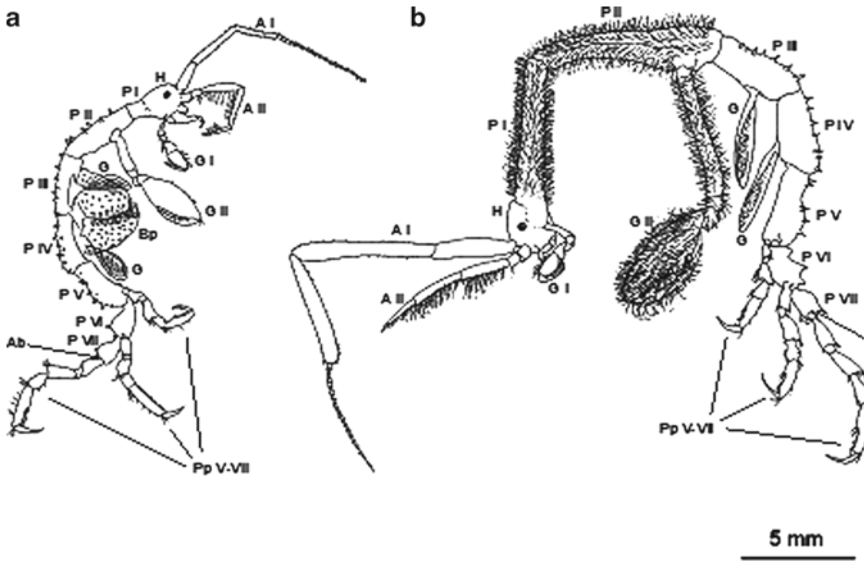

**Fig. 2** Schematic overview of (**a**) female and (**b**) male *Caprella mutica*. A I and II = antennae I and II, H = head, P I–VII = pereonites I–VII, Ab = abdomen, Pp V–VII = pereopods V–VII, Bp = brood pouch, G = gills, G I and II = gnathopods I and II (Boos 2009 modified after Platvoet et al. 1995)

replicates of adult individuals. At hatching, individuals of European specimens of *C. mutica* are on average 1.3 mm in length (Boos 2009). Visual determination of sexual differentiation (genital appendages located on pereonite V in females and VII in males) is possible from Instar V onwards (after the fourth moult). Under laboratory conditions, reflecting average summer water temperatures in the southern North Sea (16°C), the development of morphological characteristics, such as spination of the body segments, commences at Instar IV (mean body length of 4.8 mm) and initiates from posterior segments (pereonites VI and VII) followed by the anterior segments. At this early stage, spines may be small tuberculations in advance of fully developed projections. From Instar VIII onward (mean body length of 7.5 mm in females and 8 mm in males) spination is more or less developed as described in the previous section. Setation in male individuals reared under laboratory conditions (16°C) appears from Instar VI onwards at a mean body length of 5.7 mm. Maturation of females is typically reached at Instar VII (mean body length of 6.7 mm) and involves the full development of the brood pouch and the completed differentiation of the first clutch of eggs in the ovaries located dorsally in pereonites III and IV (Boos 2009).

Hatchlings reared in the laboratory at 16°C and fed *ad libitum* with freshly hatched *Artemia* sp. nauplii and diatoms (*Thalassiosira rotula*) moulted every 3–4 days until sexual differentiation, and reached maturity after approximately 1 month (Boos 2009). Moulting intervals in hatchlings reared at average spring (10°C) and winter (4°C) temperatures were of weekly and fortnightly durations, respectively. It took about 2 months for hatchlings to reach maturity at 10°C. Growth in hatchlings maintained at winter temperatures (4°C) and fed on the same diet was clearly impaired and hatchlings perished before reaching maturity. Yet, winter hatchlings survived longer (i.e. 4 months) under constant laboratory conditions than spring and summer hatchlings, which only survived for about 10 weeks or less, nonetheless reaching maturity (Boos 2009).

The moult cycle of adult female *C. mutica* maintained at 16°C is approximately 10 days, reflecting the duration of the reproductive cycle. Under the same conditions, moulting intervals in male adults may increase to nearly twice the duration of the females. Moulting intervals and, thus, reproductive cycles in mature females were found to range between nearly 40 days at 4°C and 8 days at 26°C. Laboratory studies showed that *C. mutica* was able to successfully reproduce at temperatures between 4°C and 26°C, with a maximum number of seven successful broods recorded at 16°C (Boos 2009). Upper temperature limits for reproduction were reached at 26°C, when reproductive success was rare, brood sizes very small and eggs positioned in the brood pouch were frequently aborted.

Laboratory-rearing temperature did not affect brood size in early adult instars (mean of 40 hatchlings per clutch; Boos 2009). Field studies in both native (Fedotov 1991) and European introduced ranges (Ashton 2006), have both confirmed a positive relationship between brood size and body size in female *C. mutica*. Both authors reported maximum numbers of more than 300 eggs per single clutch in individual females reflecting much higher fecundities under natural conditions.

From seasonal and annual field studies in eastern Russia, Fedotov (1991) inferred *C. mutica* to have a life span of more than 2 years. However, allocating size measurements and survival times from laboratory studies regarding different life stages and correcting these measurements to larger body sizes found in the field, we consider 6–9 months a more likely approximate lifespan of this species in general.

In the native range, maximum densities in natural near-bottom habitats have been reported to range between 1,200 and 2,600 ind. $m^{-2}$ in summer periods (Fedotov 1991; Vassilenko 2006). Along northwestern European coasts, rapid increases in population abundance (up to 144 ind $m^{-2}$ $d^{-1}$) have been observed in early summer (April to May; Cook, unpubl.), with maximum population densities of *C. mutica* exceeding 200,000 ind. $m^{-2}$ in summer when seawater temperatures range between 14°C and 20°C (Ashton 2006; Boos 2009). In late winter and early spring, population densities decline considerably (Fig. 3). This may be because of natural mortality of older individuals and prolonged reproductive cycles due to colder temperatures, as demonstrated by laboratory studies (Boos 2009). In addition, lack of suitable substratum (see Sect. 2.3) such as different macroalgae to cling to during cold water phases may contribute to the overall low abundance of *C. mutica* during winter and early spring in European waters; as has been found for other caprellid species in Asian waters (Takeuchi et al. 1990; Takeuchi and Hirano 1992). Overwintering populations may, therefore, be at lower densities, yet still numerous (about 500–1,000 ind. $m^{-2}$; Boos, unpubl.) and seek refuge in deeper and warmer (Fedotov 1991), and/or sheltered areas such as inner shanks of navigational buoys (Boos 2009).

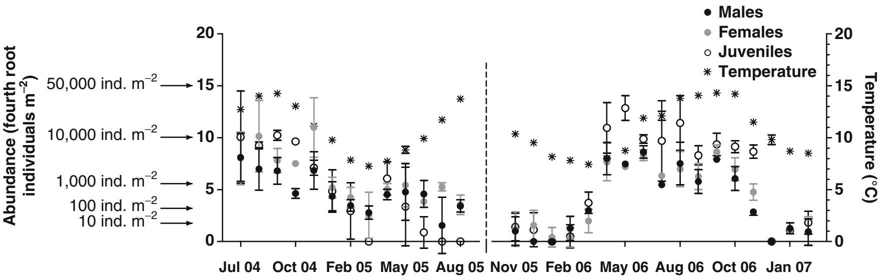

**Fig. 3** Seasonal abundance of male, female and juvenile *Caprella mutica* between July 2004 and February 2007 at Dunstaffnage fish farm, Lynne of Lorne, Scotland. Data are merged from Ashton (2006, $N=3$ at 3 m depth for July 2004 to August 2005) and Boos (2009, $N=5$ at 1 and 3 m depth pooled data for November 2005 to February 2007). Between August and November 2005 no data have been obtained (dotted line). Symbols represent average fourth root individuals $m^{-2}$ (±SD). Temperature (°C) is given as monthly average (±SD) of hourly records for July 2004 to August 2005 (Ashton 2006) and as mean (±SD) of three daily measurements around the sampling date (Boos 2009)

## 2.3 Habitat Preference

In its native range, *C. mutica* is typically reported from sheltered bays in the littoral zone to about 13 m in depth, amongst different macroalgae such as *Neorhodomela larix, Polysiphonia morrowii*, *Sargassum miyabei*, *S. pallidum*, *Cystoseira crassipes*, *Laminaria japonica*, *Dichloria viridis*, *Chondrus* spp. and others (Vassilenko 2006). In addition, uncounted mass occurrences referred to as ‘dense populations’ have been detected in fouling communities on submerged artificial structures i.e., buoy ropes and aquaculture cultivation lines (Takeuchi et al. 2001). In its European range, habitat preferences of *C. mutica* include soft structures, such as tunicates (e.g., *Ascidiella aspersa* and *Ciona intestinalis*) or the foliose surfaces of macroalgae (e.g., *Ulva lactuca*) and fine filamentous structures, such as turf-like bryozoans and hydroids (e.g., *Obelia* spp. and *Tubularia indivisa*) and filamentous algae (e.g., *Ceramium* spp. and *Sargassum muticum*) to which it can grasp compared with organisms with much harder exteriors such as bivalves (Shucksmith 2007; Cook, pers. obs.). Laboratory choice experiments offering different structural substrates for settlement confirmed these observations (Schrey 2006). In addition, when offered three different types of structures to cling to, *C. mutica* settled in higher densities on filamentous turf-like structures than on mussel mimics with hard and smooth surfaces (Shucksmith 2007). A further advantage of the association with filamentous substrates is that *C. mutica* is well camouflaged against this background and individuals have been observed to exhibit different exoskeleton colouration when associated with different substrates. The mechanism for colour development or change in *C. mutica*, however, is not well understood.

Many of the ‘preferred’ substrate species described for *C. mutica* are known to rapidly colonise artificial structures (e.g., buoys, pontoons, ropes and boat hulls) in areas of human activity such as harbours, aquaculture facilities or offshore wind farms (Buschbaum and Gutow 2005; Ashton 2006; Schrey 2006; Schneider 2007; Dong Energy et al. 2006; Page et al. 2006). While substrate preference of *C. mutica* may be responsible for this association with artificial structures, the environments in these habitats are also modified by anthropogenic disturbance. Disturbance may promote species invasions (Crawley 1987; Cohen et al. 2002; Stachowicz et al. 2002), and non-native species are generally first identified in human-impacted, highly disturbed sites suggesting that these habitats may act as corridors or stepping stones for future dispersal for example into natural benthic habitats (Buschbaum 2002).

In its native and introduced ranges, population densities of *C. mutica* in fouling communities attached to artificial structures are of magnitudes higher than in natural benthic habitats. Small numbers or even only single specimens have been found in kelp communities (*Laminaria* spp.) along the north coast of Scotland (S. Dworjanyn, pers. comm. 2006), attached to floating macroalgae off the west coast of Scotland (Ashton 2006), or on individual algal tufts in the southern North Sea (Boos 2009). Recently, however, populations have become more conspicuous inhabiting macroalgal patches (i.e., *Sargassum muticum*) in natural benthic habitats of the coasts of Sylt, German Bight, North Sea, suggesting *C. mutica* to potentially become an important representative of natural shallow subtidal communities (C. Buschbaum, pers. comm. 2009).

Non-native populations of *C mutica* have been recorded from environments with a variety of flow regimes, including those experiencing strong tidal and wind currents (e.g., exposed fish farms) and those that are more sheltered (e.g., enclosed bays and harbours) (Ashton 2006; Shucksmith 2007). In particular, they have been recorded at exceedingly high densities at an exposed fish farm site in the Lynne of Lorne, Scotland (see Figs. 3 and 4) where high current speeds (21.0 cm $s^{-1}$) have been measured (Cook et al. 2006). Laboratory studies have found strong aeration and/or increased water flow to be beneficial for maintaining *C. mutica* in aquarium tanks (Shucksmith 2007; Nakajima and Takeuchi 2008; Boos 2009). The increased survival was attributed to increased oxygen supply and circulation and also to enhanced filter feeding efficacy. These observations suggest that the hydrography of the environment may influence the relative success and, therefore, ‘invasiveness’ of *C. mutica* in a new habitat.

## *2.4 Environmental Tolerance Limits*

Adult *Caprella mutica,* collected from the west coast of Scotland, have been shown to have a broad tolerance to temperature and salinity conditions in 48 h laboratory trials (Ashton et al. 2007a). 100% mortality was observed at 30°C (48 h LT50, 28.3 ± 0.41°C) and salinities lower than 16‰ (48 h LC50, 18.7 ± 0.24‰).

Maintained over longer periods under laboratory conditions, mortality of adult females increased significantly at temperatures exceeding 20°C (Boos 2009). Although lethargic at low temperatures (2°C) no mortality was observed in *C. mutica* after 48 h of laboratory maintenance and also over longer periods at low temperatures (4°C) females survived up to 5 months in the laboratory (Ashton et al. 2007a; Boos 2009). Annual temperatures in the species’ native area can range between −1.8°C and 25°C (Schevschenko et al. 2004), which would support the

**Fig. 4** Dense population of *Caprella mutica* on a heavily fouled fish farm mooring line in the Lynne of Lorne, west coast of Scotland (Photo: E. Cook). Scale bar 1 cm

observations on survivorship made in the laboratory studies (Ashton et al. 2007a; Boos 2009). The upper 48 h $LC_{50}$ was greater than the highest salinity tested (40‰), thus it is unlikely that high salinity will limit the distribution of *C. mutica* in open coastal waters. However, the species will be excluded from brackish water environments such as the heads of sea-lochs or estuaries and semi-enclosed areas, such as marinas with freshwater input. In addition, so far *C. mutica* has not been found in the Baltic Sea, were salinities are known to vary within brackish ranges.

The physiological tolerances of *C. mutica* to temperature and salinity are beyond the physical conditions experienced in most Northwestern European coastal waters. While abiotic factors in other European regions may define the present distribution and future spread of *C. mutica*, its ability to persist in interspecific interactions will also determine the successful establishment here.

## 2.5 Feeding

Stomach content analysis has shown that *Caprella mutica*, along with a number of other caprellid species, is predominantly a detritivore (Guerra-Garcia and De Figueroa 2009). In addition, it is known that *C. mutica* is capable of filtering particles out of the water column by swaying its body through the water and using its second pair of setose antennae as a sieve (Nauwelaerts et al. 2007). *Caprella mutica* is also frequently observed grooming its body, possibly feeding on epibiotic organisms (Nauwelaerts et al. 2007; Boos, pers. obs.). According to antennal setation and mandible morphology, it has been suggested that caprellid amphipods which have setae on their second antennae obtain a significant part of their diet through filtering and scraping epiphyton, whereas caprellids without setae and most of all without molar processes are mainly predators (Caine 1977). *Caprella mutica*, however, possessing both of the latter, has been successfully reared and maintained in the laboratory on *Artemia* sp.-nauplii (Boos 2009; H-D Franke, pers. comm. 2005) and has been observed to consume on average 15 *Artemia* sp.-nauplii $h^{-1}$ in laboratory feeding trials (Schneider 2007). In fact, *C. mutica* has been observed feeding on a variety of different sessile and mobile benthic organisms including hydroids, bryozoans, gammarid amphipods and even conspecifics (Ashton and Boos, pers. obs.). This suggests that *C. mutica* is a true omnivore, frequently using predation as a feeding mechanism along with filter feeding. In addition, European populations of *C. mutica* have been found frequently associated with different macroalgae which may also serve as a food supply by either directly providing a substrate to feed on and/or providing substrate for other epibenthic organisms on which *C. mutica* may feed (Sano et al. 2003), or indirectly by elevating the caprellids into the current stream where they can filter-feed more effectively.

Often, *C. mutica* is found in habitats subjected to anthropogenic disturbance, which might improve access to resources such as space or food (Davis et al. 2000). *C. mutica* has also been found in nutrient enriched artificial environments (via fish feeds). Differences in habitats were suggested to influence the population dynamics of *C. mutica* at four sites on the West coast of Scotland (Ashton et al. 2010). Two of these sites were fish farms where *C. mutica* may be feeding directly on the fish feed, on the algal growth which is enhanced by dissolved organic nutrients (e.g., Rhodophyta, Troell et al. 1997), and/or on enhanced plankton abundance in the close vicinity of the cages (Cook et al. 2006; Navarro et al. 2008; Cook et al. 2009). Populations at the other two sites which experience no artificial nutrient enrichment (a marina and an unused pontoon structure) were significantly less abundant and had a shorter period of summer population growth.

*Caprella mutica* can be highly opportunistic in its feeding strategy in non-native habitats. Analyses of the lipid biomarkers in individuals from artificial habitats including mooring lines, fish farm cage netting and marina pontoon floats on the West coast of Scotland demonstrate consumption of a wide variety of food types from diatoms, dinoflagellates and copepods to fish farm derived particulate waste (Cook et al. 2009). Laboratory studies have shown that *C. mutica* is able to survive starvation for up to 3 weeks from hatching (Boos, unpubl.) and as adults (Cook et al. 2007). Thus, *C. mutica* would be able to overcome periods of low food availability. The flexibility observed in these feeding strategies may, therefore, play an important role in its invasion success.

## 2.6 Intraspecific Behaviour and Aggression

In populations of *C. mutica*, threat display and combat between conspecifics of both sexes is common (Boos, pers. obs.). Caprellids typically use their large second gnathopods as weapons in combat. A pointed protrusion on the palmar surface of the second gnathopods of the males, the so-called ‘poison tooth’ has been found in numerous genera of caprellid amphipods and may be used to impose lethal or at least harmful injuries (Caine 1980, 1991a; Dingle 1983; Lewbel 1978). While the poison tooth has been reported to mechanically cause injuries through impaling, there is as yet no evidence that a venomous toxin is produced (Lewbel 1978; Caine 1991a; Schulz and Alexander 2001).

Several studies on caprellid amphipods have linked aggressive behaviour to reproductive success and survival of offspring (Lewbel 1978; Caine 1979; Lim and Alexander 1986; Aoki 1997; Schulz and Alexander 2001). This behaviour may include mating behaviour, male-male competition and mate guarding as well as maternal care. Copulation in crustaceans can only take place after females have moulted i.e. when genital openings of females are accessible. Mate guarding is believed to have evolved when females show temporarily restricted periods of receptivity (Conlan 1991; Zimmer 2001), or in the case of longer receptive periods, when guarding costs are sufficiently lower than searching costs (Yamamura 1987).

In observational studies on *C. mutica*, males were found to court premature or mature females only. During precopulatory courtship, the male aggressively fought other interfering males with its second gnathopods and repeatedly brushed the female’s dorsal surface with its antennae, potentially for signs of ecdysis, until the female moulted (Boos, unpubl.). Matthews (2008) observed that male *C. mutica* are able to distinguish and select non-brooding receptive females with larger oocytes from females with small oocytes. Matthews (2008) also showed aggressive and competitive male-male interactions to be most intense when receptive females were present (i.e., during courtship) as opposed to the presence of brooding or parental females. When no females were present, aggression was lowest between males.

Male *C. mutica* typically perform postcopulatory mate guarding for a short period of time (approx. 15 min) before abandoning their position or are fought off by the females, which by then begin to show aggressive behaviour toward their own mates (Boos, unpubl.). Matthews (2008) also found that aggression in females changed with their reproductive status. Receptive females were least aggressive while aggression in brooding females increased. The highest number of attacks was found in parental females. Matthews (2008) found female aggression towards conspecifics and congenerics to be generally confined to male specimens and suggested that males were posing more of a threat to the juveniles than the females. Aoki (1997) showed strong mother-young associations in *Caprella monoceros* and *C. decipiens* with post-hatching co-habitation periods of up to 20 and 30 days, respectively. In addition, hatchlings of *C. monoceros* were found to cling to the body of the mother and moult there for a period of about 11 days before even moving on to the surrounding substratum. In contrast, *C. mutica* showed only very short periods of juveniles clinging to the mother (approx. 1 h) after hatching (Cook, pers. obs.). Further, Matthews (2008) found newly emerged hatchlings of *C. mutica* to disperse after only 1 day in laboratory studies and dispersion of one clutch was within 7 days. The author, therefore, suggested maternal care in *C. mutica* to be short-lived. Yet, other observational studies have shown individual females to remain in close proximity to groups of hatched juveniles in the field and also in large aquarium tanks (Boos, pers. obs.) suggesting protective behaviour. While parental periods of females are rather short and females may become receptive within 2 or 3 days after hatching or even on the same day (Boos 2009), the role of maternal care in *C. mutica* for juvenile survival remains unclear.

Food limitation within a population of *C. mutica* poses a clear threat from the adults towards juvenile individuals (Schneider 2007). In laboratory experiments, the author found nearly 100% juvenile mortality after 3 days when additional food was offered only once a day for a duration of 1 h. In contrast, treatments allowing for constant supply of food *ad libitum* revealed only about 40% juvenile mortality after 3 days (Schneider 2007). Juvenile individuals are generally most susceptible to cannibalism in amphipods and isopods (Otto 1998; Franke and Janke 1998). This self-regulation of high population growth in food-limited habitats would explain the differences observed in population dynamics in the field experiments described above. It also explains why *C. mutica* populations may attain such immense abundances in habitats, which are nutrient enriched.

## *2.7 Interspecific Interactions*

The success of non-native species is often explained by the lack of native competitors and/or predators, allowing for mass occurrences and uncontrolled population growth (Van der Velde et al. 2000). It has further been suggested that competitive superiority and even the displacement or extinction of native species significantly contributes to invasion success, potentially resulting in altered biodiversity, community structure, local food webs and interactions between species (Dick 1996; Dick et al. 1999; Morrison 2000; Füreder and Pöckl 2007). Several authors have found biodiversity (species richness) in native habitats as well as heterogeneity of environments (different types of structures) to play a crucial role in the invasibility of an ecosystem (Ullmann et al. 1995; Levine and D'Antonio 1999; Levine 2000). Consequently, these factors also influence the effects of an invasion, promoting both exclusion and coexistence of species (Tilman 2004; Stachowicz and Tilman 2005). Unfortunately, very few studies have documented any interactions between *C. mutica* and other species.

In laboratory-based competition experiments, *C. mutica* successfully displaced two ecologically similar native European caprellids (*Caprella linearis* and *Pseudoprotella phasma*) from space limited artificial patches after 48 h (Shucksmith et al. 2009). When maintained with *C. linearis*, displacement took place even though numbers of *C. mutica* were ten times less than those of *C. linearis*. Added refuges (artificial turfs) to the artificial patches were found to reduce the number of *C. linearis* displaced. In addition, when including different habitat structure types to a set of competition experiments between *C. mutica* and *C. linearis*, Shucksmith (2007) found increased displacement of the native by the non-native when homogeneous patches (low structural diversity) were offered. In contrast, when heterogeneous patches (high structural diversity) were offered, the number of displaced *C. linearis* was significantly reduced. In a similar series of density-dependent experiments, Boos (2009) showed that the underlying mechanism of displacement of *C. linearis* by *C. mutica* was direct interference (interference competition), caused by aggressive and even predatory attacks by *C. mutica*. Increased numbers of *C. mutica* introduced to substratum supporting the native *C. linearis* resulted in increased mortality and/or displacement of *C. linearis*. These results suggest that the competitively superior *C. mutica* could have a negative impact on native caprellids in its introduced habitat.

Caprellids are important trophic links in food webs and prey for numerous predatory fishes and invertebrates in coastal waters (Caine 1987, 1989, 1991b; Holbrook and Schmitt 1992; Kvenseth et al. 2003). Laboratory-based feeding trials revealed that the shore crab *Carcinus maenas* and the goldsinny wrasse *Ctenolabrus rupestris* (native predators), which are both known to feed upon amphipod crustaceans, selectively fed on large individuals of *C. mutica* rather than on small individuals and consumed more caprellids in near-bottom benthic habitats compared with habitats close to the sea surface (Boos 2009). Artificial structures, widely isolated from natural near-bottom habitats, may serve as refuges from predators in the field supporting dense populations of *C. mutica*, while benthic predation pressure restricts mass occurrences and the spread of the non-native species into natural habitats. Generally, low abundances have been found in natural near-bottom habitats compared with artificial structures directed away from the seabed. In addition, there is support from field studies on the west coast of Scotland, which suggested that at least the green shore crab, *Carcinus maenas*, was affecting the populations of *Caprella mutica* in natural kelp beds adjacent to source populations found in artificial habitats (e.g., fish farms) (Shucksmith 2007).

## 3 Distribution and Dispersal

### *3.1 Current Distribution*

*Caprella mutica* has become successfully established throughout the temperate northern hemisphere and in New Zealand in the southern hemisphere (Table 1; Fig. 5). It achieved a global distribution in just 30 years (1973–2003) and has continued to increase its range on all coastlines since that time. The first introduction records of *C. mutica* were during the 1970s from the Pacific coast of the United States (Carlton 1979). Since then, new populations have been described from the Pacific and Atlantic coasts of the United States and Canada (Carlton 1979; Marelli 1981; Cohen and Carlton 1995; Cohen et al. 1998; Cohen et al. 2002; MIT Sea Grant 2003; USGS 2005; Frey et al. 2009; B. Sainte-Marie; pers. comm. 2005), and from Alaska (Ashton et al. 2008a). In the mid-1990s, the first European populations of *C. mutica* were found in the Netherlands (Platvoet et al. 1995). In the following years, occurrences from Norway, Germany, Belgium, Ireland and Scotland were

**Table 1** Global (and European) distribution records of introduced *Caprella mutica* including year and source of first sighting (in italics), present distribution and substrates where it has been found

| Location/ Country | Latitudinal range | Date of first record | Distribution source(s): *first* and present | Substrates | | | |
|---|---|---|---|---|---|---|---|
| | | | | Marina | Aquaculture | Buoy | Other |
| **Europe** | | | | | | | |
| Netherlands | 51°25′N–51°40′N | 1995 | *Platvoet et al.* 1995<br>M. Faasse (pers. obs.) | ✓ | ✓ | ✓ | ✓ Power station |
| Belgium | 51°13′N–51°37′N | 1998 | *F. Kerckhof (pers. obs.)* | ✓ | | ✓ | |
| Norway | 60°14′N–62°50′N | 1999 | *Heilscher* 2000<br>ICES 2003 | ✓ | | | |
| Scotland | 55°31′N–58°22′N | 1999 | *O'Reilly* 2007<br>Ashton 2006<br>Ashton et al. 2006 | ✓ | ✓ | ✓ | ✓ Boat Hulls<br>✓ Algae |
| Germany | 54°10′N–55°00′N | <2000 | *Buschbaum and Gutow* 2005 | ✓ | | ✓ | ✓ Boat Hulls<br>✓ Algae |
| England | 50°22′N–51°56′N | 2002 | *Ashelby* 2005<br>Arenas et al. 2006 | ✓ | | | |
| Ireland | 51°50′N–54°03′N | 2003 | *Tierney et al.* 2004<br>Minchin and Holmes 2006<br>Minchin 2007 | ✓ | ✓ | | |
| France | 49°29′N | 2004 | *G. Breton (pers. comm.* 2005*)* | ✓ | | | |
| Denmark | 55°27′N | 2005 | *R. Frederiksen (pers. comm.* 2006*)* | | | | ✓ Windfarm |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **North America** | | | | | | | |
| Pacific Coast | 32°76′N–69°37′N | 1973 | Carlton 1979 | ✓ | ✓ | | ✓ Boat Hulls |
| | | | *Marelli* 1981 | | | | |
| | | | Watling and Carlton 2007 | | | | |
| | | | Ashton et al. 2008a | | | | |
| | | | Frey et al. 2009 | | | | ✓ Algae |
| | | | Page et al. 2006 | | | | ✓ Oil Rigs |
| Atlantic Coast | 41°30′N–49°54′N | 2000 | *MIT Sea Grant* 2003 | ✓ | ✓ | | |
| | | | B. Sainte-Marie (pers. comm. 2005) | | | | |
| **Southern Hemisphere** | | | | | | | |
| New Zealand | 41°0′S–44°22′S | 2002 | *Inglis et al.* 2006 | ✓ | ✓ | ✓ | |
| | | | Willis et al. 2009 | | | | |

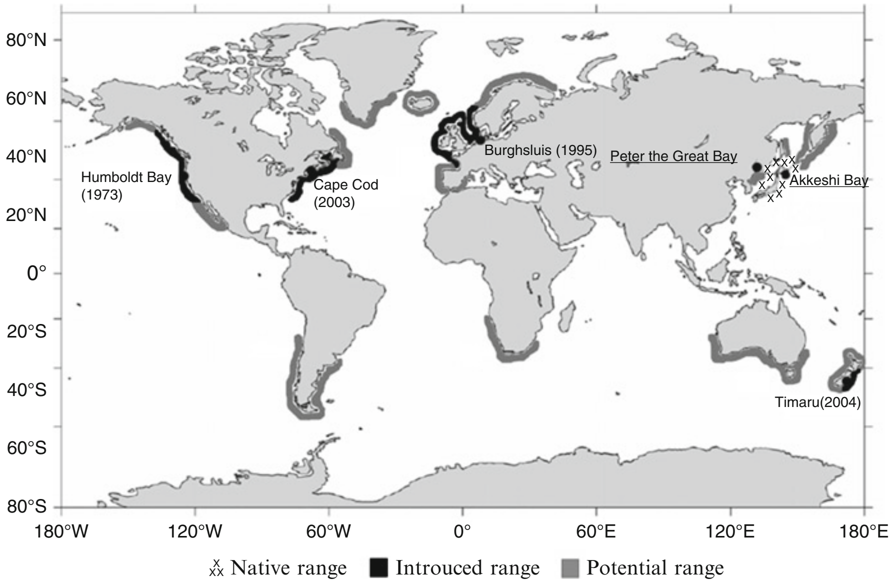

**Fig. 5** Current global distribution of *Caprella mutica* indicated by 'x' and black solid lines. Underlined text labels show the native distribution; normal text labels show locations and dates of first record on each coastline. According to suitable temperature conditions (0°C winter minimum to 25°C summer maximum), the potential range of *C. mutica* is indicated by grey solid lines (modified after Ashton 2006). See text for detailed explanation

reported (Heilscher 2000; ICES 2003; Tierney et al. 2004; Willis et al. 2004; Buschbaum and Gutow 2005; Ashton et al. 2007b). The only location in the southern hemisphere is New Zealand, where *C. mutica* has been found since 2002 (Inglis et al. 2006; Willis et al. 2009).

## 3.2 *Dispersal Vectors*

Long-distance introductions of *C. mutica* are most likely a consequence of increased global and local shipping traffic (transit in ballast water or on fouled boat hulls) as well as of co-transports of introduced aquaculture organisms such as the Pacific Oyster *Crassostrea gigas*, native to the Sea of Japan (Takeuchi and Sawamoto 1998; Cohen and Carlton 1995; Gollasch et al. 2002; Tierney et al. 2004; Ashton et al. 2006). Because of the various routes, vectors and introduction events, which may have been responsible, it has not been possible to establish the exact route which *C. mutica* followed into Europe (Ashton et al. 2008b).

Once established in a new location, smaller boats (including aquaculture crafts, fishing boats and recreational boats) enable *C. mutica* to continue to spread to new habitats (secondary dispersal). *C. mutica* individuals have been observed on static or dry-docked small crafts in Europe and on the West coast of North America (Ashton, pers. obs.). The association with small crafts enables *C. mutica* to disperse beyond the locations of large commercial ship docks and aquaculture facilities that receive stock from international suppliers. While it is considered unlikely that these small crafts are responsible for cross-ocean dispersal, these vectors will continue to disperse *C. mutica* away from introduction foci.

Dispersal of species via rafting has long been suggested as a dispersal mechanism (e.g., Wheeler 1916; Highsmith 1985). Artificial (buoys, ropes, litter) and natural (macroalgae) floating materials may facilitate the dispersal of different caprellid species (Thiel et al. 2003; Astudillo et al. 2009) and *C. mutica* has been reported attached to floating macroalgae off the west coast of Scotland (Ashton 2006). Amounts of floating anthropogenic debris (e.g., styrofoam, plastic and glass bottles, bags, buoys) are increasing in the world's oceans and coastal areas (Thiel and Gutow 2005a). In addition, the dispersal of species associated with floating substrata is a natural process allowing for range extensions beyond the species' native borders (Thiel and Gutow 2005b). Thus the efficiency of this dispersal mechanism will be significantly enhanced on local and global scales. Rafting provides potential for both long- and short-distance dispersal, but it is unknown how important rafting is to the global or local distribution of *C. mutica*. The most abundant populations have only been observed on artificial structures, suggesting human-mediated dispersal mechanisms (albeit most search effort has also been focussed on these structures compared to natural habitats). Natural dispersal is also likely responsible for the very local distribution of *C. mutica*. Small numbers have been observed up to 1 km from a source population, which may have been due to natural drift as individuals have been found swimming free for short distances (M. Janke, pers. comm. 2007). This free swimming dispersal mechanism may be responsible for the introduction of *C. mutica* into natural habitats adjacent to source populations located on artificial structures.

## *3.3 Future Spread*

Most of the recorded sightings of introduced populations of *C. mutica* are from the northern hemisphere. Based on annual seawater temperatures in the species' native and introduced range, and its absence from areas with comparable temperatures (Schevschenko et al. 2004; NOAA/ National Weather Service 2009), *C. mutica* is expected to expand its known European and global range (Fig. 5). When trying to predict a potential range expansion, the physiological ability to reproduce at a certain thermal range can be used to estimate distributional limits. According to life history traits of *C. mutica* observed at different temperatures presented in Sect. 2.2, the ability of hatchlings to survive and mature at low temperatures will limit the establishment of sustainable year-round populations. Winter periods of less than 4 months at approx. 4°C are required, as this was the maximum laboratory survival time recorded for *C. mutica* hatchlings at this temperature. Periods of temperatures below 4°C must be of even shorter duration. In addition, summer periods of at least

2 months at 10°C are needed for the hatchlings to reach maturity. Once individuals have reached maturity, reproduction is possible even at lower temperatures (Boos 2009). Areas with low temperatures that would limit *C. mutica* may be found along the Arctic Circle, including European coastlines of Iceland, the northern coast of Norway and northwestern coastlines of Russia. Depending on the location, summer temperatures along the Artic Circle are reported to fluctuate between 4°C and 15°C (Freiwald and Henrich 1994; NOAA/National Weather Service 2009). In the warmer of these regions, e.g. the northern coastlines of Norway warmed by the Gulf Stream, temperatures around 10°C or greater may last 2.5 months on average and would, therefore, allow maturation in *C. mutica*. However, if a subsequent decrease in temperature to less than 4°C persists for too long (> 4 months), adult females may not survive for repeated reproduction and hatched juveniles will not mature before perishing. If populations were to establish in these regions, they may be more prone to regular extinction events and recruitment will strongly rely on repeated introductions as opposed to self-sustaining populations. The Arctic Circle may be used as a proxy for the thermal limit to the establishment of *C. mutica*, and it is considered highly unlikely that *C. mutica* will establish beyond this border in Arctic regions in the near future, as prevailing summer water temperatures in the Arctic do not exceed 4°C (NOAA/National Weather Service 2009). With global warming, however, average seawater surface temperatures are expected to rise between 1.8 and 4.0°C by the year 2100 (Bates et al. 2008). This would alter the potential future range of *C. mutica*. More so, as the warming arctic areas will experience longer ice-free periods during summer (Zhang et al. 1998; Fyfe et al. 1999; Kerr 2002a), enabling shipping passages along northern sea routes and opening pathways for potential introductions (Rahmstorf and Ganopolski 1999; Kerr 2002b).

*Caprella mutica* is known to be tolerant of climatic conditions found in many parts of Europe and may indeed survive at wide thermal ranges. It is not yet known whether populations of *C. mutica* can persist permanently at temperatures of 25°C and higher and no information on survival of reared hatchlings at these temperatures is available. Laboratory studies have shown increased mortality of adult *C. mutica* at temperatures exceeding 20°C and subsequent difficulties and/or failures in reproducing (Ashton et al. 2007a, Boos 2009). This could suggest that *C. mutica* may be limited from invading areas with high summer temperatures (>25°C), for example the Mediterranean Sea (NOAA/ National Weather Service 2009). However, the fact that *C. mutica* has not been reported from the Mediterranean Sea does not necessarily imply their inability to settle in this area. More so, as *C. mutica* is also apparently absent from adjacent areas with suitable temperature conditions such as the French and Iberian Atlantic coastlines. Similarly, recent surveys of caprellid species' distributions in Chile (Thiel et al. 2003), Tasmania (Guerra-Garcia and Takeuchi 2004) and South Africa (C. Griffiths, pers. comm. 2009), all with areas of suitable temperature conditions, have not reported *C. mutica* either (Fig. 5). It is also possible that the range of *C. mutica* is already greater than that described to date. Inconspicuousness due to small population sizes in certain habitats, seasonal variation in population dynamics, absence of taxonomic expertise and incomplete coverage of habitat during surveys are all reasons why *C. mutica* may be present but not yet reported. The range expansion of *C. mutica* is, therefore, considered an on-going process.

## 4 Risk Assessment and Potential Management Options

Some of the most common characteristics found in successful marine crustacean invaders include life history traits such as rapid growth, early maturation, short generation times and high fecundity as well as broad environmental tolerance and rapid dispersal (Williamson and Fitter 1996; Alpert et al. 2000). In addition, non-native species appear to be successful in regions with environmental conditions similar to where they originate (Van der Velde et al. 2000).

Within Europe, *C. mutica* has successfully established and extended its range throughout the North Sea, Celtic Sea and English Channel coasts over the last 15 years and it is highly likely that it will continue to spread on a European and global scale. *Caprella mutica* is an aggressive species, outcompeting native caprellid amphipods for space and its presence in these native communities is of some concern. The overall absence of the native European *C. linearis*, formerly inhabiting artificial structures in areas of human activity at Helgoland in the German Bight (North Sea), is hypothesized to be the result of interspecific competition with the non-native congener *C. mutica*. While interspecific competition on disturbed artificial habitats may endanger the persistence of local populations of *C. linearis*, natural benthic habitats may provide sufficient space and suitable substratum, allowing for habitat segregation and coexistence between the two species in the same area. In addition, populations of *C. mutica* in near-bottom natural habitats were found to be strongly controlled by benthic predators, whereas reduced predation pressure on artificial structures allowed for high population densities and competitive superiority. However, as populations of *C. linearis* generally occur in patchy distribution and are subject to strong annual fluctuations, the displacement of *C. linearis* from artificial structures may have permanent effects on the overall persistence of populations of *C. linearis* in European coastal waters and this species may, therefore, be at higher risk than previously assumed. However, more detailed information is needed on annual and seasonal population dynamics of the native *C. linearis.*

Whilst the wider environmental implications of *C. mutica* have not yet been confirmed, it is likely that it will have an important impact on benthic and plankton communities, particularly during the summer months when population densities are at their highest (Cook et al. 2009). On a more positive note, lipid studies have shown that *C. mutica* will consume fish farm derived particulate material (Cook et al. 2009), and may, therefore, actually reduce the environmental impact of the farm on the surrounding benthic environment (Black 1998). This, however, requires further investigation.

*Caprella mutica* is highly adaptable and tolerant of a wide range of environmental conditions, including highly disturbed (e.g., ports/marinas) and organically enriched sites (e.g., finfish farms). With the increasing development of our coastlines, it is highly likely that the provision of suitable substrata within European coastal waters will continue to rise and to provide a series of ‘stepping stones’ to enable the further spread of this species. Sites that are less favourable to this species, though, are water bodies with significant riverine input (e.g., estuaries, heads of sea-loch systems, enclosed marinas/ harbours) where salinity fluctuates between 3 and 35 psu on a regular basis (Ashton 2006). It is not known how tolerant *C. mutica* is to reduced levels of dissolved oxygen, but breeding activity of *Caprella equilibra* was found to decrease at higher temperatures and in oxygen deficient waters (Sconfietti and Luparia 1995). Caprellids are known to survive in ballast tanks (Gollasch et al. 2002), and are, therefore, presumably tolerant to the conditions experienced during trans-oceanic passages. *C. mutica* is intolerant to aerial exposure during summer months and will die within an hour of emergence from water (Cook, pers. obs.). However, cool and damp conditions typically found in anchor lockers or bundles of mooring lines and fish farm netting are likely to prolong their survival out of water for up to 7 h (Boos and Cook, pers. obs.).

Marine invertebrates have been shown to accumulate toxic butyltins (BT), which have been extensively used as industrial wood preservatives and antifouling agents in paints applied to boats and aquaculture nets since the 1960s (Takahashi et al. 1999). In polluted harbours near Otsuchi Port, Japan, *C. mutica* were found to have accumulated BTs, with significantly higher portions of tributyltins (TBT) than other caprellid and gammarid amphipod species from similar habitats (Takahashi et al. 1999). Low capacity to degrade TBTs and, thus, enhanced risk of contamination and accumulation may pose a risk to other species at higher trophic levels when feeding on *C. mutica*. While comparably high concentrations of TBTs can still be traced in Japanese waters, regulations have enforced restrictions of TBT in most western European countries in the 1990s and its use has been banned in many countries since 2008. Therefore, effects of accumulated TBTs in trophic cascades may be comparably low in modern-day European marine environments.

One of the most prominent characteristics related to the invasion success of *C. mutica* is the species' predominant occurrence on artificial structures in areas of human activity. Here, populations increased exponentially over short time periods (<3 months) suggesting that these habitats may act as source points for further dispersal. While often serving as first point of entry in marine non-natives (Carlton and Geller 1993; Ruiz et al. 1997; Bax et al. 2002; Floerl et al. 2005), such habitats are generally subject to frequent anthropogenic disturbances. These include boating activities, marina related construction work and aquaculture or offshore wind farm operations (Ruiz et al. 1997; Vitousek et al. 1997; Byers 2002a; Floerl et al. 2005), leading to temporarily enhanced availability of resources including space and food in these habitats (Davis et al. 2000). Non-native species such as *C. mutica*, often showing wide phenotypic plasticity and rapid adaptation to environmental change (Sakai et al. 2001), may be superior at colonizing and establishing populations in temporarily disturbed (anthropogenic) habitats (Parker et al. 1993; Carlton 2000). It is expected, however, that refuges in spatially diverse and species-rich natural benthic habitats will reduce the probability of competitive encounters (Roda et al. 2000; Jackson et al. 2001; Byers 2002b) and promote co-existence of *C. mutica* and native congeneric species (Shucksmith 2007).

No studies have looked at the impact of *C. mutica* on the economy to date. In the summer months, high densities of this species have been known to block water intakes on the pumps for the feeding system on caged finfish sites. Furthermore, they have settled on mussel lines on the west coast of Scotland and Canada, which should have been covered with juvenile mussels (*Mytilus edulis*) (Sainte-Marie and Cook pers. obs). Unfortunately, no studies have been performed to date to show whether there is a relationship between the abundance of caprellids and the lack of juvenile mussels. Preliminary studies, however, suggest that other reasons, such as strong freshwater influence or natural predators may have been responsible for the lack of juvenile mussels, and the presence of *C. mutica* was a consequence of free settlement space (Boos, pers. obs.). There may also be an economic 'cost' to the aquaculture industry, through having to clean the caprellids (which form a major part of the fouling biomass in the summer months) from the cage nets but this has not been calculated to date. The economic cost to the shipping and recreational boating community could also be quite high in the future if this species, and other hull fouling species, have to be disposed of to landfill rather than to the marine environment; the current practice in many European countries.

No efforts to eradicate *C. mutica* from established sites have been attempted to date. As population densities of this species are very high during the summer months, efforts to control *C. mutica*, if necessary, are more likely to succeed over the winter months, when growth and reproduction rates are at their minimum and population densities are at their lowest. Control methods, using freshwater, aerial exposure, traps and/or pheromones have not been tested as yet. However, it is likely that the former two methods would be the most promising for this and other non-native marine invertebrates. There is no known disease selective for *C. mutica*, although a parasitic copepod has been found within the brood pouch of certain caprellids, which mimics the morphology of the eggs (R. Huys pers. comm. 2009). Further investigations on the impact that this parasite may have on the success of *C. mutica* in colonising new habitats requires further investigation. There are no biocides that are selective for this species. In contrast to potential risk or negative impacts, Woods (2009) suggested the use of caprellid amphipods as a potential marine finfish aquaculture resource. Its high and overall availability on artificial structures, broad environmental tolerance and opportunistic feeding behaviour could give *C. mutica* promising economic value for future aquaculture management.

## 5 Conclusions

During the past 40 years, *Caprella mutica* has become established along numerous coastal areas worldwide. Where introduced, *C. mutica* is typically associated with areas of human activity. Anthropogenic vectors such as shipping traffic, recreational boating and aquaculture activities provide efficient dispersal mechanisms for *C. mutica*, which lacks a planktonic larval stage. This species typically inhabits artificial structures, reflecting its ability to colonize instable, fluctuating environments. High reproductive output, rapid growth, early maturation and short generation times may have significantly contributed to the successful establishment of *C. mutica* outside its native range. In addition, the wide environmental tolerances of *C. mutica,* as well as its omnivorous feeding behaviour, provide excellent prerequisites for colonizing a variety of different microhabitats. The comparably large body size, as well as its highly aggressive behaviour may also give this species an advantage in interference competition with other species. Efficient and rapid dispersal, decreased predation pressure and competitive superiority of *C. mutica* inhabiting artificial structures may have contributed to the establishment of dense populations. In addition, *C. mutica* has life history traits, such as the ability to reproduce at low temperatures, the enhanced survivorship of winter hatchlings and the high reproductive activity during summer, which have enabled it to successfully adapt to seawater temperatures in Europe. The variable establishment success of *C. mutica* at different European locations does not diminish the potential risk of further range expansion. Yet, the invasion success of *C. mutica* in European coastal areas is determined by the presence of suitable habitats providing reduced risk of predation. Only on artificial structures does *C. mutica* meet conditions which allow for the establishment of high population densities.

While this knowledge may provide encouragement for control and management actions, the ongoing human globalisation (Perrings et al. 2005) and particularly ever-increasing number of anthropogenic constructions in marine and estuarine environments (e.g., offshore wind parks, maricultures and boating harbours) provide an increasing number of 'invasion opportunities' for *C. mutica* and non-native species in general along all coastal zones of the world (Carlton and Geller 1993; Wilhelmsson and Malm 2008).

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# Part III
# Alien Faunas by Region

# Barnacle Invasions: Introduced, Cryptogenic, and Range Expanding Cirripedia of North and South America

## James T. Carlton, William A. Newman, and Fábio Bettini Pitombo

**Abstract** Barnacles are some of the most conspicuous and well-known ship fouling organisms in the world and thus many species no doubt owe parts of their modern distribution to human-mediated translocations over the past several centuries. Reviewed here, as a window into global patterns, are the introduced, cryptogenic, and range expanding barnacles of the Atlantic and Pacific coasts of North and South America. Five species of thoracic barnacles have invaded the Pacific coasts of the Americas: *Amphibalanus improvisus*, *A. eburneus*, and *A. subalbidus*, all from the Atlantic, and *A. amphitrite* and *A. reticulatus* from the Indo-West Pacific. Seven species have invaded the Atlantic coasts of the Americas; six of these are from the Pacific: *A. amphitrite* and *A. reticulatus* (shared as invaders with the Pacific coast), and *Balanus trigonus*, *B. glandula*, *Striatobalanus amaryllis*, and *Megabalanus coccopoma*. The Western North Atlantic *A. subalbidus* has invaded the Western South Atlantic. Striking are the few barnacle invasions that have occurred on the Pacific coast of South America and these species (*A. improvisus*, *A. amphitrite* and *A. reticulatus*) are reported only from northernmost locations (Ecuador, Colombia, and Peru). For the first 100 years (1853–1955) two species, *A. amphitrite* and *A. improvisus*, constituted the majority of invasion events in the Americas, the sole exception being the arrival of the Pacific *Balanus trigonus* in the 1860s and 1870s in the Atlantic. After 1955, the first records of invasions of *A. reticulatus*, *A. eburneus*, *B. glandula*, *M. coccopoma*, and *S. amaryllis* appear, an increased diversity of introductions in close concert with general observations of increasing

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invasions globally of marine organisms after World War II. Known since the 1970s in Brazil, *M. coccopoma* appears to be responding to warming northern latitudes and has expanded to North Carolina as of 2005. The native Western Atlantic barnacle *Chthamalus fragilis* arrived in New England in the 1890s, a range expansion perhaps facilitated by an earlier coastal warming period concomitant with the decline in abundance of its colder-water competitor *Semibalanus balanoides*, although the latter also appears to have expanded south on the North American Atlantic coast in the twentieth century due to increased habitat availability. *Chthamalus* is predicted to move north, and *Semibalanus* is predicted to return to its historical range, both due to continued warming. In turn, the native Eastern North Pacific barnacle *Tetraclita rubescens* is expanding north due to coastal warming as well. Future invasion scenarios include increased introductions facilitated through a newly expanded Panama Canal, the potential arrival of *Austrominius modestus* on the North American Atlantic coast (despite its failure to do so throughout the last half of the twentieth century), and the arrival on the warmer North and Central American Pacific coasts of *Chthamalus proteus*.

**Keywords** Cirripedia • Barnacles • Invasive • Introduced • Range expansion • Climate change • *Balanus* • *Amphibalanus* • *Megabalanus* • *Loxothylacus* • *Austrominius* • *Chthamalus* • *Tetraclita* • *Semibalanus* • *Fistulobalanus* • *Paraconcavus* • *Striatobalanus*

## 1 Introduction

Barnacles are some of the most conspicuous fouling organisms in the world, known to all who are familiar with the common marine life on boat hulls or pier pilings. Barnacles are often equally common on commercial shellfish, such as oysters, and as such, along with their proclivity to be transported by ships, are subject to being introduced to new regions of the world through maritime commerce. No global review of alien barnacles is available, although many species, at least, no doubt owe parts of their modern distribution to human-mediated translocations over the past several centuries. While Hosie and Ahyong (2008) stated that known cases of barnacle introductions worldwide "are surprisingly few" the opposite is actually the case for the Americas alone, as documented here.

Nineteenth and early-twentieth century cirripedologists and other workers were well aware of the role of ships in coastal, transoceanic, and interoceanic (intercontinental) dispersal of barnacles (Darwin 1854; Pilsbry 1916; see also Bishop 1951; Kühl 1963; Carlton 2011). Harrington and Griffin (1897) noted that a barnacle, identified as "*Balanus tintinnabulum*" was "so effective in covering the keels of ships, plying between Puget Sound and the Orient, that the bottoms must be scraped after every four voyages". Pilsbry (1909), in a paper on the barnacles of Peru, speculated that "*Balanus tintinnabulum*" was "probably derived from an oriental center", noting that it was "one of the most abundant forms carried on ship bottoms.

Whether it reached the west coast of South America by natural means, or was carried there by commerce has not been ascertained. If it proves to be wanting in Pleistocene or Pliocene deposits of the west coast, the theory of recent introduction may safely be held". While we now know that Pilsbry was working with the native Pacific South American *Megabalanus concinnus* (Darwin, 1854) (Henry and McLaughlin 1986), important here is his awareness of the potential for human-mediated modifications of barnacle distributions, as well as the value of the fossil record in helping to resolve barnacle biogeography. In the same paper, Pilsbry noted the presence of *Lepas anatifera* on the bottoms of local vessels, known as lanchas (launches), which were used as lighters at the Chincha Islands for embarking guano.

Reviewed here, as a preliminary window into global patterns, are the alien (introduced) thoracic (and one rhizocephalan) barnacle on the Atlantic and Pacific coasts of North and South America. Also considered are examples of intracontinental range expansions and introductions within the Pacific and Atlantic Oceans, and noted are several species previously referred to as introductions that are considered either questionable records or native taxa.

## 2 Vectors That Transport Barnacles Across and Between Oceans

Numerous human-mediated or human-influenced vectors are known to transport living barnacles into regions where they do not or did not previously occur (Tables 1 and 2). Examples are presented of such vectors where transport of balanomorph barnacles has been documented (Table 1) as well as examples of species involved in such episodes (Table 2). Neither table is exhaustive, but all major vectors are shown in Table 1: these include fouling and ballast transport on a wide variety of sea-going vessels, the movement or detachment of buoys, commercial movements of living organisms with attached barnacles, and human-generated debris on the ocean surface. While balanomorph barnacles can drift on "natural" substrates such as tree limbs, drifting plastic persists far longer than natural substrates, is often more abundant than natural substrates, and is present where natural substrates are often rare, such as in the Antarctic and Arctic (Barnes and Milner 2005). Not shown on the table are two additional vectors that may have transported or do transport barnacles, but for which we have not yet found direct evidence of barnacle transport: the movement for centuries of shore rocks for ballast (Carlton 2007) and the movement of marina floats (pontoons) (Carlton 2001: 11). Both are highly probable barnacle habitats.

Table 2 presents a sample of 46 species (excluding subspecies) associated with seven vectors, sufficient to suggest some broad potential patterns. Four families are represented: Chthamalidae (*Chthamalus*, *Euraphia*), Tetraclitidae (*Epopella*, *Newmanella*, *Tesseropora*, *Tetraclita*), Archaeobalanidae (*Austrominius*, *Hesperibalanus*, *Semibalanus*, *Solidobalanus*, *Striatobalanus*) and Balanidae (*Amphibalanus*, *Balanus*, *Austromegabalanus*, *Fistulobalanus*, *Megabalanus*,

**Table 1** Documented human-mediated transport vectors of balanomorph barnacles

- **(I) External fouling on vessel (Ship, platform, drydock) hulls or other surfaces**
  - (A) Cargo, cruise, research, fishing, barge, tug, replica, and military vessels
  - (B) Recreational vessels
  - (C) Derelict vessels towed between oceans
  - (D) Semisubmersible oil platforms and drill vessels
  - (E) Floating dry docks
- **(II) Internal fouling in vessel sea chests or sea water pipe systems**
  - (A) Sea chests
  - (B) Sea water pipe systems
- **(III) Ballast tanks or ballasted cargo holds**
  - (A) Plankton: nauplii and cyprids
  - (B) Fouling: juvenile or adult barnacles
- **(IV) Buoys**
  - (A) On navigation buoys(moved from one site to another)
  - (B) On aquaculture buoys (detached and floating at sea)
- **(V) Commerce: seafood, mariculture, fish egg harvesting, marine biosupply**
  - (A) Live seafood
    - (i) Lobster shipments: on seaweed packed as dunnage
    - (ii) Oyster shipments
  - (B) Mariculture: commercial oysters for open-sea planting
  - (C) Oyster shell transplants (for cultch)
  - (D) Fish egg harvesting: in kelp transplanted for herring egg industry
  - (E) Marine biosupply shipments
- **(VI) Habitat-ecosystem restoration projects**
  - (A) Oyster shell transplants (for restoration)
- **(VII) Other human-influenced or human–mediated vectors**
  - (A) On drifting plastic or other anthropogenic materials
  - (B) On marking-tracking tags on marine animals
    - (i) On migratory birds
    - (ii) On fish

*Notomegabalanus*, *Perforatus*). Nearly 75% of the species in Table 2 are balanids, and, of these, fully two-thirds are amphibalanines or megabalanines. Of no small interest is that approximately one-quarter (11) of the species shown in Table 2 have been introduced on the Atlantic or Pacific coasts of Americas, as detailed below.

Common species appearing in many shipping records are *Amphibalanus amphitrite*, *A. eburneus*, *A. improvisus*, *A. reticulatus*, *Balanus trigonus*, and *Megabalanus tintinnabulum* (Table 2). Not surprisingly, these species have all been introduced to new regions around the world. Associated with the widest range of vectors are *Amphibalanus amphitrite* and *A. improvisus*.

Certain species, such as *Balanus crenatus*, are considered to be naturally distributed over broad ranges, and yet are also associated with global transport mechanisms such as shipping (Table 2). In these cases, cryptic patterns of invasions may be buried within seemingly natural distributions; we predict that careful assessment of

**Table 2** Examples of balanomorph barnacle species transported on human-mediated vectors

| Vector | Barnacle species[a] associated with vector (nomenclature updated) | Reference |
|---|---|---|
| **(I) External fouling on vessel (ship, platform, drydock) hulls or other surfaces** | | |
| (A) Cargo, research, fishing, barge, tug, replica, and military vessels (numerous papers document ship-borne barnacle transport; a few examples are listed here:) | | |
| **West Africa, India, China ==>England** | *Megabalanus tintinnabulum* | Darwin (1854) |
| **Bengal and China ==> England** | *Megabalanus coccopoma*<br>*Megabalanus tintinnabulum* | Darwin (1854) |
| **England ==> Africa ==> Patagonia ==> England** | *Austromegabalanus psittacus*<br>*Megabalanus tintinnabulum* | Darwin (1854) |
| **Indo-Pacific ==> Ireland** | *Megabalanus zebra* | Pilsbry (1916) |
| **San Francisco ==> Hong Kong ==>Java ==> India ==> Philadelphia** | *Megabalanus occator*<br>*Megabalanus tintinnabulum*<br>*Tetraclita squamosa patellaris* | Pilsbry (1916) |
| **West Indies ==> Massachusetts** | *Newmanella radiata* | Pilsbry (1916) |
| **Germany (vessels arriving from the Atlantic, Indian, and Pacific Oceans)** | *Amphibalanus amphitrite*<br>*Amphibalanus improvisus*<br>*Balanus crenatus*<br>*Austromegabalanus psittacus*<br>*Megabalanus tintinnabulum* | Hentschel (1923) |
| **Atlantic coast of the United States (military vessels arriving from the Atlantic, Indian, and Pacific Oceans)** | *Amphibalanus amphitrite*<br>*Amphibalanus eburneus*<br>*Amphibalanus improvisus*<br>*Balanus crenatus*<br>*Megabalanus tintinnabulum*<br>*Megabalanus tulipiformis* | Visscher (1928) |
| **England ==> Netherlands** | *Amphibalanus improvisus*<br>*Austrominius modestus* | Bishop (1947) |
| **New Zealand ==> Panama Canal ==> England** | *Amphibalanus amphitrite*<br>*Austrominius modestus*<br>*Balanus trigonus* | Bishop (1947) |
| **South Africa (regional vessels and some overseas traffic)** | *Amphibalanus amphitrite*<br>*Austromegabalanus cylindricus*<br>*Balanus trigonus*<br>*Notomegabalanus algicola* | Millard (1952) |
| **Japan/Korea ==> Australia** | *Fistulobalanus albicostatus*<br>*Megabalanus tintinnabulum*<br>*Megabalanus volcano* | Allen (1953) |
| **South Pacific/West Pacific ==> Puget Sound (Washington)** | *Amphibalanus amphitrite*<br>*Megabalanus rosa*<br>*Megabalanus tintinnabulum*<br>*Megabalanus volcano*<br>*Striatobalanus amaryllis* | Eyerdam (1959)[b] |

(continued)

**Table 2** (continued)

| Vector | Barnacle species[a] associated with vector (nomenclature updated) | Reference |
|---|---|---|
| **New Zealand (coastal and some overseas traffic)** | *Amphibalanus amphitrite*<br>*Amphibalanus cirratus*<br>*Austromegabalanus decorus*<br>*Austrominius modestus*<br>*Balanus trigonus*<br>*Euraphia hembeli*<br>*Solidobalanus auricoma* | Skerman (1960) |
| **Far Eastern seas north of The Japan Sea** | *Balanus balanus*<br>*Balanus crenatus*<br>*Balanus rostratus*<br>*Chthamalus dalli*<br>*Semibalanus balanoides calcaratus*<br>*Semibalanus cariosus*<br>*Hesperibalanus hesperius* | Rudyakova (1967) |
| **Adriatic Sea (coastal and some overseas traffic)** | *Amphibalanus amphitrite*<br>*Amphibalanus eburneus*<br>*Tetraclita squamosa* | Igic (1968) |
| **China (coastal traffic)** | *Amphibalanus amphitrite*<br>*Fistulobalanus kondakovi* | Huang et al. (1979) |
| **China (coastal traffic in Daya Bay)** | *Amphibalanus amphitrite*<br>*Amphibalanus cirratus*<br>*Balanus trigonus*<br>*Chthamalus sinensis*<br>*Megabalanus tintinnabulum* | Yan and Huang (1993) |
| **California coast (Oregon ==> California)** | *Balanus crenatus* | Carlton and Hodder (1995) |
| **Western Pacific: Russian shipping lines on routes from Bering Sea to Vietnam** | *Amphibalanus amphitrite*<br>*Amphibalanus eburneus*<br>*Amphibalanus improvisus*<br>*Amphibalanus reticulatus*<br>*Balanus crenatus*<br>*Balanus rostratus*<br>*Balanus trigonus*<br>*Fistulobalanus albicostatus*<br>*Megabalanus rosa*<br>*Megabalanus tintinnabulum*<br>*Semibalanus cariosus* | Zvyagintsev (2000) |
| **Hawaiian Islands <==> California** | *Chthamalus proteus* | Godwin (2003)[c] |
| **Hawaiian Islands: interisland barges/tugs** | *Amphibalanus amphitrite*<br>*Amphibalanus reticulatus*<br>*Chthamalus proteus*<br>*Euraphia hembeli*<br>*Megabalanus tanagrae*<br>*Tesseropora pacifica* | Godwin et al. (2004) |

(continued)

**Table 2** (continued)

| Vector | Barnacle species[a] associated with vector (nomenclature updated) | Reference |
|---|---|---|
| **Marshall Islands ==> Hawaiian Islands** | *Euraphia hembeli*<br>*Tesseropora pacifica* | Godwin et al. (2004) |
| **Southern Ocean (south of Australia)** | *Amphibalanus amphitrite*<br>*Austrominius modestus* | Lewis et al. (2005) |
| (B) Recreational vessels | | |
| **New England coast** | *Amphibalanus improvisus* | Carlton, Kapoor, Mintz |
| **(Maine <==> Long Is Sound)** | *Amphibalanus eburneus* | (unpubl.) |
| **Japan ==> Hawaii** | *Amphibalanus amphitrite*<br>*Amphibalanus eburneus*<br>*Amphibalanus reticulatus* | Godwin et al. (2004) |
| **California ==> Mexico ==> Hawaii** | *Amphibalanus amphitrite*<br>*Balanus trigonus*<br>*Chthamalus proteus*<br>*Megabalanus californicus* | Godwin et al. (2004) |
| **Galapagos ==> Hawaii** | *Megabalanus peninsularis* | Godwin et al. (2004) |
| (C) Derelict vessels towed between oceans | | |
| **California ==> Panama Canal ==> Texas** | *Amphibalanus improvisus* | Davidson et al. (2008a) |
| (D) Semisubmersible oil platforms and drill vessels | | |
| **Japan ==> New Zealand** | *Amphibalanus amphitrite*<br>*Amphibalanus improvisus*<br>*Amphibalanus reticulatus*<br>*Amphibalanus variegatus*<br>*Fistulobalanus albicostatus*<br>*Megabalanus rosa*<br>*Megabalanus volcano*<br>*Tetraclita squamosa japonica* | Foster and Willan (1979) |
| **Brazil** | *Balanus trigonus*<br>*Megabalanus coccopoma*`<br>*Megabalanus tintinnabulum* | Farrapeira (2006) |
| **Brazil ==> Tristan da Cunha** | *Balanus* sp.<br>*Megabalanus tintinnabulum*<br>*Tetraclita* sp. | Wanless et al. (2010) |
| (E) Floating dry docks | | |
| **Hawaiian Islands ==> Guam** | *Amphibalanus eburneus*<br>*Amphibalanus reticulatus*<br>*Chthamalus proteus* | DeFelice (1999); see also, Paulay et al. (2002): 414 |
| **China ==> Korea ==> Puerto Rico ==> Maine** | *Chthamalus* sp.<br>*Megabalanus volcano*<br>*Megabalanus zebra* | M. Bowen, 2001, pers. comm. |

(continued)

**Table 2** (continued)

| Vector | Barnacle species[a] associated with vector (nomenclature updated) | Reference |
|---|---|---|
| **(II) Internal fouling in vessel sea chests or sea water pipe systems** | | |
| (A) Sea chests | | |
| **Southeastern Australia** | *Amphibalanus cirratus*<br>*Austrominius modestus* | Coutts et al. (2003) |
| (B) Sea water pipe systems | | |
| **"Orient" ==> San Francisco Bay** | *Amphibalanus amphitrite* | Newman (1963) |
| **(III) Ballast tanks or ballasted cargo holds** | | |
| (A) Plankton: nauplii and cyprids | | |
| **Massachusetts** | *Semibalanus balanoides* | Carlton (1985) |
| **Europe ==> Great Lakes** | *Austrominius modestus* | Carlton (1985) |
| **Japan ==> Oregon** | *Amphibalanus* spp.?; | Carlton and Geller (1993); |
| | unidentified species | Carlton (unpubl.) |
| **Black Sea/Turkey/Adriatic Sea ==> Adriatic Sea** | unidentified species | David et al. (2007) |
| **Asia ==> Puget Sound, Washington** | unidentified species | Cordell et al. (2009) |
| **Vladivostok, Russia: vessels sailing on Russia-Japan and Russia-China routes** | *Balanus crenatus* | Zvyagintsev et al. (2009) |
| (B) Fouling: juvenile or adult barnacles | | |
| **Japan ==> Oregon** | *Amphibalanus* sp. (settled during 11 day voyage) | Carlton (unpubl.) |
| **Washington <==> California** | *Balanus* sp. | Carlton (unpubl.) |
| **Germany (coastal and overseas traffic)** | *Amphibalanus amphitrite*<br>*Amphibalanus cirratus*<br>*Amphibalanus eburneus*<br>*Amphibalanus improvisus*<br>*Amphibalanus reticulatus*<br>*Amphibalanus variegatus*<br>*Austromegabalanus campbelli*<br>*Austrominius modestus*<br>*Balanus balanus*<br>*Balanus crenatus*<br>*Balanus trigonus*<br>*Fistulobalanus kondakovi*<br>*Epopella simplex*<br>*Megabalanus tintinnabulum*<br>*Perforatus perforatus*<br>*Semibalanus balanoides*<br>*Striatobalanus amaryllis* | Gollasch et al. (2002)[d] |
| **(IV) Buoys**[e] | | |
| (A) On navigation buoys (moved from one site to another) | | |
| **California coast ==> Salton Sea CA** | *Amphibalanus amphitrite* | See herein |

(continued)

**Table 2** (continued)

| Vector | Barnacle species[a] associated with vector (nomenclature updated) | Reference |
|---|---|---|
| (B) On aquaculture buoys (detached and floating at sea) | | |
| **Chile**, coastal waters | *Austromegabalanus psittacus* | Astudillo et al. (2009) |
| **(V) Commerce: seafood, mariculture, fish egg harvesting, marine biosupply** | | |
| (A) Live seafood | | |
| (i) Lobster shipments: on/in seaweed packed as dunnage | | |
| **New England ==> California** | *Amphibalanus venustus* | Miller (1969) |
| (ii) Oyster shipments | | |
| **Puget Sound ==> Connecticut** | *Balanus crenatus* | Carlton, Mohammad, Huynh (unpubl.) |
| **Puget Sound ==>Washington, D.C.** | *Balanus glandula*[f] | Carlton (unpubl.) |
| (B) Mariculture: commercial oysters for open-sea planting | | |
| **Japan ==> California** | *Fistulobalanus albicostatus* | Bonnot (1935) and Henry and McLaughlin (1975)[g] |
| **Japan ==> France** | *Amphibalanus amphitrite*<br>*Amphibalanus improvisus*<br>*Fistulobalanus albicostatus* | Gruet et al. (1976) |
| (C) Oyster shell transplants (for cultch) | | |
| **California** | *Balanus glandula*<br>*Chthamalus dalli* | Cohen and Zabin (2009) |
| (D) Fish egg harvesting: in kelp transplanted for herring egg industry | | |
| **Southern California ==> Oregon** | *Megabalanus californicus*[h] | Carlton 1992, p. 35 (as "barnacles"); Carlton (unpubl.) |
| (E) Marine biosupply shipments: phoretic species | | |
| **California ==> Connecticut** | *Balanus trigonus*[i]<br>*Megabalanus californicus*[i] | Carlton, Mohammad, Huynh (unpubl.) |
| **(VI) Habitat-ecosystem restoration projects** | | |
| (A) Oyster shell transplants (for restoration) | | |
| **California** | *Balanus glandula*<br>*Chthamalus dalli* | Cohen and Zabin (2009) |
| **(VII) Other human-influenced or – mediated vectors** | | |
| (A) On drifting plastic or other anthropogenic materials (see text discussion) | | |
| **North Atlantic: Shetland Islands** | *Austrominius modestus* | Barnes and Milner (2005) |
| **Arctic and sub-Arctic** | *Semibalanus balanoides* | Barnes and Milner (2005) |

(continued)

**Table 2** (continued)

| Vector | Barnacle species[a] associated with vector (nomenclature updated) | Reference |
|---|---|---|
| **Spain ==> Wales** | *Perforatus perforatus* | Rees and Southward (2008) |
| (B) On marking-tracking tags on marine animals[j] | | |
| (i) On migratory birds[k] | | |
| **Africa ==> Finland, Norway** | *Fistulobalanus albicostatus* | Tøttrup et al. (2010) |
| | *Fistulobalanus pallidus* | |
| (ii) On fish[l] | | |
| **New Zealand** | *Austromegabalanus decorus* | Jones and Foster (1978) |

Key: ==> one-way traffic, <==> two-way traffic

[a] With the exception of Vector VI-A (oyster shell transplants), listed are only those species found alive at the end of the noted voyage, transit, or incident. Species are listed twice in one instance: Vector V-C and VI-A, as the same incident applies to two distinct vectors

[b] Eyerdam (1959) believed the vessel sampled came from the Hawaiian or Marshall Islands, an origin mistakenly repeated by Carlton (1987: 454, Table 1); while the bivalves could be from the Hawaiian Islands, the barnacles on the vessel do not occur in the Hawaiian or Marshall Islands, but rather are found in the Western, South and/or Indo-Pacific, as the bivalves do as well

[c] *Chthamalus proteus*: on ocean-going barges that had departed the Hawaiian Islands, sailed to California and the Pacific Northwest, and were still alive on the same barges when they returned to Honolulu Harbour

[d] From species list referred to as “Table A1” in Gollasch et al. (2002), available at: http://www.corpi.ku.lt/nemo/aqua_app_gollasch.pdf (accessed July 20, 2010), not the website provided in Gollasch et al. 2002: 224. For detailed vessel origin and other data, see Lenz et al. (2000)

[e] Intertidal and subtidal barnacles are common on navigation and other buoys (Pilsbry 1916; Gray 1940; WHOI 1952; Fradette and Bourget 1980; Bourget et al. 2003; Knott 2006), which when and if dislodged may transport their fouling communities along coastlines; see especially Kerckhof and Cattrijsse (2001) for a description of the cirriped fauna on buoys on the Belgian coast

[f] *Balanus glandula* survived 13 days out of water (from oyster harvest in Puget Sound until re-submergence in seawater in a laboratory nearly 2 weeks later in Connecticut)

[g] Of interest is that Bonnot (1935) found *Fistulobalanus albicostatus* on a shipment of Pacific oysters (*Crassostrea gigas*) planted in Elkhorn Slough, Monterey Bay, California in 1930, while Henry and McLaughlin (1975: 109, 114) reported a single species collected from “*Ostrea* sp.” (almost certainly *Crassostrea gigas*) 225 km to the south of Elkhorn Slough in Morro Bay, California. These records suggest that *F. albicostatus* was likely released on a regular basis into oystering bays from California to Canada throughout the twentieth century; no established populations are known. Gruet et al. (1976) similarly reported it transported on *C. gigas* to France

[h] Epizoic on crab *Pugettia producta* amongst kelp *Macrocystis*

[i] Barnacles on stalked seasquirts (*Styela*) shipped from biosupply company

[j] A further example of barnacle transport on tagged animals is provided by Reisinger et al. (2010), who reported *Lepas australis* on tags (satellite-relay data loggers) on elephant seals in the Southern Ocean

[k] On plastic leg rings on the Lesser Black-backed Gull *Larus fuscus*

[l] On plastic tag attached to a trevally (*Caranx georgianus*) collected in New Zealand

the fossil record, combined with molecular genetic work, will reveal that some portions of seemingly cosmopolitan or near-cosmopolitan distributions will be found to be due to modifications in the past few hundred years. Where the fossil record supports wide distributions prehistorically, it may nevertheless be that extensive genetic mixing has occurred.

## 3 Introduced and Cryptogenic Cirripedia of the Americas

Treated here are case histories of 17 species of barnacles (Tables 3 and 4): five species have been introduced to the Pacific coasts of the Americas, and seven species have been introduced to the North and South American Atlantic coasts (Tables 3 and 4; Fig. 1). Several species are considered cryptogenic (species for which clear evidence of being

**Table 3** Summary of Barnacle species treated herein and their status on the Pacific and Atlantic coasts of North and South America

| Pacific coasts | Atlantic coasts |
|---|---|
| ***Introduced*** | ***Introduced*** |
| *Amphibalanus amphitrite* | *Amphibalanus amphitrite* |
| *Amphibalanus eburneus* | *Amphibalanus reticulatus* |
| *Amphibalanus improvisus* | *Balanus glandula* |
| *Amphibalanus reticulatus* | *Balanus trigonus* |
| *Amphibalanus subalbidus* | *Megabalanus coccopoma* |
| | *Striatobalanus amaryllis* |
| | *Loxothylacus panopaei* |
| | ***South America:*** |
| | *Amphibalanus subalbidus* |
| ***Cryptogenic*** | ***Cryptogenic*** |
| *Balanus calidus/Balanus spongicola* | ***Western–Eastern Atlantic:*** |
| | *Fistulobalanus pallidus* |
| | *Megabalanus tintinnabulum* |
| | ***Western Atlantic: South America:*** |
| | *Amphibalanus eburneus* |
| | *Amphibalanus improvisus* |
| ***Establishment uncertain:*** | |
| ***Panama canal locks:*** | |
| *Balanus calidus* | |
| *Fistulobalanus pallidus* | |
| ***Range expansions of native species*** | ***Range expansions of native species*** |
| *Tetraclita rubescens* (South ==> North) | *Chthamalus fragilis* (South ==> North) |
| | *Semibalanus balanoides* (North ==> South) |
| ***Temporary range expansions of native species*** | ***Temporary range expansions of native species*** |
| *Megabalanus coccopoma* (South ==> North) | ***North of Cape Hatteras:*** |
| *Megabalanus californicus* (South ==> North) | *Amphibalanus subalbidus* (South ==> North) |
| | ***South of Cape Hatteras:*** |
| | *Semibalanus balanoides* (North ==> South) |

**Table 4** Introduced barnacles (Cirripedia) of North and South America: Origins and summary of sites and timing of introduction

| Species | Origin | Introduced to (selected first records):(date of first record, location) |
|---|---|---|
| *Amphibalanus amphitrite* (Darwin, 1854) | Indo-Pacific | **EP:**<br>1914 California (Henry and McLaughlin 1975)<br>1946 Gulf of California (*Ibid.*)<br>1960 Mexico (*Ibid.*)<br>1974 Balboa, Panama (Spivey 1976)<br>1999 Peru (Pitombo unpubl.)<br>**WA:**<br>1940 Brazil (de Oliveira 1941)<br>1952 Bermuda; Gulf of Mexico (*Ibid.*)<br>1955 North Carolina (*Ibid.*; see text for date)<br>1966 Argentina (Bastida 1969) |
| *Amphibalanus eburneus* (Gould, 1841) | Northwest Atlantic | **EP:**<br>1959 Gulf of California (Henry and McLaughlin 1975)<br>1963 Mexico (*Ibid.*)<br>1964 Panama (Newman 1964)<br>2000 California (Cohen et al. 2005) |
| *Amphibalanus improvisus* (Darwin, 1854) | Northwest Atlantic | **EP:**<br><1854 Ecuador and West Colombia (Darwin 1854)<br>1853 California (San Francisco) (Carlton and Zullo 1969)<br>1889 Gulf of California (Henry and McLaughlin 1975) |
| *Amphibalanus reticulatus* (Utinomi, 1967) | Indo-Pacific | **EP:**<br>1984 Mexico (Laguna 1985)<br>1998 Gulf of California (Gomez-Daglio and Gonzalez 2006)<br>2000 Panama (Cohen 2006)<br>**WA:**<br>1956 Puerto Rico (Henry and McLaughlin 1975)<br>1965 Trinidad (Henry and McLaughlin 1975)<br>1969 Florida (east coast) (Moore et al. 1974)<br>**[*within Brazil, north to south; see text for references:*]**<br>1990 Pernambuco State<br>1992 Bahia State<br>1996 Rio de Janeiro State<br>2004 Parana State |
| *Amphibalanus subalbidus* | Northwest Atlantic | **EP:**<br>1989 Gulf of California (Van Syoc 1992)<br>**WA (South America):**<br>1994 Paraíba (Young 1994)<br>2004 Pernanbuco (Farrapeira et al. 2007) |

(continued)

**Table 4** (continued)

| Species | Origin | Introduced to (selected first records):(date of first record, location) |
|---|---|---|
| *Balanus glandula* Darwin, 1854 | Eastern Pacific | **WA:** |
| | | 1974 Argentina (Bastida et al. 1980) |
| *Balanus trigonus* Darwin, 1854 | Pacific | **WA (see Table 2 for references)** |
| | | 1864 Brazil |
| | | 1879 West Indies |
| | | 1961 Florida (east coast); North Carolina |
| *Megabalanus coccopoma* (Darwin, 1854) | Indo-Pacific | **WA:** |
| | | 1974 Brazil (Lacombe and Monteiro 1974) |
| | | 2001 Gulf of Mexico (Perreault 2004) |
| | | 2005 North Carolina (Knott 2006) |
| *Striatobalanus amaryllis* (Darwin, 1854) | Indo-Pacific | **WA:** |
| | | **[*within Brazil, north to south; see text for references:*]** |
| | | 1982 Piaui State |
| | | 1990 Pernambuco State |
| | | 1992 Bahia State |
| | | 2005 Parana State |
| *Loxothylacus panopaei* (Gissler, 1884) | Northwest Atlantic | **WA:** |
| | | 1964 Chesapeake Bay (Van Engel et al. 1966) |
| | | 1983 North Carolina (Hines et al. 1997) |
| | | 2004 Florida (Kruse et al. 2011) |

Cryptogenic species, such as *Amphibalanus improvisus* and *A. eburneus* on the South American Atlantic coast, are not included here

*Abbreviations*: *WA* Western Atlantic Ocean (North, Central, and South America, including the Gulf of Mexico and Caribbean), *EP* Eastern Pacific Ocean (North, Central, and South America, including the Gulf of California and the Galapagos Islands)

native or introduced is absent), and examples of permanent and temporary range expansions of native species on both Atlantic and Pacific shores are discussed.

While Ferreira et al. (2009) reported that three species of barnacles were introduced to the Brazilian coast (to which we add two species, *Amphibalanus amphitrite* and *A. subalbidus*), Farrapeira (2010) reports 25 alien species of barnacles in Brazil. Her list includes many species known only from the Western Atlantic Ocean, parasitic taxa (*Sacculina hirsuta*), symbiotic and commensal species (such as *Platylepas* spp. and *Octolasmis* spp.), and coral-embedded species (such as *Ceratoconcha* spp., *Lithotrya dorsalis*). While authors of this present study agree with Farrapeira (2010) that many invasions may have occurred in the early days of sail, long before the first distributional records are available, Farrapeira (2010) notes that many of the species she lists as non-native to Brazil are capable of natural rafting or are "wide-ranging symbionts of mobile hosts". Farrapeira (2010) attempted to assign the "original distribution" of species in part based upon a taxon's type locality, but type localities do not necessarily indicate a species' origin, nor do they imply that dispersal occurred from that site. The treatment of previous workers is retained, and consequently this study regards most of the "exotic" species of Farrapeira as native to Atlantic South America.

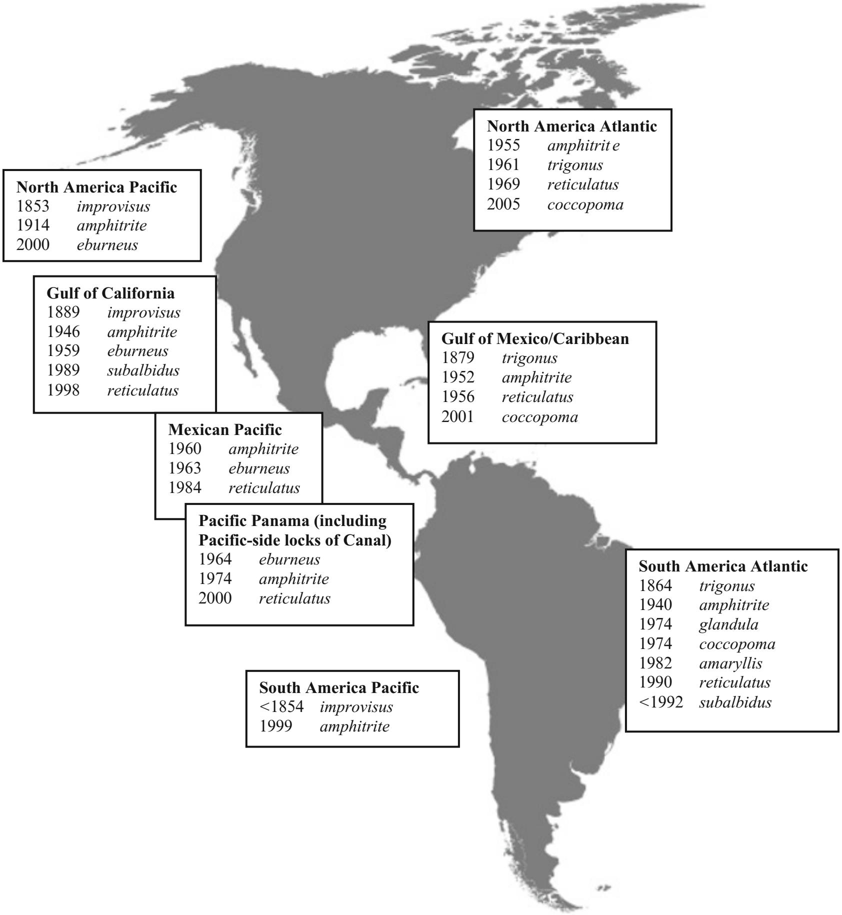

**Fig. 1** Distribution and chronological appearance of introduced thoracic barnacles on the Pacific and Atlantic coasts of North and South America. Base map from http://www.kontree.com/world/americas/index_files/America_blank_map.png

# 4 Balanomorpha: Balanidae: Amphibalaninae

## 4.1 *Status of* Amphibalanus eburneus *and* Amphibalanus improvisus *on the Atlantic Coast of South America*

Young (1995: 249) proposed that *Amphibalanus eburneus* was native to the North Atlantic Ocean and was introduced to Atlantic South America, noting that on the Southwestern Atlantic coast it has “a very restricted distribution usually being found [in] polluted bays with harbors.” Henry and McLaughlin (1975) record no specimens from the Atlantic coast of South America. Young (1994) cited Luederwaldt (1919) as the first record of *A. eburneus* for Brazil, in a mangrove community at Santos, São Paulo State. de Oliveira (1941, as *Balanus amphitrite niveus*, in part: see Henry 1974; Henry and McLaughlin 1975) appears to be the next to report it from Brazil, based upon collections made circa 1937–1940 in Guanabara Bay, Rio de Janeiro. In 2006 it was found on test panels in a mussel farm in Santa Catarina State, South Brazil (Cangussu et al. 2007) and in 2006 it was also reported in estuarine areas in northeast Brazil (Farrapeira 2006).

Orensanz et al. (2002) proposed that *Amphibalanus improvisus* may be cryptogenic in Uruguay and Argentina, in both of which countries Darwin (1854) found it in 1833 on the voyage of the *Beagle*. Neves and da Rocha (2008) list it as cryptogenic in Brazil. The west coast of South America had been visited regularly by North Atlantic vessels since the 1500s, making introduction of both *A. eburneus* and *A. improvisus* possible.

As the fossil record of these species on the Atlantic coast of South America requires review (for example, Tavora et al. 2005, who identify *A. eburneus* and *A. improvisus* from the "Eomiocene" of Brazil based only on shells and not opercular valves; they also note earlier reports of both species from the South American fossil record), both species are provisionally regarded as cryptogenic on the South American Atlantic coast. Regardless, noted here is that, at the least, extensive genetic mixing may well have occurred between North and South Atlantic stocks as a result of movement on ship hulls.

Farrapeira (2010) reviews the distribution of both species in northeast Brazil.

## 4.2 *Amphibalanus amphitrite* (Darwin, 1854)

There are no modern surveys of the amphibalanine barnacles of North American estuaries and bays. It would thus not be surprising to find that other pink-striped species have invaded but remain confounded with *A. amphitrite*. For example, a re-examination of populations of *A. amphitrite* from southern California to South America may reveal the cryptic presence of *A. venustus*, as well as additional populations of *Amphibalanus reticulatus*, discussed below.

**PACIFIC** This Indo-Pacific ("Near East", Zullo 1966b) warm-water species has been transported by ships for centuries, making its aboriginal distribution throughout the Indian Ocean and the Western Pacific Ocean difficult to determine (cf. Kühl 1963). It has been found in the Mediterranean at an archaeological site of the "Carthaginian naval base near Tunis" in North Africa, dated to the second century B.C., or more than 2,000 years ago (Southward 1998: 23; Wirtz et al. 2006), although the provenance of the vessels that may have brought it to that naval base is not known. *Amphibalanus amphitrite* appeared in the Northeastern Pacific in the years around World War I. It now occurs from the Los Angeles, California area (Cohen et al. 2005) to Panama (Henry and McLaughlin 1975); an additional isolated, but locally abundant population exists in San Francisco Bay, California.

The earliest collections are 1914 from Los Angeles Harbour (Henry and McLaughlin 1975, as *Balanus amphitrite saltonensis*) and 1919 from the San Diego area (La Jolla, Henry and McLaughlin 1975); Zullo et al. (1972) reported it in the San Diego area as well, based upon collections made in 1921 and 1927.

Establishment on the summer-warm margins of San Francisco Bay by 1938 (Carlton 1979a; not 1929, as given in Mooi et al. 2007) may have been from either overseas shipping or secondary dispersal from southern California; Rogers (1949) described San Francisco Bay populations as the subspecies *Balanus amphitrite herzi* and *B. a. franciscanus*, both synonyms of *A. amphitrite.*

The earliest record from the Gulf of California is 1946; the first record from western Mexico, at Acapulco, is 1960 (Henry and McLaughlin 1975). Ross (1962) reported it living on the native barnacle *Tetraclita squamosa stalactifera* in 1957 at San Carlos, Sonora, Gulf of California. Henry (1960) reported specimens collected in 1959 at Guaymas in the Gulf of California, and speculated that the failure of Steinbeck and Ricketts (1940) to find this species in 1940 (although *A. improvisus* was collected by them at that time) may be evidence that it was introduced after between 1940. Gomez-Daglio and Gonzalez (2006) found it at La Paz (1998–1999) from the intertidal zone to 40 m, including on red mangrove bark and prop roots and embedded in the gorgonians *Muricea* sp. and *Lophogorgia* spp. *Amphibalanus amphitrite* was first collected at La Punta, Lima, Peru, in 1999, in an embayment on artificial rock, establishing its southernmost range to date.

Whether *A. amphitrite* populations at Balboa, at the Pacific entrance of the Panama Canal, (1) represent direct transport through the Panama Canal from Atlantic populations (Cohen 2006), (2) are derived from southern expansion of earlier populations established to the north in Mexico, or (3) represent a separate introduction from the Western Pacific, may be resolvable by genetic analyses. Spivey (1976) first reported specimens at Balboa based upon 1974 collections, where it was associated with five other barnacle species.

Henry (1960) noted that *A. amphitrite* co-occurred with *Chthamalus fissus* and *Tetraclita squamosa* in the Gulf of California. Henry and McLaughlin (1975) note its association with seven additional species of barnacles from California to Mexico. Newman (1967) documented the distributional ecology, osmoregulatory and feeding physiology, and desiccation tolerance of this species and *A. improvisus*, in San Francisco Bay.

In World War II (WWII) this species was transported accidentally to a large inland saline lake, the Salton Sea, in the Colorado Desert of southern California. The Sea was created in 1905 by flooding of the Salton Basin by the Colorado River; in the decades that followed, many salt water species were introduced accidentally or intentionally. It was introduced "when buoys from San Diego Bay used to mark seaplane lanes were hastily transported there" (Newman and Abbott 1980), not by ballast water as stated by Tøttrup et al. (2010). The barnacles were abundant by 1944 (Hilton 1945), and they remain abundant in the hypersaline (43–44 psu) waters of the Sea, so much so that some beaches in the Sea are composed almost entirely of barnacle shells, resulting in perhaps the only shores in the world created by an introduced species.

Although having been transported from the coast to an inland location only about 5 years earlier, Rogers (1949) described the Salton Sea population as a new subspecies, *Balanus amphitrite saltonensis*, arguing that the "orifice is proportionately much larger, the radii are somewhat broader, the adductor pit on the scutum is almost lacking and the intermediate ridge is usually more prominent" than typical *A. amphitrite*.

While generally treated as a synonym of the stem species, *B. a. saltonensis* was retained as a valid subspecies by Henry and McLaughlin (1975), who distinguished *B. a. saltonensis* from *B. amphitrite amphitrite* by the former having parietal tubes usually with transverse septa (typically absent in the stem species), inner lamina with strong flat ribs (weak to moderate ribs in *B. amphitrite amphitrite*), and the tergum usually with the spur greater than its own width from the basiscutal angle (vs. in *B. amphitrite amphitrite*, the tergum's spur being less than its own width from the basiscutal angle). They accompanied this diagnosis with an analysis of 15 morphological characters: the statistical difference between *B. amphitrite saltonensis* and *B. amphitrite amphitrite* largely rested upon six ratios of four tergal measurements. Henry and McLaughlin identified material collected from coastal waters in Southern California (Wilmington Harbor 1914) as this "subspecies" as well, and noted that a Bermuda population of *A. amphitrite*, also existing in a highly restricted environment, was morphologically similar. Flowerdew (1985), however, concluded that *B. amphitrite saltonensis* was genetically identical and thus synonymous with *B. amphitrite amphitrite*. In 1990, R. Van Syoc transferred newly settled "*saltonensis*" barnacles from the Salton Sea to San Diego, where they grew into morphometrically-matching typical coastal populations of *B. a. amphitrite* barnacles (Van Syoc 1992).

Raimondi (1992) re-examined the question of whether Salton Sea population had diverged from the stem stock. He noted that while Flowerdew (1985) had concluded that there was no "significant genetic differentiation" between coastal and Salton Sea populations (based upon the observation that the values of genetic identity (I) and genetic distance (D) indices were in the range of variation expected for conspecific populations), the implication that no evolutionary divergence had occurred between the populations was not correct (because nonsignificant I and D values simply demonstrate that there is no divergence for the tested alleles). Raimondi determined experimentally that differences between the two populations disappeared when reared under similar environmental conditions, as had Van Syoc (1992).

Remarkably, however, while adult plasticity indicated that the populations appeared identical, rapid larval evolution has taken place through selection (Raimondi 1992): Salton Sea cyprids are unpigmented (cyprids from coastal populations in Mission Bay, near San Diego, are green-brown), Salton Sea nauplii take longer to become cyprids than do individuals from Mission Bay, and Salton Sea cyprids are larger than those from Mission Bay. These differences persisted after two generations in the laboratory, indicating that they were underlain by genetic variation.

Raimondi proposed several hypotheses for the processes that may have driven selection for these traits: for example, he speculated that pigmentation may have been lost by Salton Sea cyprids because the potential for damage by ultraviolet radiation (harmful to many marine organisms) was much lower in the Sea's highly turbid waters.

Simpson and Hurlbert (1998) examined the effects of high salinity on the growth, mortality, and shell strength of *A. amphitrite* in the Salton Sea: barnacles at higher salinities were shorter and had thicker walls relative to their diameters, potentially increasing their structural stability. They predicted that *A. amphitrite* will begin to show a marked decline in abundance when salinities reach 50 psu, and will become extinct when the salinity becomes 70–80 psu, leading to the interesting situation of the eventual loss of a distinct, albeit relatively new, genetic lineage.

**ATLANTIC** Zullo (1966a) reviewed the biogeographic, historic, and palaeontological evidence for the prior absence of *A. amphitrite* in the Atlantic theatre. *Amphibalanus amphitrite* arrived in England during WWII (Bishop 1947). It also arrived in the Western Atlantic in the mid-twentieth century, likely as a result of the massive increase in global shipping associated with World War II in the early 1940s and the years that followed. It was first collected in the Northwest Atlantic in 1952 both in Bermuda (Henry 1958, as *Balanus amphitrite hawaiiensis*; date from Henry and McLaughlin 1975) and on the Florida west coast (Henry and McLaughlin 1975). It was collected in 1955 in Beaufort, North Carolina (Henry and McLaughlin 1975; date from National Museum of Natural History Invertebrate Zoology (USNM 97625) on-line collection database, retrieved April 2010), and in 1957 in Curacao (Henry and McLaughlin 1975). The record of "late 1940s" in the Western Atlantic in Cohen (2006) appears to be based upon an interpretation of *A. amphitrite* being a post-WWII invasion.

Paul Fofonoff (Smithsonian Environmental Research Center) alerted us to the existence of one specimen of *A. amphitrite* in the Smithsonian Institution (National Museum of Natural History) collected in 1931 by J P Visscher at the Dry Tortugas, Florida Keys, in the Gulf of Mexico (USNM catalog number 155404, record accessed August 2010). While of interest, the date of arrival of *A. amphitrite* in the western Atlantic is not reset as 1931, 21 years before the next record, based upon this one specimen. Visscher was for many years involved in the surveying and collection of fouling organisms from ships' bottoms (e.g., Visscher 1928, and through the 1930s and 1940s: http://siarchives.si.edu/findingaids/FARU7239.htm [accessed August 2010]), and, absent any collection details (the authors of the present are moved by the improbability of Visscher finding a single individual in the wild at the Dry Tortugas), the authors here speculate that the specimen in question may have come from the hull of a visiting vessel.

The fact that it was found to be so widespread (North Carolina, Bermuda, Gulf of Mexico, and in the southern Caribbean off Venezuela) between 1952 and 1957 suggests that study of museum material of barnacled oysters and other shells will reveal earlier records. Indeed, by at least 1956 it was "the most abundant fouling organism in the inter-tidal region of Beaufort, North Carolina" (Costlow and Bookhout 1958). Zullo (1966a) suggested that Hedgpeth's (1950) report of *Balanus amphitrite niveus* from the Port Aransas jetties in Texas referred to *A. amphitrite*, rather than *A. venustus*. Whitten et al. (1950) and Hedgpeth (1950) reported upon the collections made at Port Aransas between 1938 and 1947, but the exact date of collections of *B. a. niveus* was not recorded.

Zullo (1966a: 233) noted that the initial invasion of *A. amphitrite* in the western Atlantic went unnoticed, and that *A. amphitrite* "has often been misidentified as *B. a. niveus*". It is thus possible that the *Balanus amphitrite niveus* [= *Amphibalanus venustus*] of Weiss (1948), in a study of fouling in Biscayne Bay, Miami, on the east coast of Florida, based upon collections commencing in 1942, as well as the "*Balanus amphitrite*" of Moore and Frue (1959, who although referring to their material as *B. amphitrite*, subsumed "all its subspecies together", including *niveus*), based upon collections made in 1952 and later, also in Biscayne Bay, both included the true *A. amphitrite*, as well as *A. venustus*. Moore et al. (1974), in a study of long-term changes in settlement of barnacles in the Miami area, referred to their material as *Balanus amphitrite sensu lato*, and thus may have confounded *A. amphitrite* and *A. venustus*. The same may be true of McDougall's fouling community studies in 1941–1942 at Beaufort, North Carolina, which also reported *Balanus amphitrite niveus* (McDougall 1943). Gittings et al. (1986: 29) review its occurrence as of the 1980s in the Gulf of Mexico.

*Amphibalanus amphitrite* occurs from Cape Hatteras south to Argentina (Orensanz et al. 2002, who review the earlier literature from Patagonia, and who mistakenly note that Newman (1979), rather than Richards (1968), reported it from Plio-Pleistocene sediments off the Argentina shelf). It was first collected on the Atlantic coast of South America in 1940, where de Oliveira (1941) identified it as Darwin's var. *communis* (which was also being confused with *A. venustus*). He described two "varieties" (subspecies) of *A. amphitrite*, *fluminensis* and *aeratus*, both later synonymized with *A. amphitrite* by Henry and McLaughlin (1975). Bastida (1969) reported it from Argentina in 1966. Neves and da Rocha (2008) record it as cryptogenic in Brazil, but it is in fact not native to the Atlantic Ocean. Young (1994) and Farrapeira (2010) provide detailed records for Brazil.

Southward (1986) reported that in Bermuda it was "uncommon, represented by a few large individuals at low tide or sublittoral inshore".

Although generally regarded as having established, reproducing populations only south of Cape Hatteras (Zullo 1966a, 1979), *A. amphitrite* may be one of the many species now moving north along the North American Atlantic coast. Previously absent as a permanent resident of Chesapeake Bay (Kennedy and DiCosimo 1983), it may now be established there (Ruiz et al. 2000), but longer term data, including *in situ* studies on gametogenesis and larval production, will be required to verify this. Although found regularly on panels at Norfolk, Virginia, at the mouth of Chesapeake Bay, between 2000 and 2004 (Fofonoff et al. 2010), it is possible that these individuals represent summer recruits from the south (Costlow and Bookhout (1958) showed that larval life was 10 days or longer, a sufficient length of time for potential recruits to be brought north by coastal currents). It was found earlier, in 1967, at Lynnhaven, Virginia, in Chesapeake Bay (Henry and McLaughlin 1975), and was reported by Van Engel (1972) as occasionally appearing in the lower Chesapeake in the same era as well.

*Amphibalanus amphitrite* occasionally recruits further north to southern New England as well. Verrill et al. (1873) noted that in Massachusetts this species was "found upon the bottoms of ships, but probably does not live long after arriving upon our coast". Zullo (1966a: 234) noted that living individuals were found on pilings on the south shore of Cape Cod in 1962, and suggested that they "probably represented the spat of shipborne individuals carried north from warmer waters" (see also Zullo 1963, 1979: 2, 25). *Amphibalanus amphitrite* appears to be a regular, albeit uncommon, element of Long Island Sound fouling communities by mid to late summer (J. T. Carlton, 1990, Mystic River Estuary, pers. obs.; R. Whitlatch, 2000, pers. comm.).

Henry (1958) noted that *A. amphitrite* co-occurs in Bermuda with *Chthamalus stellatus thompsoni*; Henry and McLaughlin (1975) note its co-occurrence with *Chthamalus fragilis, Amphibalanus eburneus*, *A. improvisus*, *A. subalbidus*, and *B. crenatus* at various stations from Virginia to Brazil. Ross (1962: 14), in a paper on Pacific barnacles, reported on his observations, of an unstated date, of *A. amphitrite* in Florida, where he noted that it occurred between "mean sea level and 0.5–1 fathom" [1.8 m]. On the Atlantic coast of Florida Ross described it as a "common fouling organism in competition" with *A. improvisus*, *A. eburneus*, and *A. venustus*; on the Gulf coast of Florida he found it to be rare in "unprotected, open-sea habitats". Zullo and Lang (1978) reported that in South Carolina *A. amphitrite* is "common in middle and lower intertidal zone on rocks and pilings. Less abundant at immediate subtidal zone on rocks and pilings". Farrapeira (2008) examined the distribution of *A. amphitrite*, *A. improvisus*, and *A. reticulatus* along an estuarine mangrove gradient in Brazil, with all three species occurring in both polyhaline and mesohaline portions of the system. Spivak et al. (1975), Calcagno et al. (1997, 1998) and Lopez Gappa et al. (1997) investigated growth, production, and population dynamics of *A. amphitrite* in Argentina.

Lang (1979) reported that "at North Inlet [near Georgetown, South Carolina] *A. amphitrite* is a common intertidal species, generally situated between upper intertidal *Chthamalus fragilis* and lower intertidal *A. eburneus* on wood pilings". Whether *C. fragilis* extended into the midlittoral before the arrival of *A. amphitrite* has not been investigated.

Boudreaux et al. (2009) asked whether the introduction of *A. amphitrite* on the Atlantic coast of Florida had a negative impact on the abundance of the native oyster *Crassostrea virginica*. They found that a general increase since prehistoric times (as documented by barnacle abundance in native American shell middens) in barnacle numbers that included both the native *Amphibalanus eburneus* and *A. amphitrite* reduces oyster settlement, but that there was no species-specific difference relative to reducing growth and survival of oysters.

## 4.3 *Amphibalanus eburneus (Gould, 1841)*

**PACIFIC** Matsui et al. (1964: 142) predicted that this barnacle would "eventually become established in west American waters"; in an addendum in the same paper, Newman (1964) was then able to report its collection in April 1964 at the Pacific end of the Panama Canal, at Balboa. Henry and McLaughlin (1975) extended the first collection records in the Eastern Pacific to 1959 (Guaymas, Mexico, in the Gulf of California) and 1963 (Manzanillo Lagoon, West Mexico); all of these records, in concert, suggest introduction in the years following WWII. That *A. eburneus*, a species native to the Northwestern Atlantic Ocean, had been arriving in the Eastern Pacific is indicated by its presence on a ship's bottom in dry dock at Hunter's Point, about 1938, in San Francisco Bay (Carlton 1979b). Now well-established on the piers at Mazatlan and in nearby lagoons (Henry and McLaughlin 1975; Paez-Osuna et al. 1999; Salgado-Barragan and Hendrickx 2002), it remained unreported outside of Mexico until 2000, when a well-established population was discovered in Colorado Lagoon, in Long Beach, in southern California (Cohen et al. 2005).

## *4.4 Amphibalanus improvisus* (Darwin, 1854)

**PACIFIC** This Northwest Atlantic barnacle is one of the earliest documented invasions of any marine species on the Pacific coast of both North and South America. It was collected in 1853 in San Francisco Bay (Carlton and Zullo 1969), only a few years after the start (1849) of the "Gold Rush" that brought hundreds of ships from the Atlantic Ocean (and elsewhere) to California. These ships were often abandoned, providing a striking opportunity for colonization by Atlantic fouling organisms. Mooi et al. (2007) indicated that *A. improvisus* was introduced with commercial oyster shipments from the Atlantic, but these did not commence until after 1869. Zullo and Miller (1986) argued for its Western Atlantic origin, noting the lack of verified fossils in the Eastern Atlantic and Mediterranean.

On the North American Pacific coast, *A. improvisus* occurs from central California to British Columbia (Carlton 1979a). There are occasional records of it in southern California as far south as San Diego Bay (Carlton 1979a; Newman 1979), but these are sporadic and do not represent established populations, perhaps due to the seasonal and arid nature of estuarine conditions there (Newman 1979). It resumes established populations from the Gulf of California (1889 collections) to Peru (1926 collections: Henry and McLaughlin 1975), with Darwin (1854) reporting material from Guayaquil, Ecuador and western Colombia based upon specimens in the Cuming and British Museum collections, which may date from the earlier 1800s. The port of Guayaquil was founded in 1535 by the Spanish, and thus it is likely that *A. improvisus* became established in the Pacific Ocean long before Gold Rush ships brought it in the 1850s to San Francisco.

In passing, note that *A. improvisus* was not first described from hull fouling, as stated by Hosie and Ahyong (2008); no type or type locality was designated by Darwin. Newman (1967) documented the distributional ecology and osmoregulatory physiology of this species in San Francisco Bay. *Amphibalanus improvisus* has been found in the freshwater Delta Mendota irrigation canals in central California (Zullo et al. 1972), in concert with reports of adult *A. improvisus* in fresh water in other parts of the world (Carlton 1979a). It occurs at the mouth of the Columbia River, in Astoria, Oregon, on the native crayfish *Pacifastacus trowbridgii* (Miller 1965). Nonetheless, it is apparently not as well adapted to freshwater as *Amphibalanus subalbidus* (Poirrier and Partridge 1979; Dineen and Hines 1992).

## *4.5 Amphibalanus reticulatus* (Utinomi, 1967)

This Indo-West Pacific species had been confounded with *Amphibalanus amphitrite* by Darwin (1854), and had subsequently been reported under that name as well as other names (such as *communis* and *variegatus* in the *amphitrite*-series) (Henry and McLaughlin 1975). It was distinguished as a distinct taxon (a *nomen novum*) with a type locality of Japan, by Utinomi (1967). Its specific origins in the broad Indo-Pacific theatre remain obscure, as it is likely to have been widely dispersed by ships within the Indian and Pacific Oceans centuries before the first barnacle collections were made by naturalists and professional zoologists.

**PACIFIC** *Amphibalanus reticulatus* was first collected in the Northeastern Pacific in 1984 at Mazatlan, in Western Mexico (Laguna 1985, 1990). Gomez-Daglio and Gonzalez (2006) report it from La Paz, in the Gulf of California, based upon 1998–1999 collections, on intertidal rocks and on *Megabalanus peninsularis*. It was next collected in 2000 at the Pacific entrance to the Panama Canal (Cohen 2006). Gomez-Daglio and Gonzalez (2006) report it from Ecuador, but Pitombo and Ross (2002: 107, Figure 3.) listed it as questionable, and its presence in Ecuador is not verified.

**ATLANTIC** Determination of early records in the western Atlantic awaited its recognition as a distinct species in 1967. In hindsight, the earliest collections appear to be from Puerto Rico in 1956 (Henry and McLaughlin 1975), with more widespread recognition not commencing until the 1970s, after the name *reticulatus* was proposed (Moore et al. 1974; Southward 1975; Zullo and Lang 1978; Spivey 1979: 506–507).

In concert with the mid-1950s record in Puerto Rico, Spivey (1979) suggested that the *Balanus amphitrite* reported in the 1950s from Louisiana oil platforms by Gunter and Geyer (1955) may have been *Amphibalanus reticulatus*, based upon subsequent studies in 1972 by Thomas (1975) of the same platforms, where only *A. reticulatus* was found. While Gunter and Geyer's material may have been *A. reticulatus*, it may also be that *A. amphitrite* was replaced on the platforms by *A. reticulatus*.

*Amphibalanus reticulatus* was found in 1962 "on a ship in the harbor at Charleston, South Carolina" (Moore et al. 1974, based upon an unpublished record by D. P. Henry). Gittings et al. (1986) report this record as simply the "east coast of the United States", also based upon an unpublished communication from D. P. Henry (Britton and Morton 1989, report this date as the "first Western Atlantic record", a mis-interpretation of the statement in Gittings et al. 1986, that it was first found on the *east coast* of the United States in 1962). While it is tempting to take 1962 as the first North American Atlantic coast record, the provenance of the ship is not reported, and thus if it became fouled in South Carolina is not known. Rather, the first clear record appears to be that of Moore et al. (1974) who found it in February 1969 on experimental panels at Miami Beach, on the east coast of Florida. In the Gulf of Mexico, the first records are 1972, on pilings and platforms in Louisiana (Thomas 1975; Spivey 1979) and in 1976 in Apalachee Bay, Florida (Spivey 1979) (the report of a Gulf of Mexico record in 1952 in Cohen 2006, appears to be a typographical error for 1972). Gittings et al. (1986) review its 1980s-era distribution in the Gulf of Mexico. Spivey (1976) reported it from the Caribbean end of the Panama Canal, based on 1974 material. No clear picture of the direction or timing of spread can be deduced from these records.

In South America, it was found at Maraca Bay, Trinidad in 1965 (Henry and McLaughlin 1975) and Young and Campos (1988) reported the first material from Atlantic Colombia, based on 1986 collections on vermetid shells. *Amphibalanus reticulatus* has apparently been expanding south since its first colonization along the Colombian-Trinidad shores. Absent from northeast Brazil as of 1984 (Young 1995), it was found sequentially, north to south, at Recife (Pernambuco) in 1990 (Farrapeira-Assunção 1990), at Todos os Santos Bay (Bahia) in 1992 (Young 1995), in Rio de Janeiro in 1996 (Ferreira et al. 2009: 469) or 1997 (Neves and da Rocha 2008: 629, based upon a pers. comm. to those authors in 2005 by FBP) and in 2004 in Parangua Bay (Neves et al. 2007; Neves and da Rocha 2008). The report by Southward and Newman (1977) of its earlier presence in northeast Brazil thus may be in error. Farrapeira (2010) reviews its distribution in northeast Brazil.

Thomas 1975 (*fide* Spivey 1979) reported that *A. reticulatus* was “the most abundant barnacle and dominant fouling species found on submerged platform structures” on the Louisiana coast, “where *B. eburneus* and *B. improvisus* also occur”. Henry and McLaughlin (1975: 195) note that *A. reticulatus* “appears, at least in some parts of south Florida, to be replacing *B. a. amphitrite*; whereas, in Japanese waters the reverse situation has occurred” (citing Utinomi 1967, 1970, “Prior to World War II, *B. reticulatus* was more prevalent than *B. a. amphitrite* in Japanese bays and harbours but now is apparently not found on the Japan Sea coast; it occurs in stenohaline habitats only.”). Farrapeira (2010) suggests that *A. reticulatus* has displaced *A. amphitrite* in northeast Brazil, in marine and estuarine environments. Zabin (2009) experimentally demonstrated that the Caribbean barnacle *Chthamalus proteus*, introduced in the 1990s to the Hawaiian Islands, can outcompete *A. reticulatus* (itself earlier introduced to Hawaii) via substrate pre-emption in a zone of overlap.

In the southern United States, Gittings et al. (1986) describe the distributional ecology as follows: “In the clearer, warmer water areas of the Gulf of Mexico off Mexico and Florida, *B. a. amphitrite* dominates the fouling community. Between Panama City, Florida and Port Aransas, Texas, *B. reticulatus* may largely exclude *B. a. amphitrite*. In the northwestern Gulf, *B. improvisus* dominates the nearshore fouling assemblage during the coldest portion of the year (January to March), while *B. reticulatus* dominates during the summer and fall". Similarly, Britton and Morton (1989) described *A. reticulatus* in the southern U.S.: "Since the mid-1970s, it has attained a position of dominance in the clear-water biofouling communities attached to offshore drilling platforms from central Louisiana to eastern Texas (George and Thomas 1979). Within its natural range, *B. reticulatus* is an intertidal species on natural rocky shores, but it has apparently encountered difficulty in becoming established on the unnatural rock substrata along northern Gulf shores".

Ferreira et al. (2009) report densities on hard substrates in Sepetiba Bay (state of Rio de Janeiro), Brazil up to 4,410/m².

## *4.6 Amphibalanus subalbidus* (Henry, 1974)

**PACIFIC** The Western Atlantic *Amphibalanus subalbidus* was discovered in 1989 in an arm of the Colorado River Delta, including the Rio Hardy and a normally dry lake known as Laguna Salada (Van Syoc 1992) at the head of the Gulf of California. Laguna Salada floods during exceptionally heavy rainfall, such as that of the El Nino of 1983–1984, especially when the rainfall coincides with high tides in the Gulf. The lake subsequently dries out exposing previously drowned chaparral; it was on such an occasion the trunks and branches were found to be partially encrusted with barnacles. Van Syoc (1992) suggested that the Mio-Pliocene species *Balanus canabus* Zullo and Buising, 1989, from the proto-Colorado River Delta, was a junior synonym of *Amphibalanus subalbidus* and that the population in Laguna Salada represented a natural relict Pacific population of this otherwise Atlantic species. However, *B. canabus* can be morphologically distinguished from *A. subalbidus* and therefore Pitombo (2004), in his revision of the Balaninae, made them subspecies of *Amphibalanus*; *A. s. subalbidus* and *A. s. canabus* respectively. The extant Mexican Pacific population of *A. subalbidus* is here regarded as introduced, probably from the Gulf of Mexico, perhaps in connection with shrimp mariculture operations directly across the Delta in Sonora. *Amphibalanus subalbidus* ranges from Chesapeake Bay (Henry and McLaughlin 1975) to the Gulf of Mexico (Gittings et al. 1986; Gittings 2009) and Trinidad (Henry 1974), with introduced populations in Brazil (below). It is a distinctive estuarine, oligohaline species (Poirrier and Partridge 1979; Dineen and Hines 1992), although not recognized as such until fairly late.

**ATLANTIC** While Southward and Newman (1977) did not list *A. subalbidus* for northeast Brazil, Young (1994) subsequently listed it for Paraiba State, "found rarely in the Rio Paraiba do Norte estuary attached to small rocks". The collection date is considered to be 1992 or earlier (based on Young's having submitted his manuscript in January 1993). Farrapeira et al. (2007) note collections from 2004 to 2006 in the Port of Recife, Pernambuco. Farrapeira (2010) proposed that *Amphibalanus subalbidus* was introduced to Brazil, a designation with which the present study concurs.

### *4.7 Fistulobalanus pallidus* (Darwin, 1854)

**ATLANTIC** The history of this Atlantic species (with outlier, and probably introduced, populations in the Indian Ocean) remains uncertain, due to long-term confusion with other amphibalanine species and its late recognition as a full species (Henry and McLaughlin 1975). Whether native to the Eastern or Western Atlantic remains unknown (Zullo 1984), and it is tempting to suggest that this species may owe its amphiatlantic distribution to the Atlantic slave-trade era, which peaked in the 1700s and 1800s. While the earliest records appear to be 1948 collections from Surinam (Henry and McLaughlin 1975), exploration of older barnacle-covered substrates in museums, such as oysters, may uncover older material. Henry and McLaughlin (1975) report specimens from Venezuela (1963) and French Guiana (no date, but collected by H. G. Stubbings, and thus likely in the 1940s–1960s era). It is not reported from the Gulf of Mexico (Gittings et al. 1986; Britton and Morton 1989; Gittings 2009). Its present range in the Western Atlantic is the Caribbean to Suriname; the record of *F. pallidus* from Brazil (Lacombe and Monteiro 1974) is in fact *F. citerosum* (Young 1994).

This species is here tentatively regarded as cryptogenic in the American fauna (see also Orensanz et al. 2002).

**PACIFIC** *Fistulobalanus pallidus* was found in the Panama Canal in the Miraflores Locks on the Pacific Ocean side in 1972 (Jones and Dawson 1973) and in 1974 (Spivey 1976). Whether it occurs at present in the Canal is not known.

## 5 Balanomorpha: Balanidae: Balaninae

### *5.1 Balanus glandula* Darwin, 1854

**ATLANTIC** The well-known Northeastern Pacific *Balanus glandula* is thought to have appeared in the late 1960s or early 1970s in Argentina (the crediting of E. Spivak for its occurrence in Rio de Janeiro, Brazil, by Newman and Ross (1976) being a *lapsus*), where exposed rocky intertidal shores were notable for the (former) absence of intertidal barnacles (Spivak and L'Hoste 1976; Bastida et al. 1980). The first date of actual identified specimens in hand appears to be 1974 (Bastida et al. 1980); the date "1970" as a "first record" in Schwindt (2007: Figure 5), citing Spivak and L'Hoste (1976) as the source, is an estimate and not based upon actual specimens collected in 1970 (E. Schwindt, pers. comm. 2010). It subsequently appeared in Japan (Kado 2003) and in South Africa (Simon-Blecher et al. 2008).

*Balanus glandula* now occurs along the entire Argentinean coastline, from San Clemente del Tuyu in the north to Rio Grande in the south (Schwindt 2007), yielding an estimated rate of spread of 244 km/year between 1974 and 2004. Densities reach nearly 20,000 barnacles/m², twice the densities reported on the North American

Pacific coast (Elias and Vallarino 2001). A number of workers have examined abundance (larval and adult), recruitment patterns, population dynamics, and observed or predicted changes in community structure in Argentina (Vallarino and Elias 1997; Rico et al. 2001; Elias and Vallarino 2001; Hoffmeyer 2004; Rico and Gappa 2006; Bertness et al. 2006; Hidalgo et al. 2007; Penchaszadeh et al. 2007; Schwindt 2007; Schwindt et al. 2009; Savoya and Schwindt 2010).

It appears that in the Mar del Plata region, *B. glandula* has displaced the native mussel *Brachidontes rodriguezi* on the exposed coast in the high intertidal, and *Amphibalanus amphitrite*, which appeared only a few years earlier in Argentina, from sheltered port areas (Vallarino and Elias 1997; Elias and Vallarino 2001). At Puntas Pardelas, densities of the native snail *Siphonaria lessoni* have decreased significantly; *Siphonaria* "dominated" upper midlittoral shores in the 1960s, where *B. glandula* is now abundant (Cuevas et al. 2006). Predators include the carcinophagous Olrog's gull (*Larus atlanticus*) (Delhey et al. 2001) and the seastar *Anasterias minuta* (Gil and Zaixso 2008).

Geller et al. (2008) established, using molecular markers, that the Argentinean populations came from California (as opposed to a new invasion of *B. glandula* in Japan that came from the Alaska/Puget Sound region).

## *5.2 Balanus trigonus* (Darwin, 1854)

**ATLANTIC** Werner (1967) and Zullo (1992a) reviewed the history of this Pacific species in the Atlantic basin, where it now occurs from North Carolina (Zullo 1992a) to Argentina (Spivak et al. 1975; Young 1994) and abundantly throughout the Gulf of Mexico (Gittings 1985); Farrapeira (2010) reviews its distribution in northeast Brazil. Although in retrospect the historical record is now reasonably clear, the invasion of *B. trigonus* into the Atlantic illustrates the challenges of reconstructing the history of many potentially ship-borne species prior to the 1900s. The chronology of Atlantic collections of *B. trigonus* reported in Werner's and Zullo's papers and figures are corrected and expanded here (Table 5). *Balanus trigonus*, a distinctive and easily recognized species, was collected no later than 1864 in southern Brazil by Müller (1867, 1868) who, in a pattern characteristic of the nomenclatural history of many alien species (Carlton 2009), inadvertently re-named it as a new taxon (*Balanus armatus*). Müller (1867) questioned whether his new species was different from *B. trigonus*, but felt compelled to describe it as new, in part because *B. trigonus* was previously unknown from the Atlantic.

It was next found in 1879 on the hull of a vessel arriving in Massachusetts from the West Indies (Pilsbry 1916; Zullo 1992a, mistook this report as possibly applying to a vessel from the Pacific Ocean, noting that the oysters (*Ostrea folium*) reported on the ship's hull was a Pacific species: however, in Pilsbry's time, that name was used for the native Caribbean oyster, *Dendostrea frons*). Henry (1954) reported it from the Gulf of Mexico, leading Zullo (1992a) to use and plot that date in his paper for that region. However, Henry's record was based upon collections made at *Albatross* Station 2411 in 1885, at a depth of 49 m, 88.5 km off of the west coast

**Table 5** Records of *Balanus trigonus* in the Atlantic Ocean (excluding the Mediterranean Sea). National Museum of Natural History invertebrate zoology (USNM catalogue numbers) on-line collection database retrieved April 2010

| Collection date | Location | Reference and notes |
|---|---|---|
| 1864 | Brazil: Desterro (now Florianópolis), Santa Catarina Island | Müller (1867, *Balanus armatus* n.sp. = *B. trigonus*); Müller (1868, the translation); Müller paper is signed February 1865, and we thus take 1864 as the latest possible date of collections |
| 1879 | West Indies | Pilsbry (1916): USNM 21550, specimens from hull a whaling ship returning from the West Indies |
| 1885 | Gulf of Mexico: West Florida Shelf | USNM 79267: *Albatross* station 2411, depth 49 m, 88.5 km west of Fort Myers, Florida (18 March 1885) |
| 1887 | Azores | Gruvel (1920), *fide* Zullo (1992) |
| 1897 | Brazil: Rio Grande do Sul | USNM 59192 |
| <1897 | Brazil: Rio de Janeiro | Weltner (1897); labels bear no collection date (see text) |
| <1897 | West Africa (Guinea) | Weltner (1897) |
| <1897 | Madeira | Weltner (1897); labels bear no collection date (see text) |
| <1897 | Delaware: Delaware River | Weltner (1897); labels bear no collection date (see text) |
| <1905 | West Africa (Congo: Loango) | Gruvel (1905) |
| 1909 | West Africa (Mauritania) | Gruvel (1912) *fide* Zullo (1992) |
| 1909 | West Africa (Angola) | Gruvel (1912) *fide* Zullo (1992) |
| 1935 | Colombia: Gorgona Is. | USNM 85966 (*Velero III* Allan Hancock Expedition) |
| 1936 | Venezuela: several locations | Nilsson-Cantell (1939) *fide* Werner 1967 |
| 1936? | Colombia: Bahia de Cartagna to La Guajira | Nilsson-Cantell (1939) *fide* Young and Campos 1988 |
| 1939 | Colombia: Bahia Honda | USNM 85956; Cornwall (1958:. 83, as "Batia Columbia") |
| 1939 | Venezuela: Coche and Cubagua Islands | USNM 85954, 95953 (*Velero III* Allan Hancock Expedition) |
| 1961 | Florida: Miami | Moore and McPherson (1963) |
| 1961 | North Carolina: off Core Banks | Williams et al. (1964) 33 km east of Cape Lookout, 31–36 m; in a bed of scallops |
| 1963 | Guyana (British Guiana), French Guiana, Brazil | Werner (1967), *R/V Oregon* Cruise 84 |
| 1966–1967 | Panama: Caribbean coast: Limon Bay | Bayer et al. (1970) |
| <1967 | Jamaica | I. M. Goodbody, pers. comm. to W. E. Werner (Werner 1967) |
| 1971 | Panama, Caribbean coast: Galeta | Henry and McLaughlin (1975: 167, at *A. venustus)* |

(continued)

**Table 5** (continued)

| Collection date | Location | Reference and notes |
|---|---|---|
| 1974 | Panama: Caribbean coast: Manzanillo Bay at Fort Randolph | Spivey (1976: 48) |
| 1977 | South Carolina | USNM 174799 and other lots, South Atlantic Benchmark Program (BLM/MMS) |
| 1980 | Georgia | USNM 190132: BLM/MMS collections |
| 1987 | Mississippi | USNM 1009464 |

of Florida (D. P. Henry, pers. comm. to W. E. Werner in 1967). Zullo (1992a) states that Henry (1954) "reported it from the carapace of a deep water crab in the Gulf of Mexico", but this is a *lapsus*, as no such statement appears in Henry's paper; crabs, however, were collected at that *Albatross* station (Rathbun 1918).

Gruvel (1920) reported *B. trigonus* from the Azores based upon 1887 material. Weltner (1897) next reported specimens from Brazil (Rio de Janeiro), Madeira, West Africa (Guinea), and Delaware. The Delaware material was collected along with *Amphibalanus improvisus* on mussel (*Mytilus*) shells (Weltner 1897); no further details are available, and *B. trigonus* has not subsequently been reported as established in the Delaware or Chesapeake regions. The specimen labels of the material from Rio de Janeiro, Guinea, and Delaware in the Berlin Museum do not have collection dates (C. O. Coleman, email correspondence, January and July 2010), and thus these collections can only be interpreted as being no later than 1897. However, USNM material (59192, collection data base accessed April 2010) from Rio Grande do Sul, Brazil, was collected in 1897.

*Balanus trigonus* was thus detected between the 1860s and 1890s across much of the North and South Atlantic Oceans, suggestive of an introduction no later than the 1850s followed by fairly rapid acquisition and entrainment in Atlantic ship fouling communities. Zullo (1992a) noted that *B. trigonus* arrived in the Atlantic prior to the opening of either the Suez Canal (1869) or the Panama Canal (1914). Zullo suggested that *B. trigonus* had first colonized the South Atlantic (via the Capes of Cape Horn or Good Hope), and was then dispersed by the 1880s into northern waters by New England and European whalers (accounting in part for its appearance at the Azores and Madeira).

Three lines of additional evidence suggest that *B. trigonus* is an introduction to the Atlantic Ocean: (1) It is present in the fossil record of the Pacific, but absent from Atlantic fossil assemblages (Zullo 1992a), (2) Zullo (1992a) noted that *B. trigonus* is commonly associated with *Megabalanus tulipiformis* and *Perforatus perforatus* in the Mediterranean and on the African Atlantic coast, and with *Amphibalanus venustus* and *Megabalanus antillensis* in the Caribbean and western Atlantic, and that Darwin (1854) listed numerous Atlantic basin localities for these species that now support populations of *B. trigonus* as well, but did not find it, and (3) Darwin (1854) examined many collections taken from ships' hulls around the

Atlantic basin, and *B. trigonus*, a conspicuous and easily recognized species, was absent in all of the material available to him. By 1879, however, it was being taken from vessels coming out of the West Indies (Pilsbry 1916), and it is otherwise a well-known ship fouling organism (Pilsbry 1916; Bishop 1947; WHOI 1952; Millard 1952; Skerman 1960; Relini 1968, see also additional records in Table 2).

Starting in the 1960s *B. trigonus* began to be reported from the southeast Atlantic coast of the United States (Table 5). Zullo (1992a) suggested that this apparently late appearance "may be related to the lack of major southern ports where the salinities are high enough to allow colonization by *B. trigonus*". He further noted that in the 1960s *Balanus calidus* was abundant on the South and North Carolina shelves, but by the 1970s (Table 5) and 1980s, in numerous federal government collections of barnacles from the inner to outer shelves, "*B. trigonus* occurred in high densities on all types of substrata ... (but) *B. calidus* was found only rarely, and only empty shells were observed". Zullo suggested that *B. trigonus* may be "extending its range along the Atlantic coast at the expense of *B. calidus*", but also suggested that the decrease in *B. calidus* may simply be fluctuations in its population density. This study further suggests that it may be that yet to be determined environmental conditions were changing along the southeast Atlantic coast in the 1970s and 1980s that favoured *B. trigonus* over *B. calidus*, rather than the two species undergoing competition. However, if the arrival of *B. trigonus* on the southeast coast was due to changes in the nearshore ocean (that also led to the decrease of *B. calidus*), then it could be expected that other members of the marine biota would be decreasing or increasing as well in the same era, and a search of the literature for similar phenomena amongst other taxa (plant or animal) in this region would be of interest in this regard. It is tempting to suggest that the warm-water *B. trigonus* was responding to increasingly warmer temperatures in the twentieth century along the American Atlantic coast, but *B. calidus* is also a warm-water species and so would not be expected to have declined due to increased ocean temperatures.

*Balanus trigonus* is regularly carried north of Cape Hatteras on sea turtles. In the summer *B. trigonus* occurs as far north as Cape Cod, arriving on specimens of *Chelonibia* and *Platylepas* attached to marine turtles (Zullo and Bleakney 1966). Indeed, the presence of *B. trigonus* on about 10% of immature loggerhead turtles has been used to corroborate the northward movement of turtles into Chesapeake Bay, based on the absence of *B. trigonus* north of Cape Hatteras, and reconstructed from ${}_{18}$O and ${}_{13}$C profiles from barnacle shells (Killingley and Lutcavage 1983).

*Balanus trigonus* is now common in the open ocean off the southeast coast (Werner 1967; Williams et al. 1984; Zullo 1992a). While open ocean subtidal invasions are known around the world (Carlton 2002; Preisler et al. 2009), they are less frequently recognized in part because of the assumption that invasions are generally restricted to ports and harbours. Williams et al. (1984) found it to be the only barnacle settling on experimental panels in 27–30 m depth near Beaufort, North Carolina. In the adjacent rock outcrop community *B. trigonus* (averaging 409 barnacles per $m^2$) and the octocoral *Titanideum frauenfeldii* were the most common species. The sea urchin *Arbacia punctulata* appeared to be the major predator on *B. trigonus*; summer sediment scour further contributed to barnacle mortality.

Gittings et al. (1986) noted that "in the Gulf of Mexico it is now widespread in both turbid and clear waters, although it is seldom the principal fouler of manmade structures in turbid waters. In clear waters off the southwestern coast of Florida, it may also be the dominant biofouling species". Spivak et al. (1975) reported on aspects of its biology and ecology in Argentina; Garcia and Moreno (1998) studied the recruitment, growth, and mortality of *B. trigonus* in Colombia.

### *5.3 Balanus calidus* Pilsbry, 1916 *and Balanus spongicola* Brown, 1844

**PACIFIC** *Balanus calidus* occurs in the Western Atlantic Ocean from North Carolina to the West Indies, including the Gulf of Mexico (Newman and Ross 1976; Zullo 1979). Spivey (1979: 46) reported a population at the Pacific end of the Panama Canal, "in the lower (seaward) end of the lower east chamber of Miraflores Locks, 12 m below minimum water level", in 1974 (as discussed below, it is not treated here as an established invasion of the Canal, pending more modern-day records). Zullo (1986: 60, 1991: 182, 189) next reported living specimens of *B. calidus* from the Galapagos Islands, at three stations, intertidally and subtidally, based upon 1964 collections. He also tentatively referred one Quaternary-aged shell (without opercular valves) to *B. calidus*, from limestone on Isla Santa Cruz (Zullo 1986), but later simply stated that *B. calidus* occurred in the fossil record on the Islands (Zullo 1991). Transport through the Panama Canal (as evidenced by its earlier report in Miraflores Locks) by vessels, and in particular by recreational boats visiting the Galapagos (Zullo 1991) could have introduced *B. calidus* to the Islands.

Laguna (1985), however, questioned Spivey's record of *B. calidus* from the Panama Canal, suggesting that it was "probably *B. cf. ? spongicola*". *Balanus calidus* is considered here as cryptogenic on the Galapagos Islands, and further note that genetic studies may be required to determine the species involved.

## 6 Balanomorpha: Balanidae: Megabalaninae

### *6.1 Megabalanus coccopoma* (Darwin, 1854)

**ATLANTIC** This barnacle, native to the tropical Eastern Pacific (Newman and McConnaughey 1987), and recently appearing in Japan and Australia (Yamaguchi et al. 2009), was first recorded on the South American Atlantic coast in 1974 on the southern coast of Brazil in Guanabara Bay at Rio de Janeiro (Lacombe and Monteiro 1974). Young (1994) did not find *M. coccopoma* in the earlier collections of Luederwaldt (1929) in São Paulo state (São Sebastião), and concluded that its arrival in Brazil must have occurred after Luederwaldt's work.

*Megabalanus coccopoma* is now commonly found on exposed rocky shores of southeast Brazil, from Espirito Santo to Rio Grande do Sul States (Young 1994). Silveira et al. (2006) reported it on offshore structures off the north coast of Brazil, in Rio Grande do Norte state, in 2004. Farrapeira (2010) reviews its distribution in northeast Brazil.

Perreault (2004) reported that it had arrived in Louisiana, in the northern Gulf of Mexico, by 2001; Celis et al. (2007) record its presence in Mexico as of 2005. It subsequently appeared in South Carolina in 2005 (Knott 2006), and was then detected in 2006 both to the south in Georgia (Gilg et al. 2010) and to the north in North Carolina (Knott 2006). Its movement north in the beginning of the twenty-first century is in concert with the northward movement, apparently climate-mediated, of a number of other marine invertebrates, as discussed below.

Newman and McConnaughey (1987) reported the temporary colonization of the San Diego, California, area by *M. coccopoma* following the El Nino-Southern Oscillation (ENSO) event of 1982–1983. Similarly, they note that *Megabalanus californicus* was collected well north of its usual northern limit (Monterey Bay, California, at 37° N) in 1939 (near Humboldt Bay, at 41° N; Zullo 1968) and in 1980–1981 on Cordell Bank (at 38° N), the latter records broadly also associated with ENSO eras. Of interest is an earlier report by Cornwall (1955: 2) of a ship from California with *Megabalanus californicus* on its hull which arrived in 1925 in British Columbia. The ship "stood for some time off William Head, Vancouver Island ... After a few weeks young specimens of [*M. californicus*] were found growing on the rocks at Weir's Beach, but they did not persist".

Silveira et al. (2006) state that in Brazil "it is competing in the southeast with *M. tintinnabulum*, which has a lower population density than" *M. coccopoma*.

## 6.2 *Megabalanus tintinnabulum* (Linnaeus, 1758)

**ATLANTIC** The global historical biogeography of this barnacle, which has a tortured taxonomic history, remains to be worked out, requiring a synthesis of the fossil record, historical collections, and genetic studies. It occurs in the Western Atlantic from at least Florida to Uruguay (Henry and McLaughlin 1975: 61; Young 1994), and is common throughout the northern Gulf of Mexico (Gittings et al. 1986). The genus *Megabalanus*, including *M. tintinnabulum*, may originate in the Pacific, but even after monographic treatment, Henry and McLaughlin (1975) could do no better than describe the distribution of *M. tintinnabulum* as "worldwide". Laguna's (1985) report of it from central West Mexico has not been confirmed (Pitombo and Ross 2002; Pitombo 2010), and subsequently he himself (Laguna 1990) does not mention the species. In referring to both *M. tintinnabulum sensu stricto* and its "varieties" (some now considered synonyms and some now regarded as "good" species), Darwin (1854) noted that this barnacle was one of the most common ship fouling organisms, and suspected that it owed at least parts of its distribution to the history of shipping: "It is attached in wonderful numbers to ships' bottoms arriving at our ports, from West Africa, the West Indies, the East Indian Archipelago, and China" (Darwin 1854: 200). It was already present in the Atlantic by Darwin's time, but this reveals little of its history, as European vessels had been returning from the Pacific for the previous 300 years. It has been reported from the Tertiary and Quaternary of Europe and Atlantic South America (Newman and Ross 1976), but these reports either pre-date modern revisionary work of the group (Henry and McLaughlin 1986), or are often based only upon shells (Tavora et al. 2005) and not opercular valves.

Pilsbry (1916) described Western Atlantic populations as *Balanus tintinnabulum antillensis*, with a distribution from the West Indies to Rio Janeiro (although he was uncertain about assigning specimens from Brazil to *antillensis*). Appearing in the literature occasionally as *Megabalanus antillensis*, it was synonymized with *M. tintinnabulum* by Henry and McLaughlin (1986), a synonymy that is supported here (its retention as a full species in Pitombo (2004) was a *lapsus*). Young (1995) considered it introduced to the "Southwestern Atlantic"; Ferreira et al. (2009) treated it as a cryptogenic species in Brazil.

While the authors here hypothesize that *Megabalanus tintinnabulum* will be found to be an introduction from the Indo-West Pacific, perhaps as early as the 1500s, into the Atlantic Ocean, and that fossils previously assigned to *M. tintinnabulum sensu stricto* will be found to be members of other taxa (a situation reminiscent of earlier erroneous reports of *Balanus trigonus* as fossil in the Atlantic theatre), pending genetic work from around the world, it is also regarded as cryptogenic in the Atlantic Ocean.

## 7 Balanomorpha: Balanidae: Archaeobalanidae

### *7.1 Striatobalanus amaryllis* (Darwin, 1854)

**ATLANTIC** This species, like *Amphibalanus reticulatus*, appears to have a history of spreading south along the South American coast. Young (1989) reported (as *Chirona (Striatobalanus) amaryllis*) finding this Indo-Pacific barnacle intertidally in Piaui State, Brazil in 1982 (the date of "1987" as the first record in Brazil, as reported by Neves et al. 2007and Neves and da Rocha 2008 appears to be in error, as Young 1989 specifically notes August, 1982, as the date of his first collection of this species in Brazil). Farrapeira-Assunção (1990) next reported it in 1990 in Pernambuco State, Brazil, and Young (1995) found it in 1992 in Bahia State (or 1993 at Ilha do Medo, *fide* Neves et al. 2005). Neves et al. (2005, 2007) extend the range south to Paranagua Bay, Brazil, based upon material collected in 2004. Further collections (F. Pitombo) made on natural rocky shores on Paranagua Bay demonstrate that *S. amaryllis* continues to spread to natural substrata. Specimens of *S. amaryllis* were also found (F. Pitombo, unpubl.) on an oil platform docked in Rio de Janeiro state. While it is not yet found in this or neighboring states (Espirito Santo and

São Paulo), its presence on platforms sheds light on mechanisms of dispersal and introduction along the Brazilian coast.

Young (1989, 1994) observed that *S. amaryllis* is found intertidally in Brazil, co-occurring with *Megabalanus tintinnabulum*, but is reported as largely subtidal in the Indo-Pacific. Neves and da Rocha (2008) report that it co-occurs in Brazil with *Fistulobalanus citerosum*. Farrapeira (2010) suggests that *S. amaryllis* has replaced the "previous dominant *M. tintinnabulum*" in northeast Brazil in the low intertidal and on reefs with lesser wave exposure.

## 8 Rhizocephala: Sacculinidae

### *8.1 Loxothylacus panopaei* (Gissler, 1884)

**ATLANTIC** The accidental introduction into Chesapeake Bay in the 1950s of the pathogen *Haplosporidium nelsoni* (which causes "MSX" disease in oysters) ironically led to the introduction in the 1960s of this rhizocephalan parasite. Beginning in the 1960s, large number of oysters (*Crassostrea virginica*) were imported into Chesapeake Bay from the Gulf of Mexico (GOM) to replace disease-ridden oyster stocks. These oysters contained sacculinid-infected crabs. In 1964 *Loxothylacus panopaei*, previously known from the Caribbean and Gulf of Mexico, was found infecting the native panopeid crab *Eurypanopeus depressus* (Van Engel et al. 1966) in Chesapeake Bay. The report of *L. panopaei* by Newman in McLaughlin et al. (2005: 369) from Massachusetts in the 1970s, citing Weisbord (1975) is in error; the distributional records in Weisbord refer to the host crabs, not the parasite.

Since the 1990s, the biology and ecology of *Loxothylacus* in *Eurypanopeus* as well as in another native panopeid, *Rhithropanopeus harrisii*, have been examined in Chesapeake Bay (Alvarez et al. 1995; Grosholz and Ruiz 1995; Hines et al. 1997). By 1983, *Loxothylacus* had reached North Carolina (Hines et al. 1997); by 2004 it had arrived in Edgewater, Florida, just north of what was then thought to be the endemic range of this parasite, an average expansion rate of 33 km/year (Kruse and Hare 2007). However, Kruse et al. (2011) have established, using molecular markers, that the east coast of Florida south of Edgewater is occupied by a different species than that known from Chesapeake Bay and the GOM, and that the Chesapeake Bay population did indeed originate from the Gulf of Mexico.

Young (1993) further reported this rhizocephalan to be in Para State in Brazil in the xanthid crab *Panopeus occidentalis*. Farrapeira et al. (2008) recorded it infesting the crab *Aratus pisonii* in Recife, Pernambuco, Brazil in 2006, and concluded that *L. panopaei* was a non-indigenous species, speculating that it was introduced to the Recife area in adult crabs transported in vessel fouling (they noted that the host crab, *A. pisonii*, typically found in mangrove communities, has been found in fouling on coastal vessels in Brazil. Farrapeira (2010) also noted that Davidson et al. (2008b) had found *L. panopaei* in the xanthid crab *Rhithropanopeus* *harrisii* in vessel fouling; however, the derelict vessel in question was a stationary platform). *Loxothylacus panopaei* is eurytopic relative to hosts, and thus acquisition of potentially novel hosts in South America is not surprising. Farrapeira (2010, Table on p.3) scores *L. panopaei* as native, but we take this to be a typographical error given her text discussion. Pending further data, however, on the historical absence of *L. panopaei* in crabs along the Brazilian and northern Atlantic South American coast, and further pending genetic confirmation that it is the northern hemisphere species *L. panopaei*, it is treated here as cryptogenic in South America.

## 9 Intracontinental Range Expansions

### *9.1* Balanidae: *Amphibalanus subalbidus* (Henry, 1974)

**ATLANTIC** Henry and McLaughlin (1975) reported living individuals of *A. subalbidus* found in 1972 in Boston, Massachusetts, on tree branches in the Charles River. There are no records since 1972 north of Maryland (its otherwise northernmost limit), but this may be due to a lack of exploration of estuarine barnacles north of Chesapeake Bay, and confusion with other estuarine amphibalanine species, such as *A. improvisus* and *A. eburneus*; in fact it is more estuarine than *A. improvisus* (Poirrier and Partridge 1979; Dineen and Hines 1992) with which it may co-occur.

### *9.2* Chthamalidae: *Chthamalus fragilis* Darwin, 1854

**ATLANTIC** Most modern literature on this well-known American Atlantic species (Pilsbry 1916; Zullo 1963, 1979; Newman and Ross 1976; Dando and Southward 1980) fails to mention that this species was not known in New England until 1898 (Sumner et al. 1913a: 191, footnote a). Wethey (1984: 184) and Carlton (2002) independently reviewed its curious history north of the mid-Atlantic coast. Commencing in 1898, it was sequentially recognized in the decade that followed as common around southern Cape Cod and on the Massachusetts mainland (Table 6).

**Table 6** Earliest records (1898–1909) of *Chthamalus fragilis* north of Chesapeake Bay

| Date | Location (all in Massachusetts) | Authority |
|---|---|---|
| 1898 | Woods Hole | M. A. Bigelow in Sumner et al. (1913a) |
| 1906 | Woods Hole | Sumner (1909: 374), column 1, bottom |
| 1909 | Woods Hole region: Penzance Point, Nobska Point, Nonamasset Is., Buzzards Bay | Sumner (1909) and Sumner et al. (1913a, b) |
| 1909 | Vineyard Haven | Sumner (1909) |
| 1909 | New Bedford | Sumner (1909) |

A now common species from the north shore of Cape Cod Bay (Zullo 1963; Carlton 2002) and south, it is inconceivable that it would have been overlooked, as Sumner (1909) and Sumner et al. (1913a) argued, by several earlier generations of New England invertebrate zoologists. *Chthamalus* is not mentioned in the monographs of Gould (1841), Gould and Binney (1870) or Verrill et al. (1873), nor in scores of other publications on the invertebrates of the intertidal zone from Massachusetts to New Jersey in the nineteenth century. It was, historically, well known as a southern species, occurring from the mid-Atlantic (Chesapeake Bay area) and south. As Sumner (1909) remarked,

> It is surely difficult to explain how this barnacle has been so long overlooked upon our own Atlantic shores. It is hard to believe that the present species has been habitually confused with Balanus balanoides by the long succession of field naturalists and systematic zoologists who have exploited (sic) the shores of New England for over a century.

Sumner noted that *Chthamalus* and *Balanus* were so "plainly distinguishable" by colour and external morphology that the "confusion of the two ... seems incredible". Sumner suggested that "An alternative explanation is that *Chthamalus* has only recently invaded New England waters ...", pointing out the recent arrivals of the European snail *Littorina littorea* and the Asian sea anemone *"Sagartia luciae"* (= *Diadumene lineata*) as "doubtless the most striking local examples of this phenomenon".

Southern New England has been warming since the 1850s, since the cessation of the climatic minimum (the "Little Ice Age") (Carlton 2002). This warming led Wethey (1984) to make the compelling suggestion that *Chthamalus* was able to invade New England "as a result of release from competition with *Semibalanus* [*balanoides*] brought about by" increasing coastal temperatures. As Wethey (1983, 1984) showed, the northern limit of *Chthamalus fragilis* is controlled by the southern high-intertidal limit of *Semibalanus balanoides*: north of Cape Cod, *S. balanoides* survives along the entire intertidal gradient, from the high to the low shore, such that *C. fragilis* has no refuge from competition. South of Cape Cod, *S. balanoides* succumbs in the high intertidal zone due to summer heat, creating a high-shore refugium from competition for *Chthamalus*. The exception to this pattern, as discussed below, is populations of *C. fragilis* found on the warm margin of the north shore of Cape Cod. A previously colder southern New England would, in this model, mimic the conditions that now obtain north of Cape Cod, and *Chthamalus* would have been eliminated by competition with *Semibalanus*, and thus from New England, until the shores south of Cape Cod began to warm.

The timing of the northern appearance of *C. fragilis* in southern New England is roughly coincident with the movement north of the shore crab *Carcinus maenas*, which prior to the end of the nineteenth century was restricted to the south side of Cape Cod, but began moving north by the 1870s, arriving in the Boston region by 1893 (Carlton and Cohen 2003), further suggestive that a period of coastal warming had commenced.

Carlton (2002) proposed an alternative (or additive) model. In the last half of the nineteenth century the European periwinkle snail *Littorina littorea* was moving south down the Atlantic shore, and become common to abundant south of Cape Cod by the 1880s (Steneck and Carlton 2001). It may thus be that the arrival of this large, abundant, facultative omnivore (which can consume large numbers of newly setttled cyprids and recruits of *S. balanoides*) "altered the uppermost rocky shores in some manner such as to facilitate the colonization of *Chthamalus*" (Carlton 2002).

Regardless of the processes that permitted *C. fragilis* to colonize New England, larvae may have arrived either naturally with northbound currents or adults may have been transported in ship fouling. In this regard, it is of interest to note that Woods Hole was the home of the Pacific Guano Company from 1863 to 1889, importing product from Europe and South America, and phosphate rock from South Carolina (Pacific Guano Company 1876; New York Times 1889), the type locality of *C. fragilis* (Darwin 1854).

Zullo (1963) noted that *C. fragilis* was "abundant in the upper intertidal zone in the warmer water areas of the Cape, such as the coastline along Buzzards Bay and Vineyard Sound, and ... also ... at Barnstable Harbor [north shore of Cape Cod], Brewster, and on the northern shores of Martha's Vineyard", but it did not occur north of the Cape Cod Canal. Zullo (1963, 1964) was the first to report its presence on the southern shore of Cape Cod Bay (the north shore of Cape Cod). Extensive field surveys in 1984 revealed *Chthamalus* to occur on the southern shore of Cape Cod Bay from Sandwich (at the north jetty at the east end of the Cape Cod Canal) to Provincetown, being particularly abundant in the regions of Brewster, Orleans, and Wellfleet (J. T. Carlton, unpubl. observation).

## *9.3 Archaeobalanidae: Semibalanus balanoides (Linnaeus, 1758)*

**ATLANTIC** The southern limit of this well-known North Atlantic barnacle along the Atlantic coast of North America was considered for many years to be New Jersey (Pilsbry 1916). By the mid-twentieth century, however, *S. balanoides* had become well established along the Maryland, Virginia, and North Carolina coasts (Barnes 1958; Wells et al. 1960). Gordon (1969) referred to *S. balanoides* as "newly arrived", based upon it first being reported south of New Jersey as late as 1949. It appears that *S. balanoides* extended its range along the mid-Atlantic coast since Pilsbry's time due in part to the vast expansion of hard substrates (particularly rock jetties) along shores that were primarily originally sand and mud (Barnes 1958; Wells et al. 1960). *Semibalanus balanoides* now reaches its southern limits at Cape Hatteras, with occasional temporary excursions south to the Beaufort area (Mohammad 1965). With warming conditions, *S. balanoides* should now be expected to be retreating north, once again to New Jersey (if not further north) as its southernmost limit.

### *9.4* Tetraclitidae: *Tetraclita rubescens* (Darwin, 1854)

**PACIFIC** Connolly and Roughgarden (1998) reported that this distinctive intertidal barnacle, long known to be rarely north of San Francisco (Newman 1975: 269) had become established 300 km to the north at Cape Mendocino based upon collections made in 1995 (see also Dawson et al. 2010). It is now not only common at many sites north of San Francisco where it was historically rare, but it reached Brookings in southern Oregon by 2007 (Sanford and Swezey 2008). In concert with many other species moving north along the Pacific North American coast (Barry et al. 1995; Carlton 2000; Sorte et al. 2010), this is regarded here as a clear example of range expansion facilitated by warming coastal waters.

## 10 Balanidae Species Removed from Further Consideration

### *10.1 Paraconcavus pacificus (Pilsbry, 1916)*

**ATLANTIC** Ross (1962: 17) reported specimens of the East Pacific species *Paraconcavus pacificus* on the venerid clam *Dosinia elegans* from the entrance of Tampa Bay, Florida. Since there were no previous records of this East Pacific species in the Gulf of Mexico, he inferred that it had been recently introduced there. Not only has this report apparently been overlooked by subsequent authors citing him (Newman 1982; Henry and McLaughlin 1975; Spivey 1981; Zullo 1992b), but neither it nor any other extant member of the genus has been reported from the Gulf of Mexico. This study considers that the report is questionable enough to be in error, and it is reported as such here.

### *10.2 Balanus crenatus Bruguière, 1789*

**PACIFIC** Mooi et al. (2007) reported this species as introduced to San Francisco Bay; this appears to be a *lapsus*, as it is a well-known native species (Cornwall 1951; Zullo 1960, 1966b; Newman 1979).

## 11 Discussion

### *11.1 Temporal Patterns*

The record of barnacle invasions in the Americas reported here covers a 150 year period from the 1850s to the early 2000s. There is little doubt that a number of the "dates of first records" (Table 4, Fig. 1) are artifacts of the timing of exploration and collection, and that thorough examination of museum collections, utilizing fouled barnacle-covered oysters and other shells, will reveal earlier dates for a number of species.

An analysis of the first known dates of collection for thoracic species over broad geographic regions (Fig. 1), albeit coarse-grained, reveals some compelling patterns. For the first 100 years (1853–1955) two species (*A. amphitrite* and *A. improvisus*) constituted the majority of invasion events in the Americas, the sole exception being the collection of *B. trigonus* in the 1860s and 1870s in the Atlantic. After 1955, the first records of invasions of *A. reticulatus*, *A. eburneus, B. glandula, M. coccopoma,* and *S. amaryllis* appear (excluding the collection of the Atlantic barnacles *F. pallidus* and *B. calidus* in locks on the Pacific side of the Panama Canal, although these, too, were first detected post-1950s). While, again, certain artifacts can influence this apparent post-mid-twentieth century rise in barnacle invasions, an increased *diversity* of barnacle invasions in the last half of the twentieth century is in close concert with general observations of increasing invasions globally of marine invertebrates, fish, and algae after WW II related to vastly expanded global trade facilitated by more, larger, and faster ships.

Carlton and Cohen (2003) noted that the appearance of the Atlantic *A. improvisus* on the California coast in the 1850s and of the Pacific *B. trigonus* on the Brazilian coast in the 1860s also fell within a well-known global pulse of invasions related to an earlier surge of shipping. They observed that “with the advent of clipper ships as a mainstay, the California and Australian Gold Rushes altered global shipping patterns for over a decade” (1849–1861). The opening of the Suez Canal in 1869 then altered shipping patterns again, forcing Atlantic-based clipper ships out of the China tea trade (the Red Sea/Suez Canal being more suited to steam than sail) and into the Australian wool trade. It was during these decades that many long-distance sailing records were set: in 1866, for example, three ships sailed 25,000 km in 99 days during the “Great Tea Race” between China and London (Carlton and Cohen 2003). This present study predicts that analyses of global barnacle invasion patterns, outside of the Americas, will reveal that introductions surged between the 1850s and 1870s, in addition to a post-WWII global surge.

## 11.2 Temporal Patterns: Post-Discovery Spreading

The collection of species sequentially over time in one direction or another (north or south of their original discovery sites, or east or west in bodies of water such as the Gulf of Mexico) could suggest that a given species is *moving* in one direction. Pitfalls abound in the analyses of such apparent patterns, including (1) that the species may already be widespread upon first detection, and the pattern of discovery may only coincidentally be in one direction or other, depending upon the history of subsequent investigators and investigations; (2) the site of first discovery may not be where the species was first introduced and became established; (3) once introduced, a species may naturally begin to spread (in any direction) until it reaches its physiological limits (Carlton 2000), although the spread may appear unidirectional, depending upon vectors, local hydrographic conditions, (again) exploration history, et cetera, and (4) spread may be compounded by (and thus confused with) multiple separate introductions. Relative to the latter, for example, Roman (2006) demonstrated that while the shore crab *Carcinus maenas* appeared to have moved north along the Canadian Maritimes to the Gulf of St. Lawrence, the northernmost populations in fact represented a distinct genetic stock introduced independently "on top" of the southern populations. Vector history and availability may also play an important role; Zullo (1992a) thus suggested that the Pacific barnacle *B. trigonus* was first brought to the South Atlantic Ocean and then dispersed north along whaling ship routes.

These caveats noted, of particular interest relative to climatic warming scenarios are species that, having been established in a region for a relatively long time then begin to appear in more northern locations (in the northern hemisphere) or more southern locations (in the southern hemisphere). Carlton (2000) reviews a series of alternative hypotheses that would account for such movements, independent of climate change.

Certain patterns of apparent chronological, directional histories can be detected in Table 4. This study cautions against calculating invasion rates (km/year) until data documenting site-by-site prior absence are available. While there are clear patterns of spread, such as the records of *A. reticulatus* and *S. amaryllis* in Brazil and *B. glandula* in Argentina, all of these based upon documented prior absences, whether any of these sequences represent responses to climate change remains unclear. In the Pacific, *A. eburneus* was first reported in a fairly tight cluster of years (1959, 1963, 1964) from the Gulf of California, Mexico, and Panama, and then a long gap precedes its northward detection (2000) in southern California. *Amphibalanus eburneus*, however, is not an obligatory warm-water species requiring warming conditions to colonize a new area, so this northward range expansion is not necessarily climate-related.

*Amphibalanus reticulatus* similarly is detected on the Pacific coast first in Mexico (1984) and then to the north (Table 4), but this, too, could represent simply long-term dispersal along the coast, as suggested by its collection to the south in Panama (2000). However, the Panama population could also represent an independent introduction, perhaps through the Panama Canal or from the Indo-West Pacific, not related to the earlier northern occurrences.

Similar patterns obtain for the rest of the species shown in Table 4, where while there appear to be clear patterns of unidirectional spreading, these may represent the expected dispersal of species, rather than response to warming conditions in either hemisphere. One exception may be the arrival of *Megabalanus coccopoma* on the southern Atlantic coast of the United States, where this species, known since the early 1970s in Brazil, was found in the Gulf of Mexico in 2001, and has since colonized the coasts of Georgia, South Carolina, and North Carolina, apparently only since about 2005. Carlton (2010), noting the appearances along the southern Atlantic coast of the United States of a suite of taxa with warmer-water affinities, referred to this phenomenon as "Caribbean Creep".

To determine whether the southward spread of both *Amphibalanus reticulatus* and *Striatobalanus amaryllis* from northern to southern Brazil, and the spread of *Amphibalanus amphitrite* from Brazil to Argentina, are linked to warming conditions will require a comparison of these species' minimal temperature requirements for gametogenesis, larval survival, and settlement, compared to increased temperatures in these lower latitudes. This said, the long delay in moving south along the South American coast by *A. amphitrite* is compelling, relative to climate warming that would permit it to move into Argentina.

While the data in hand do not yet substantiate climate-mediated range expansions for most of the species dealt with here, the authors of this present study predict, as discussed below, that we are likely on the doorstep of such range shifts.

## 11.3 Temporal-Geographic Patterns

There are few general temporal-spatial patterns, save for an apparent 32 year lacuna in any barnacle invasions on the Pacific coast of the Americas (*A. amphitrite* collected in 1914 in southern California, followed by its collection in 1946 in the Gulf of California). Throughout the nineteenth to twenty-first centuries barnacle invasions alternate on both Atlantic and Pacific American shores (Fig. 1, Table 4).

This said, one notable pattern, revealed by a comparison of Fig. 1 with site and time data in Table 4, is that no alien barnacle species has first colonized North America north of latitude 34°. The first records of the Indo-West Pacific barnacle *A. amphitrite* are in Los Angeles (34° N), in 1914, and in Beaufort, North Carolina (34° N), in 1955. No barnacle species from overseas has ever made landfall on the Atlantic coast north of North Carolina or on the Pacific coast north of southern California (amongst those species native to North America, *B. improvisus* colonizes San Francisco Bay (37° N) in the late 1840s or early 1850s). Whether native to North America or elsewhere, no new barnacle invasions first make landfall in the Pacific Northwest, or New England. Why in particular no Western Pacific species have first appeared in Pacific Northwest waters is not clear, especially given the long history of transplantation of Japanese oysters to Oregon, Washington and British Columbia. And, as Ruiz et al. (2009) note, there are few barnacle invasions north of California: only *A. improvisus* occurs in Oregon, California, and British Columbia, and no introductions are yet known in Alaska.

## 11.4 Geographic Patterns: Diversity and Origins

Five species of thoracic barnacles have invaded the Pacific coasts of the Americas: *A. improvisus*, *A. eburneus*, and *A. subalbidus*, all from the Atlantic, and *A. amphitrite* and *A. reticulatus* from the Indo-West Pacific. Seven species have invaded the Atlantic coasts of the Americas, and six are from the Pacific Ocean: *A. amphitrite* and

*A. reticulatus* (shared as invaders with the Pacific coast), and *B. trigonus*, *B. glandula*, *S. amaryllis*, and *M. coccopoma*. The Northwest Atlantic *A. subalbidus* has invaded the Southwest Atlantic. While the Western Pacific has contributed species to the Eastern Pacific, there are no clear examples of the mirror image of the Eastern Atlantic contributing species to the Western Atlantic, unless the cryptogenic *F. pallidus* falls in this category.

## *11.5 Geographic Patterns: Regional Diversity of Invaders*

In general, no one region has gained significantly more alien barnacles than other regions (Fig. 1). Striking, however, are the few barnacle invasions that have occurred on the Pacific coast of South America (Pitombo and Ross 2002; Castilla et al. 2005; Pitombo 2010), and, indeed, these species (*A. improvisus*, *A. amphitrite* and *A. reticulatus*) are reported only from northernmost locations (Ecuador, Colombia, and Peru). The genera *Amphibalanus* and *Fistulobalanus* contain species associated with brackish environments. The arid environment of the Chilean coast thus may not facilitate colonization by estuarine barnacles, reminiscent of the apparent inability of the estuarine *Amphibalanus improvisus* to become established in the arid estuaries of southern California. In addition, the high diversity shores of Chile may present a strongly competitive environment for more stenohaline species of barnacles.

## *11.6 Galapagos Islands*

Zullo (1991) felt that the tropical Eastern Pacific *Megabalanus coccopoma* had been introduced to the Galapagos Islands by visiting ships based upon its absence there in 1964; it appears to have been first collected on pier pilings at Baltra Island in 1966 (USNM 243980; Smithsonian Institution data base accessed July 2010). While Carlton (1988) and Zullo (1991) speculated that *A. amphitrite*, *A. eburneus*, *A. improvisus*, and *A. reticulatus* were likely candidates for introduction to the Islands or were already present there, these species have not yet been reported from the Galapagos, nor are any alien barnacles from the Western Pacific or the Atlantic known solely from the Galapagos Islands.

## *11.7 The Panama Canal*

Cohen (2006) has reviewed the history of the Panama Canal relative to permitting or inhibiting marine and estuarine invasions to the Pacific or Atlantic Oceans. Spivey (1976) reported on the barnacles of the Panama Canal; his records of

*Amphibalanus reticulatus* (at the Caribbean end) and of *Amphibalanus amphitrite* (at the Pacific end) are noted above. In addition, *Fistulobalanus pallidus* was found in the Panama Canal in the Miraflores Locks on the Pacific Ocean side in 1972 (Jones and Dawson 1973) and in 1974 (Spivey 1976). It is not treated here as an established invasion in the Canal; while it may still be present, the records are more than 35 years old, and there are no recent reports. Similarly, Spivey (1979: 46) reported a population of *Balanus calidus* at the Pacific end of the Panama Canal, "in the lower (seaward) end of the lower east chamber of Miraflores Locks, 12 m below minimum water level", based upon collections in 1974. Pending more modern reports, it is not treated here as an established invasion (and, as noted above, there are doubts about the identification of this species).

That the freshwater Gatun Lake in the middle of the Panama Canal is a permeable barrier to marine and brackish-water species has long been noted. As noted in Table 2, Bishop (1947) found *Amphibalanus amphitrite, Balanus trigonus*, and *Austrominius modestus* alive on a vessel arriving in England from New Zealand that had transited the Panama Canal. Menzies (1968) experimentally found that two species of Atlantic barnacles ("*Chthamalus* sp." and "*Balanus* sp.") survived the transit through freshwater of the Canal. Davidson et al. (2008a) found that *Amphibalanus improvisus* arrived alive in Texas on a vessel towed from San Francisco Bay through the Panama Canal.

The Panama Canal is now being enlarged, with the goal of doubling transit capacity (more ship traffic and more tonnage) by 2014, along with accommodating larger (wider) ships (Zubieta 2010). The major aspects of this work include widening and deepening the Canal's entrances at both the Atlantic and Pacific ends, as well as the navigational channel in Gatun Lake. The authors of this study predict that this larger Canal will lead to increased invasions through the Canal, as well as into the brackish waters of Miraflores Lock.

## 11.8 Future Invasions

One of the hallmarks of invasion ecology is that the next invasion is often impossible to predict. That said, we note that two well-known invaders can be expected on American shores, if they are not already present. *Austrominius modestus* (= *Elminius modestus*), an Australian-New Zealand native that colonized Europe after WWII (Bishop 1947; see O'Riordan et al. 2009; Buckeridge and Newman 2010; Gomes-Filho et al. 2010; Witte et al. 2010 for an *entrée* into the earlier literature), remains a candidate for colonization of Atlantic American shores; its failure to do so, at least as a result of transport from Europe, for more than 60 years, is not a predictor of the probability of its future invasion. Hedgpeth (1968) speculated that the "ecological catholicity of the native barnacle *Balanus glandula* on the Pacific coast of North America may inhibit the establishment of *Elminius modestus*", but whether competitive processes or other factors have so far led to its failure to appear in the Americas remains unclear. The Caribbean *Chthamalus proteus* invaded the

Pacific Ocean in the 1990s (see Carlton and Eldredge 2009, for a review of the literature), and has been found on ships going back-and-forth between Hawaii and the North American Pacific coast (Table 2); indeed, it would not be surprising to find that *C. proteus* is already present on the American Pacific coasts. While *Austrominius* can be (or should be) readily recognized on American shores, detecting *C. proteus* amongst native chthamalids in, for example, the southern California and the Panamic regions, will require detailed studies.

Finally, this study suggests that many more barnacle species, both native and introduced, are likely to move north in North America and south in South America with a warming world. As discussed here, examples may already be in hand: *Chthamalus fragilis*, *Amphibalanus amphitrite, Balanus trigonus,* and *Megabalanus coccopoma* in the Northwest Atlantic, *Amphibalanus amphitrite* in the Southwest Atlantic, and *Tetraclita rubescens* may have, may now be, or are responding to warmer coastlines. Among many potential examples, the authors of this review thus expect *Amphibalanus amphitrite* and *Balanus trigonus* to continue to move north on the Atlantic American coast, and *Amphibalanus reticulatus* to continue to move north on the Pacific American coast. Among many native species to be watched for, *Amphibalanus eburneus* is likely to move north into Maine; in turn, this study expects the cooler-water *Semibalanus balanoides* to begin to retreat, perhaps even re-establishing its once southern limit at New Jersey, if not further north. Barnacles, amongst the most conspicuous and easily collected shallow-water invertebrates, and with an extensive fossil, archaeological, and historical record, should prove to be global models for monitoring a changing ocean.

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# Marine Crustacean Invasions in North America: A Synthesis of Historical Records and Documented Impacts

**Gregory Ruiz, Paul Fofonoff, Brian Steves, and Alisha Dahlstrom**

**Abstract** We examine the history and relative importance of marine crustacean invasions for North America. Nearly 400 non-native species of invertebrates and algae have established populations in marine and estuarine waters of North America. Of these documented invasions, 28% are crustaceans, contributing the largest number of species of any taxonomic group. Crustaceans also dominate non-native species richness on each coast of North America, but there are strong differences in the total number of non-native species and in their taxonomic distribution among coasts. Crustaceans contribute prominently to the current knowledge base about marine invasions, due both to the large number (proportion) of documented introductions and also the extent of research on the group; they are thus a potentially important model for understanding marine biological invasions in general. Using an analysis of available literature, we evaluate what is known about the impacts of 108 non-native crustaceans in North America. Ecological and economic impacts are reported for many (28%) of these species, but they are rarely well documented, resulting in low certainty about the magnitude, spatial scale, and temporal scale of effects.

## 1 Introduction

Biological invasions by crustaceans are a conspicuous feature of coastal marine ecosystems throughout the world. This prominence results from a combination of multiple factors, including the relatively large body size and good taxonomic (and biogeographic) resolution that exists for many species compared to some other

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taxonomic groups (Cohen and Carlton 1995; Carlton 1996; Ruiz et al. 2000). In addition, crustacean invaders can often achieve high abundances, further increasing the likelihood of detection and observation. All of these attributes are exemplified by many crab and barnacle species that are frequently recognized introductions, such as the European shore crab *Carcinus maenas* and the Chinese mitten crab *Eriocheir sinensis*.

It is therefore no surprise that crustaceans are among the most studied of all marine invaders and often comprise a large proportion of the documented non-native species in well-studied regions of the world (Cohen and Carlton 1995; Reise et al. 1999; Orensanz et al. 2002; Bouley and Kimmerer 2006; Hewitt et al. 2004; Galil 2008). Research on non-native species of crustaceans spans a wide range of topics, from population dynamics and evolutionary biology to community ecology and economic consequences (Vermeij 1982; Seeley 1986; Grosholz et al. 2000; Talley et al. 2001; Lohrer and Whitlach 2002; Floyd and Williams 2004; Hollebone and Hay 2008). Given the scope and extent of this past work, crustaceans provide an important model for understanding invasion patterns and processes.

In this chapter, we present a brief overview of the current state of knowledge about crustacean invasions for marine and estuarine waters of North America, excluding Mexico. We synthesized and analyzed occurrence records for marine species to identify non-native species that have been documented in North America, evaluating species considered to have established populations. The results were documented in a database (NEMESIS 2009) and used to characterize (a) the identity, distribution, and native region for non-native crustaceans documented among the Atlantic, Pacific, and Gulf coasts of North America, (b) the relative importance of crustaceans to overall non-native species richness documented for each coast, and (c) the impacts (effects) that have been reported for North America.

## 2 Taxonomic and Geographic Distribution of Non-native Crustaceans

We identified 108 non-native species crustaceans that were classified as having established populations in marine and estuarine (tidal) waters of North America, including the continental United States and Canada (Appendix 1). As noted in previous analyses (Ruiz et al. 2000), crustaceans make the single largest contribution of any taxonomic group to the number of documented non-native species in North America. In our current analysis, we classified 381 non-native species of invertebrates and algae (i.e., excluding vertebrates and vascular plants) as having established populations in tidal waters of North America. Thus, crustaceans comprised 28% of this total non-native species richness on a continental scale.

The largest contribution of non-native crustaceans came from amphipods, providing 30% of documented crustacean invasions in North America (Fig. 1). Three other groups each contributed strongly to the total species richness: isopods (21%), decapods (14%), and copepods (13%). Other groups of crustaceans each contributed less than 10% of the total species, with barnacles, mysids, and ostracods providing the most (7%, 6%, and 5%, respectively; Fig. 1).

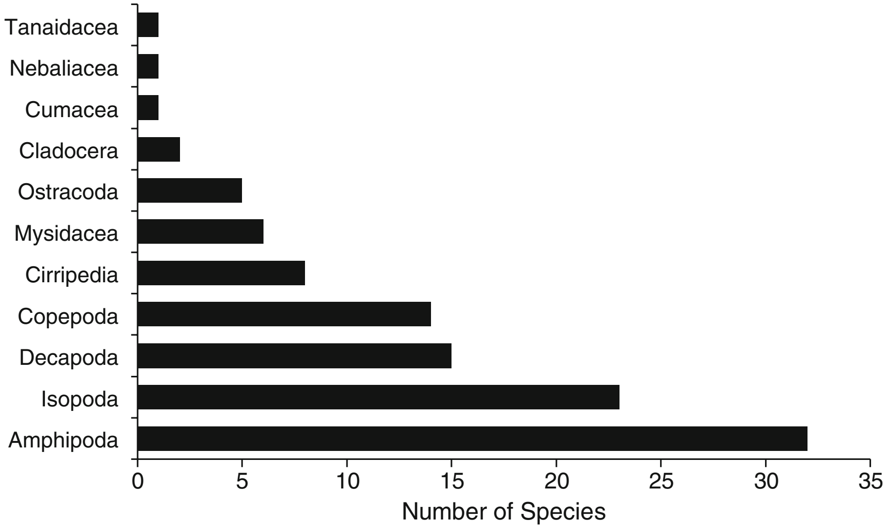

**Fig. 1** Taxonomic distribution of non-native crustaceans in tidal (marine and estuarine) waters of North America. Shown are the numbers of species in each taxonomic group classified as non-native and established in North America

## *2.1 Number of Species by Coast*

There are strong differences in the total number of non-native species among the three coasts of North America (Fig. 2). Far more non-native species have been documented for the West coast than the other two coasts, when considering established populations of invertebrates and algae. Despite such a disparity in overall numbers, the relative contribution of crustaceans to totals on each coast is similar: 42% of non-native species on the West coast, 33% on the Gulf coast, and 31% on the East coast (Fig. 2). Nonetheless, 75% of all non-native crustaceans are known from the West coast alone, and far fewer are documented on the Gulf coast (13%) and East coast (33%), with some species shared among coasts (Appendix 1).

Several factors may contribute to this disparity in the total number of non-native crustaceans and other taxa documented among coasts. One of these involves the quality of the historical record and knowledge about biogeography, both of which differ by coast. Marine biological studies on the East and Gulf Coasts began in the early-mid-1800s, centuries after the beginning of extensive European trade and shipping (1500s–1600s, Carlton 2003). Due to this long gap, many species may have invaded the Atlantic coast of North America before the biota were catalogued (Carlton 2003). In contrast, biological collections and studies began on the West Coast in the late 1800s, only few decades after the beginning of extensive settlement and shipping (mid-1800s, Carlton 1979), although we note that the West coast, too, experienced early contact (beginning in the 1500s) with European shipping. Such geographic differences in relative timing of events may greatly affect the ability to detect non-native species (Ruiz et al. 2000).

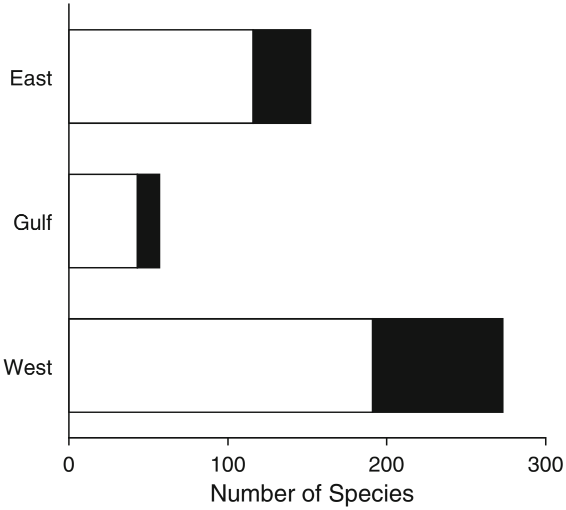

**Fig. 2** Proportion of non-native species for each coast of North America that are crustaceans. *Bars* indicate total number of invertebrate and algal species that are classified as non-native and established in tidal waters on each coast; *shaded areas* indicate numbers (proportions) that are crustaceans

Specific characteristics of species transfer mechanisms have also affected observed differences in non-native species richness among coasts in at least two ways. Both the magnitude and geographic source(s) of species transferred by human means have clearly differed among coasts, affecting the species pool and the number of propagules (individuals) delivered. This variation is perhaps most pronounced for oyster transfers and their associated biota. Massive numbers of oysters were transferred to the West coast, first from eastern North America (the Eastern Oyster, *Crassostrea virginica)* and then from Asia (Pacific Oyster, *C. gigas*), resulting in a large number of invasions by associated biota (Carlton 1979; Cohen and Carlton 1995; Miller et al. 2007). In contrast, transplants of oysters to the East and Gulf coasts from other global regions have been very limited in scale, occurring later in time with more care to prevent movement of associated species (Loosanoff 1955; Hidu and Lavoie 1991). Some transfers of native oysters (*C. virginica*) along the Atlantic coast have resulted in introductions (e.g., *Loxothylacus panopaei*, from the Gulf of Mexico to Chesapeake Bay, Hines et al. 1997). Nonetheless, while oyster introductions have been a major source of invasions to the West Coast of North America, relatively few species are attributed to this mechanism on the East or Gulf Coast.

As with oysters, strong differences in commercial shipping have contributed to variation in non-native species richness among coasts, especially with respect to source region. For example, in recent time, most overseas ship arrivals to the West coast came from ports in Asia and other Pacific Rim countries, but those to the East and Gulf coasts have been mainly from Atlantic ports (NBIC 2009). Independent of potential differences in the magnitude (number of species and densities) of organism transfers among regions, the different origin of vessel traffic indicates that a different pool of species is delivered to each coast of North America. This said, exceptions to this general pattern occur, and may deliver notable species to the "opposite" coast, such as the Asian shore crab *Hemigrapsus sanguineus* that invaded the East coast in the 1980s (Lohrer and Whitlatch 2002).

Although there are conspicuous differences in the supply of propagules among coasts, it is also possible that these geographic regions differ in susceptibility to invasions. It has been suggested that West coast estuaries are more susceptible to invasions than those elsewhere because of disturbance or a depauperate native fauna (Cohen and Carlton 1998). This hypothesis remains to be tested in a way that controls for many of the other confounding factors or differences among locations (Ruiz et al. 1999, 2000).

It has also been suggested that the West coast is relatively susceptible to invasions, especially from Asia, due to climatic regime (Vermeij 1991; Chapman 2000). In the north-temperate zone, the eastern shores of oceans (Europe, western North America) have marine-dominated climates, with milder winters and summers, while the western shores (Asia, eastern North America) have continental-dominated climates, with a wider temperature range. Species that have evolved in the latter regions (Northwest Atlantic, Northwest Pacific) may be superior colonists, while species native to marine-dominated climates (Northeast Atlantic, Northeast Pacific) may have difficulty surviving the wide temperature range in continental climates. Chapman (2000) considers this an explanation for a west-to-east pattern of invasions for peracarid crustaceans in North America, and Carlton (1999) has found a similar pattern in molluscs.

## 2.2 *Salinity Distribution of Species by Coast*

For each coast, the majority of the non-native crustaceans in our analyses occur in marine waters, ranging from 65% to 78% (Appendix 1). A small subset of species is restricted to tidal freshwater reaches of estuaries on each coast, exhibiting a very narrow range (15–16% of the crustaceans) among coasts. The West coast has more than twice the frequency of brackish water specialists (18% of species) than the East or Gulf coasts (5% and 8%, respectively). This difference results largely from the greater number of copepods and mysids that have colonized brackish water on the West coast compared to other coasts, where these groups were relatively rare (see below for further discussion).

## 2.3 Taxonomic Distribution by Coast

A striking difference exists among coasts in the relative frequency of different taxonomic groups within the non-native crustaceans (Fig. 3). On the West coast, a disproportionately large percentage of the total is comprised of amphipods (35%) and copepods (17%) compared to the other coasts. In contrast, amphipods contribute 7% and 17% of the non-native crustaceans for the Gulf and East coast, and copepods were 0% and 3% of the totals for these respective coasts. Mysids are also more prevalent on the West coast (five species, 6% of crustaceans) compared to the Gulf coast (none) and East coast (one species or 3%).

For copepods and mysids, the differences among coasts are attributed in large part to invasions from Asia. The estuarine copepod and mysid fauna of the coast of Asia includes a substantial contribution from a diverse fauna, adapted to low-salinity brackish waters, many of which range into temperate waters. Fourteen of these species (ten copepods, four mysids) have been introduced to West Coast estuaries in ballast water (Cohen and Carlton 1995; Orsi and Ohtsuka 1999; Bollens et al. 2002; Modlin 2007; Cordell et al. 2008), representing 71% of copepod introductions and 80% of mysid introductions to this coast. In contrast, only one copepod and one mysid are known introductions to the Gulf and East coasts combined (Appendix 1).

The paucity of copepod invasions for the entire Atlantic coast is especially surprising, given the magnitude of shipping and ballast water discharge at major ports along this coast (NBIC 2009). Although ballast water is considered the source for most copepod invasion along the West coast, a similar signal is completely lacking

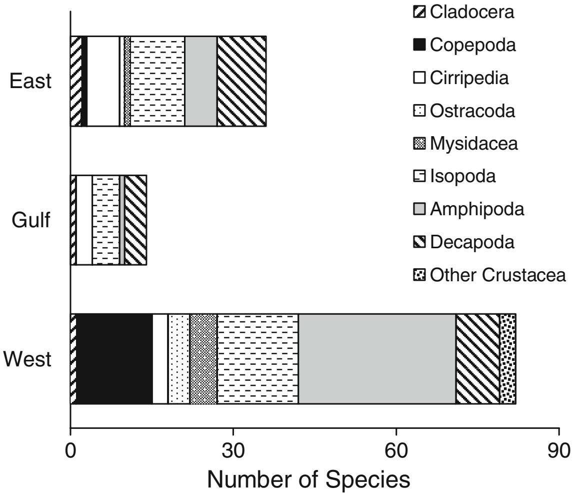

**Fig. 3** Contribution of different taxonomic groups to non-native crustaceans for each coast of North America. Shown are the numbers of species in the respective taxonomic groups that are considered non-native and established in tidal waters on each coast

for the East and Gulf coast, where the only reported invasion is a freshwater parasitic copepod on fish (*Lernaea cyprinacea).* Moreover, the only documented non-native marine zooplankton species established on the East Coast is the European mysid *Praunus flexuosus* (Wigley 1963).

Based on past and current shipping patterns, most overseas ship arrivals and ballast discharge to the East coast have come from Europe, whereas that to the West coast has been from Asia (NBIC 2009; Ruiz, 2005). It is noteworthy that the copepod fauna of Europe is considered relatively low in diversity, with many circumpolar and amphi-oceanic species and species complexes (Frost 1989; Bradford 1976; Lee 2000). While many of the copepods introduced to West coast estuaries from Asia are morphologically distinct and easily recognized (Orsi and Ohtsuka 1999), the species pool in Europe reaching the East Coast via ballast water of ships is more similar morphologically to the native fauna (Fofonoff and Ruiz, 2003). It is possible that some early introductions of European copepods have been overlooked, especially if species complexes disguise a richer biota than is presently recognized.

For amphipods, some of the same issues appear important in the observed disparity among coasts. Asia was an important source (native region) for amphipods on the West coast, and so was the Atlantic, resulting from transfers by oysters and ships (Cohen and Carlton 1995; NEMESIS 2009). Atlantic and Asian amphipods arriving on the West Coast appear to have often been morphological distinct and readily recognized from native biota (Carlton 1979; Chapman 1988, 2007). In contrast, a number of amphipod species, especially those building tubes on solid surfaces (e.g., Corophiinae, *Jassa marmorata; Ampithoe valida; Erichthonius brasiliensis*) are found on both sides of the Atlantic (Lincoln 1979; Conlan 1990; Bousfield and Hoover 1997). It is likely that some early introductions of European fouling-community amphipods to the East Coast have been overlooked, since they could have happened centuries before the onset of biological studies.

More generally, the frequency differences observed for taxonomic groups among coasts results from variation in (a) the historical supply of propagules, (b) susceptibility to invasions, and (c) detection of non-native species. The relative importance of each of these is still under debate for crustaceans and all other taxa, as discussed above (see Sect. 2.1). The patterns observed for copepods and other ballast-mediated invasions serve to further underscore the importance of propagule source in constraining the species pool and taxonomic resolution. There is also the suggestion that the biota from some regions may be superior colonists, such as species arriving from Asia to the West coast of North America (Vermeij 1991, 1996; Chapman 2000).

## *2.4 Native Region by Coast*

In considering the native region of crustaceans on a broad-scale (Fig. 4), most species are from Asia and the western Pacific, ranging from 41% to 62% of all crustaceans per coast. North America itself is the second largest native region for crustacean

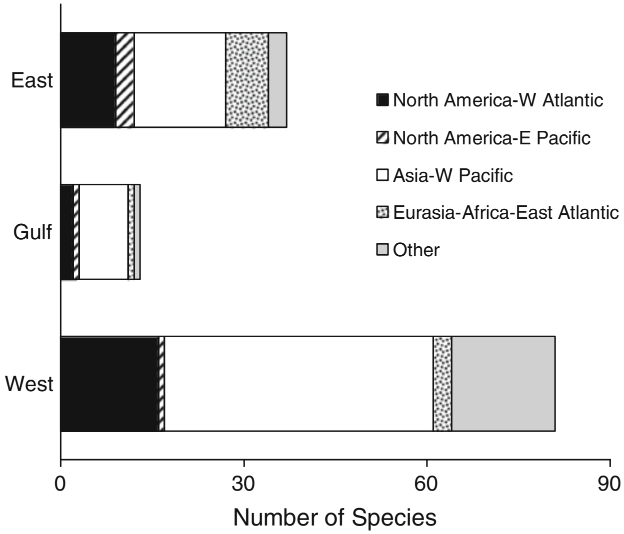

**Fig. 4** Contribution of different native regions to non-native crustaceans for each coast of North America. Shown are the numbers of species from the respective broad-scale native regions that are considered non-native and established in tidal waters on each coast

invasions, contributing 21–32% of species with the vast majority on each coast from western Atlantic coast. The eastern Atlantic (including Eurasia and Africa) was the third largest native region for all three coasts of North America, being greatest for the East coast (19% of species) and lower for the Gulf and West coasts (8% and 4%, respectively). The native region for the residual species was classified as other, including other regions and those of unknown origin.

While the prominence of Asia and western Atlantic reflect the history of shipping and oyster transfers (as discussed above), the contribution of Asia across all regions is somewhat surprising when considering the historical and current trade patterns. For the East coast, this results from the combination of direct introductions as well as secondary introductions via Europe. The latter is illustrated by the recent introduction of the Chinese mitten crab *Eriocheir sinensis* to the East coast, where genetic data suggest Europe as the likely source population (Ruiz unpubl. data).

## 3 Impacts of Non-native Crustaceans

For all of North America, an impact was reported to occur in marine and estuarine waters for 30 of the 108 crustacean species, representing 28% of all species (Appendix 1). Here, we recorded an impact if there was a significant change attributed to the non-native species, causing either (a) a detectable change in composition or population size(s) of resident species or (b) economic impact, including effects

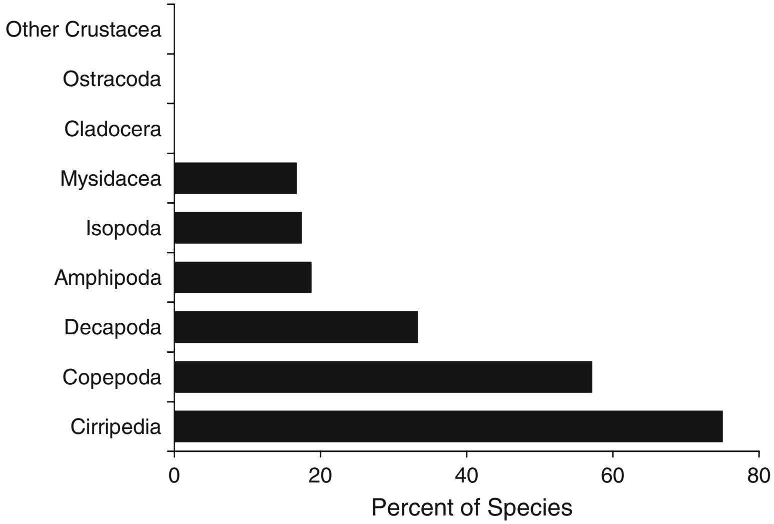

**Fig. 5** Percent of non-native species in each crustacean group that are reported to have impacts in tidal waters of North America. See Fig. 1 for total number of species in each group

on fisheries resources, agricultural products, infrastructure (e.g., docks, piers, dams, water supply), power plants, shipping, and recreation. As a first analysis, we considered impact as a binary condition, which was either reported or not reported, regardless of information type and impact magnitude (addressed separately below) or whether explicitly tested.

Considering only marine and estuarine waters of North America, some type of impact was reported most frequently for introduced barnacles (75% of species), copepods (57%), and decapods (33%) (Fig. 5; see also Appendix 1). Impacts were reported for 17–19% of the amphipod, isopod, and mysid species. No impacts were reported for cladocerans, ostracods, or other species of crustaceans.

When expanding our analysis to include the same non-native species in non-tidal freshwater (i.e., lakes and rivers), another six species have been reported to have impacts, including five in North America and one on another continent (Appendix 1). These included three species of decapods, two species of amphipods, and one species of cladoceran. As such impacts were not reported for marine and estuarine waters, we have excluded them from further analyses.

## *3.1 Impact Type*

Figure 6 shows the frequency of impact types reported for tidal waters of North America for all 108 non-native crustacean species. Slightly over 10% of species were reported to have competition or economic impacts. Approximately 5% of species were reported to have effects as a result of predation (including herbivory),

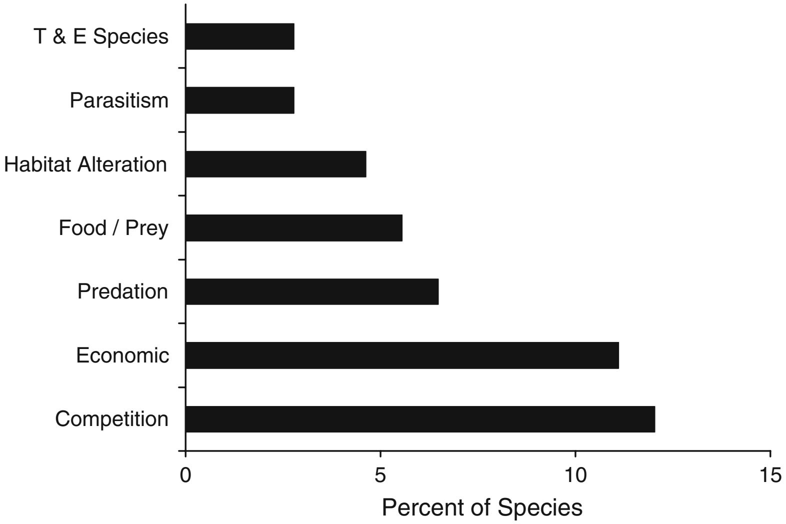

**Fig. 6** Frequency of impact types reported for crustaceans in tidal waters of North America. Shown are the percent of species reported to have impacts in seven broad impact categories (T & E = threatened and endangered). Species may be included in more than one category

providing a food/prey resource, or altering habitat. Effects on host populations by parasitism was reported for 3% of species, and effects on threatened or endangered (T & E) species were reported for 3% of species. These categories were not mutually exclusive, in that more than one impact type was reported for 13 of the 30 species with reported impacts (Appendix 1). Although we also considered changes in ecosystem processes (e.g., nutrient cycling) as a possible impact category, none of the crustaceans were reported to have a significant impact of this type.

## *3.2 Information Type and Effect Magnitude*

Most of the impacts reported were based upon qualitative observation, correlated changes associated with the arrival or abundance of a non-native species, or changes inferred from understanding the ecology of a species (Appendix 2). For seven (23%) of the 30 species with reported impacts, impact assessments were based on laboratory or field experiments. The latter included three decapods (*Carcinus maenas*, *Hemigrapsus sanguineus*, *Petrolisthes armatus*) and a single species each of amphipod, isopod, barnacle, and copepod (*Microdeutopus gryllotalpa*, *Sphaeroma quoianum*, *Loxothylacus panopaei*, *Tortanus dextrilobatus*, respectively).

We estimated the effect size or magnitude for each of the species with reported impacts, and approximately half (14) of the 30 species were considered to cause change(s) in excess of 50% in other resident populations or to have economic effects.

This was a coarse-level assessment, in which we estimated the magnitude of changes by impact type that were reported in the literature. Our goal was to gain some indication of the perceived effect size by classifying observed changes into one of five categories of increasing effect size (see Appendix 2; this is an initial application of methods being developed by Dahlstrom). Thus, this is not a precise measure but instead a rough index of reported effect size, on some spatial and temporal scale (see Conclusions).

For some species, the actual effect size was not explicitly stated. In some of these cases, we generated an estimate based on information provided. In other cases, there was simply too little information to obtain a reasonable estimate, and these were classified as "undescribed or unassessed", occurring for 10 of the 30 species. This does not mean that the species is considered to have an insignificant impact, only that that effect magnitude was elusive. This situation is perhaps best illustrated by barnacles, many of which are known to have significant economic impact as biofouling organisms, affecting vessels (e.g., increased fuel consumption, hull maintenance) and water intake systems in North America and elsewhere. While the local effect of barnacles on an individual vessel or power plant can be severe, the impacts are often caused by a broader community of species that include barnacles, and effects are occurring on a global scale. Our ability to examine such partial contributions or cumulative effects was limited in the current classification scheme.

## *3.3 Certainty*

We used a categorical index to assess the strength of inference about the magnitude of reported impacts. Our approach relied on information type (above), and certainty or confidence in reported estimates of effect magnitude was considered low in the absence of quantitative data or when the ability to partition effects among multiple (confounding) factors was limited. We assigned a certainty score from 1 to 3 (low to high) for each reported effect magnitude x impact type, for the 30 species in which an impact was reported (Appendix 3).

At the present time, the level of certainty or confidence about the effect magnitude of non-native crustaceans is very limited. We classified 8 (27%) of the 30 species as having a high level of certainty about the reported effect magnitude for at least one of the impact types. This included primarily species for which there were quantitative experimental data that evaluated ecological effects (three decapods, one copepod, one amphipod) and those which caused conspicuous erosion or destruction of docks (three isopods). All other species were classified as having low certainty about the reported effect magnitude for all impact types.

This analysis does not imply that these effect magnitudes are incorrect or did not occur, but only that the information available is too limited to have confidence in these reports. Assigning impacts to an individual invading species is especially difficult when environmental conditions, species assemblages, and foodwebs are all undergoing changes driven by multiple causes. Observed changes that are coincident or correlated with invasion dynamics are clearly useful, but the ability to attribute cause of a single factor is confounded by the many other changes that are occurring (Ruiz et al. 1999).

This complexity is illustrated in the fresh and brackish Delta regions of the San Francisco Bay estuary, where five non-native species of planktonic copepods (*Acartiella sinensis*, *Pseudodiaptomus forbesi*, *P. marinus*, *Tortanus dextrilobatus*, and *Limnoithona tetraspina*) and two non-native mysids (*Hyperacanthomysis longirostris* = *Acanthomysis bowmani*; *Orientomysis aspera* = *A. aspera*) appeared and became abundant or dominant over the course of approximately 7 years, from 1987 to 1993 (Orsi and Walter 1991; Cohen and Carlton 1995; Modlin and Orsi 1997; Orsi and Ohtsuka 1999). The calanoid copepod *Eurytemora affinis*, probably an early introduction to the estuary (Lee 2000; Orsi 2001), had been a dominant mesozooplankter (Ambler et al. 1985) and an important component of the diet of larval and planktivorous fishes in the Delta (Nobriga 2002; Nobriga and Feyrer 2008; Bryant and Arnold 2007). Within 2 years of its first detection, *P. forbesi* had become the most abundant calanoid in fresh and oligohaline regions of the Delta, while *E. affinis* had declined. Similarly, the native mysid *Neomysis mercedis*, another major prey item for fishes, had declined and was largely replaced by the two introduced mysids, *H. longirostris* and *O. aspera*, first collected in 1993 (Modlin and Orsi 1997).

The changes in species composition in the plankton coincided with declines in recruitment of two important fish species, the introduced Striped Bass, *Morone saxatilis*, a major game fish in the Bay, and the native, endangered Delta Smelt, *Hypomesus transpacificus*. Larvae of striped bass fed selectively on the copepod *E. affinis* in experiments, apparently because of superior escape abilities of *P. forbesi* (Meng and Orsi 1991). *Eurytemora affinis* was also considered to be a higher-quality prey, over *P. forbesi*, for all stages of the smelt (Moyle et al. 1992; Nobriga 2002). However, since *P. forbesi* has become dominant, it is now the primary copepod in the diet of both fish species (Hobbs et al. 2006; Bryant and Arnold 2007). The replacement of the mysid *N. mercedis* by the two exotic mysids is also considered to be adverse for juvenile striped bass, since the introduced mysids are smaller, and so require more search effort (Nobriga 2002; Feyrer et al. 2003).

At first glance, these drastic changes in species dominance and fish recruitment might be attributed to superior competitive abilities of the planktonic invaders. However, they have followed a drastic change in the estuary's foodweb, caused by another invader, the Asian brackish-water clam *Corbula amurensis*, which appeared in the Bay in 1986, and quickly developed huge biomasses, whose suspension-feeding drastically decreased phytoplankton biomass and shifted energy and nutrients from the plankton to the benthos (Alpine and Cloern 1992; Nichols et al. 1990). The decrease in phytoplankton and zooplankton biomass, and decreased planktivorous fish recruitment, has persisted to the present, and has been termed 'pelagic organism decline' (Sommer et al. 2007; Baxter et al. 2008).

The replacement of *E. affinis* by *P. forbesi* appears to be partly due to the superior ability of its nauplii to escape the feeding currents of the Asian Clam (Kimmerer et al. 1994). The role of competition in the species replacement is not clear. However, *P. forbesi* did rapidly replace a previous invader, *P. inopinus*, in the

Columbia River estuary (Sytsma et al. 2004; Cordell et al. 2008). Similarly, the mechanism of species replacement of the native mysid *N. mercedis* by the two exotic mysids has not been studied. Competition has been suggested, but the invading mysids may be better adapted to the altered foodweb, or more tolerant to other environmental changes in this highly disturbed estuary. The invading species maintain a much smaller biomass than *N. mercedis*, probably reflecting the overall plankton biomass decline (Feyrer et al. 2003).

Thus, ecological impacts of the introduced copepods and mysids in the San Francisco estuary are reported, and may have a large effect magnitude, but certainty remains low. The changes in species composition and fish recruitment associated with the invasions occurred not just in the context of the *Corbula* invasion, but also in an environment affected by many anthropogenic disturbances, including pollution, water diversions, fishing pressure, and natural drought/flood cycles, resulting in drastic changes in river flow, salinity, suspended sediment, and water quality (Hobbs et al. 2006; Sommer et al. 2007).

## 4 Conclusions

In North America, crustaceans constitute a dominant component of the documented non-native marine diversity, whether considered at the continental scale or on individual coasts. While we have summarized the relative importance (percent contribution) of crustaceans to the recorded non-native diversity, as well as the contributions of different crustacean groups to these spatial scales, we advise some caution in interpreting these results. Certainly many invasions have gone undetected, creating the potential for strong biases in the available record, and understanding the scale and effects of such biases remain a significant challenge for invasion biology (Carlton 1996; Ruiz et al. 2000; Hewitt et al. 2004). Nonetheless, crustaceans provide a significant amount of the available knowledge about invasions in coastal marine systems.

Our analysis indicated that crustaceans not only contribute to the overall spatial patterns observed but also provide an important barometer for invasion dynamics. The relative difference in total non-native species richness among coasts was also reflected in the crustaceans, contributing 31–42% of the total on each coast (Fig. 2). The invasion record for crustaceans indicates the operation and importance of different transfer mechanisms in space and time. This record appears to have been particularly sensitive for detection of ballast-mediated introductions on the West coast, signaling the increased trade with Asia and delivery of low-salinity ballast water over the past few decades. The observed pattern for ballast introductions raises interesting hypotheses about the importance of source(s) and why a similar spike in ballast water introductions is not evident along the East and Gulf coasts, especially for copepods and mysids. In short, the crustaceans provide a good model for testing ideas about coastal invasions.

This study found that significant impacts were reported within tidal marine and estuarine waters of North America for at least 28% of the 108 non-native crustacean species documented here, spanning a range of impact types. Importantly, this analysis does not imply that the other species have no impact or even that effects of species are restricted to those observed. We have merely attempted to characterize effects that were observed at some spatial and temporal scale.

While impacts from crustacean invasions occur in North America, and some are well documented (e.g., effects of predation, biofouling, boring, and erosion), it is particularly challenging to understand the magnitude and spatial scale of effects. For most cases (72% of species with reported impacts), there was a low level of certainty about the magnitude of effects reported at some scale, due largely to (a) the lack of quantitative data and (b) the potential confounding effects of many other factors associated with observed changes.

Use of quantitative experiments can help address the issue of certainty in many cases, but the spatial and temporal extent of impacts still remains difficult to estimate in the field. Most experiments or studies are conducted over relatively small spatial and temporal scales. However, the application of these results to broader scales is poorly understood, because effects are expected to vary in both space and time, due to changes in population characteristics, local conditions, and scale-dependent processes (Diamond 1986; Parker et al. 1999; Ruiz et al. 1999).

The issues of variation and scale are not new or unique to the analysis of invasion impacts. While various approaches can be considered to integrate or represent effects across a species range (e.g., Parker et al. 1999), each requires an adequate foundation of measures that appears to be limited at the present time, even for those species where impacts are known. This is illustrated by the European crab *Carcinus maenas*, one of the best studied invaders with well-documented impacts in multiple geographic regions. For example, it is evident that the crab has caused significant population and community effects as an introduced predator in eastern North America, western North America, and Australia in a wide range of habitats (Glude 1955; Grosholz et al. 2000; Walton et al. 2002; Ross et al. 2004; Trussell et al. 2004; Griffen and Byers 2009; Kimbro et al. 2009). There are unusually good quantitative estimates in many of these cases, but most are limited in spatial scale and do not assess geographic variation. Yet, such measures are needed to evaluate the full scope of identified effects across a geographic range.

Overall, increasing quantitative measures for non-native species impacts is a high priority for invasion ecology. While invaders are a conspicuous and growing component of marine and estuarine communities (Cohen and Carlton 1998; Ruiz et al. 2000), there are many critical gaps in our understanding of ecological and economic effects for most species. In advancing research to address these gaps, it would be particularly useful to implement approaches that address the issues of spatial and temporal variation. Selecting a few species for standardized measures and experiments across multiple locations would be most valuable and an obvious next step in this direction. Crustaceans offer an excellent model for this purpose, due to (a) clear impacts that have been documented for some species, (b) the widespread nature of many non-native species (both within North America and globally), and (c) the extensive background knowledge about the biology and ecology of many groups (e.g., crabs and barnacles). In addition, past studies demonstrate that many species are conducive to experimental manipulations that quantify the magnitude of effects and can be replicated in space and time.

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## Appendix 1

Classification of distribution and impact type for non-native species of crustaceans considered established in tidal (marine and estuarine) waters of North America. Information included is as follows:

(a) **Taxonomic Group and Species** is provided for each crustacean classified as non-native and established in North America.

(b) **Coast** indicates which of the three North American coasts (P)acific, (A)tlantic, or (G)ulf; asterisk (*) indicates native to part of the coast indicated; (Cr)yptogenic indicates cryptogenic to Atlantic and Gulf coasts.

(c) **Salinity Range** characterizes known salinity distribution of the species as either Marine (M), Brackish Specialist (B), Freshwater (F), or Catadromous (C).

(d) **Impact Type** indicates the type of impact reported separately for each species in each of three habitat regions, including (1) marine and estuarine waters of North America, (2) freshwater inland lakes and rivers in North America, and (3) other global regions where the species has been introduced (i.e., not including the native region). For each of these habitat regions, the impact type is classified broadly into the following categories: P = effect(s) through predation including herbivory, C = effects through competition, X = effects through parasitism, F = effects as food or prey, H = effects through habitat alteration, T = effects on threatened or endangered species, and E = economic effects on fisheries resources, agricultural products, infrastructure (e.g., docks, piers, dams, water supply), powerplants, shipping, and recreation. Occurrence of each impact type is indicated in individual columns for the marine and estuarine region and combined into one column for the other two habitat regions. An impact was recorded for any of these categories only if it was reported to result in a significant change(s) in a target population, community, or economic resource. The final column (SUM) indicates the number of impact types reported in North America.

For a-c above, data and associated references are summarized in our database (available in NEMESIS 2009). For references on impact type on each species, see Appendix 3. Note that impact references are not an exhaustive list for all species; in cases where multiple sources demonstrated the same type of impact, a subset was selected that included quantitative measures with highest levels for effect magnitude and certainty (see text and Appendices 2 and 3). Additional references are available in NEMESIS (2009) and upon request.

| Taxonomic group and species | Coast | Salinity range | Impact type | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | North America | | | | | | | | | |
| | | | Marine and estuarine | | | | | | | Fresh | Other global regions | Sum |
| | | | P | C | X | F | H | T | E | | | |
| Cladocera | | | | | | | | | | | | |
| *Daphnia lumholtzi* | A, G, P | F | | | | | | | | F,C | | 0 |
| *Ilyocryptus agilis* | A | F | | | | | | | | | | 0 |
| Copepoda-Harpacticoida | | | | | | | | | | | | |
| *Harpacticella paradoxa* | P | F | | | | | | | | | | 0 |
| Copepoda-Calanoidea | | | | | | | | | | | | |
| *Acartiella sinensis* | P | B | | | | | | | | | | 0 |
| *Sinocalanus doerrii* | P | F | | 1 | | 1 | | | | | | 2 |
| *Pseudodiaptomus forbesi* | P | B | | 1 | | 1 | | 1 | | | | 3 |
| *Pseudodiaptomus inopinus* | P | B | | | | | | | | | | 0 |
| *Pseudodiaptomus marinus* | P | M | | 1 | | | | | | | | 1 |
| *Eurytemora affinis* (A subclade) | P | M | 1 | | | 1 | | 1 | | | | 3 |
| *Tortanus dextrilobatus* | P | B | 1 | | | | | | | | | 1 |
| Copepoda-Cyclopoida | | | | | | | | | | | | |
| *Lernaea cyprinacea* | A, P | F | | | 1 | | | | | X | | 1 |
| *Mytilicola orientalis* | P | M | | | 1 | | | | | | X | 1 |
| *Pseudomyicola ostreae* | P | M | | | | | | | | | | 0 |
| *Limnoithona sinensis* | P | F | | | | | | | | | | 0 |
| *Limnoithona tetraspina* | P | B | | 1 | | | | | | | | 1 |
| *Oithona davisae* | P | M | | | | | | | | | | 0 |
| Cirripedia-Rhizocephala | | | | | | | | | | | | |
| *Loxothylacus panopaei* | A | M | | | 1 | | | | | | | 1 |
| Cirripedia-Thoracica | | | | | | | | | | | | |
| *Amphibalanus amphitrite* | A; G; P | M | | 1 | | | | | 1 | | C,E | 2 |
| *Amphibalanus eburneus* | P | M | | | | | | | 1 | | E | 1 |
| *Amphibalanus improvisus* | P | B | | | | | | | 1 | | C,H,E | 1 |
| *Amphibalanus reticulatus* | A; G | M | | | | | | | 1 | | E | 1 |
| *Balanus trigonus* | A; G | M | | | | | | | 1 | | E | 1 |
| *Chthamalus fragilis* | A* | M | | | | | | | | | | 0 |
| *Megabalanus coccopoma* | A | M | | | | | | | | | | 0 |
| Ostracoda | | | | | | | | | | | | |
| *Eusarsiella zostericola* | P | M | | | | | | | | | | 0 |
| *Aspidoconcha limnoriae* | P | M | | | | | | | | | | 0 |

(continued)

| Taxonomic group and species | Coast | Salinity range | Impact type | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | North America | | | | | | | | | |
| | | | Marine and estuarine | | | | | | | Fresh | Other global regions | Sum |
| | | | P | C | X | F | H | T | E | | | |
| *Redekea californica* | P | M | | | | | | | | | | 0 |
| *Spinileberis quadriaculeata* | P | M | | | | | | | | | | 0 |
| *Kotoracythere inconspicua* | G | M | | | | | | | | | | 0 |
| Leptostraca | | | | | | | | | | | | |
| *Epinebalia* sp A. | P | M | | | | | | | | | | 0 |
| Mysidacea | | | | | | | | | | | | |
| *Deltamysis holmquistae* | P | B | | | | | | | | | | 0 |
| *Hyperacanthomysis longirostris* | P | B | | 1 | | 1 | | | | | | 2 |
| *Neomysis japonica* | P | M | | | | | | | | | | 0 |
| *Orientomysis aspera* | P | B | | | | | | | | | | 0 |
| *Orientomysis hwanhaiensis* | P | M | | | | | | | | | | 0 |
| *Praunus flexuosus* | A | M | | | | | | | | | | 0 |
| Cumacea | | | | | | | | | | | | |
| *Nippoleucon hinumensis* | P | M | | | | | | | | | | 0 |
| Isopoda | | | | | | | | | | | | |
| *Asellus hilgendorfi* | P | F | | | | | | | | | | 0 |
| *Caecidotea racovitzai* | P | F | | | | | | | | | | 0 |
| *Caecijaera horvathi* | P | M | | | | | | | | | | 0 |
| *Dynoides dentisinus* | P | M | | | | | | | | | | 0 |
| *Eurylana arcuata* | P | M | | | | | | | | | | 0 |
| *Gnorimosphaeroma rayi* | P | M | | | | | | | | | | 0 |
| *Iais californica* | P | M | | | | | | | | | | 0 |
| *Iais floridana* | A; G | M | | | | | | | | | | 0 |
| *Ianiropsis* sp. | A | M | | | | | | | | | | 0 |
| *Ligia exotica* | A; G | M | | | | | | | | | | 0 |
| *Ligia oceanica* | A | M | | | | | | | | | | 0 |
| *Limnoria pfefferi* | A; G | M | | | | | | | | | | 0 |
| *Limnoria quadripunctata* | P | M | | | | | | | 1 | | E | 1 |
| *Limnoria tripunctata* | P (Cr) | M | | | | | | | 1 | | E | 1 |
| *Paracerceis sculpta* | A | M | | | | | | | | | | 0 |
| *Paradella dianae* | A; G | M | | | | | | | | | | 0 |
| *Paranthura japonica* | P | M | | | | | | | | | | 0 |
| *Pseudosphaeroma campbellensis* | P | M | | | | | | | | | | 0 |
| *Sphaeroma quoianum* | P | M | | | | | 1 | | 1 | | | 2 |
| *Sphaeroma terebrans* | A; G | M; F | | | | | 1 | | 1 | | | 2 |
| *Sphaeroma walkeri* | A; G; P | M | | | | | | | | | | 0 |
| *Synidotea laevidorsalis* | A; P | M | | | | | | | | | | 0 |
| *Uromunna sp. A* | P | B | | | | | | | | | | 0 |

(continued)

| Taxonomic group and species | Coast | Salinity range | Impact type | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | North America | | | | | | | | | |
| | | | Marine and estuarine | | | | | | | Fresh | Other global regions | Sum |
| | | | P | C | X | F | H | T | E | | | |
| Tanaidacea | | | | | | | | | | | | |
| *Sinelobus cf. stanfordi* | P | M | | | | | | | | | | 0 |
| Amphipoda-Gammaridea | | | | | | | | | | | | |
| *Abludomelita rylovae* | P | M | | | | | | | | | | 0 |
| *Ampelisca abdita* | P | M | 1 | 1 | | | | | | | | 2 |
| *Ampithoe longimana* | P | M | | | | | | | | | | 0 |
| *Ampithoe valida* | P | M | | | | | | | | | | 0 |
| *Aoroides secunda* | P | M | | | | | | | | | | 0 |
| *Chelura terebrans* | P (Cr) | M | | | | | | | 1 | | | 1 |
| *Crangonyx floridanus* | P | F | | | | | | | | | | 0 |
| *Crangonyx pseudogracilis* | P | F | | | | | | | | | C | 0 |
| *Echinogammarus ischnus* | A | F | | | | | | | | C | C | 0 |
| *Eochelidium miraculum* | P | M | | | | | | | | | | 0 |
| *Eochelidium* sp. A | P | M | | | | | | | | | | 0 |
| *Gammarus daiberi* | P | B | | | | 1 | | | | | | 1 |
| *Gammarus tigrinus* | A | B | | | | | | | | | C,P | 0 |
| *Gitanopsis* sp. | A | M | | | | | | | | | | 0 |
| *Grandidierella japonica* | P | M | | | | | | | | | | 0 |
| *Incisocalliope derzhavini* | P | M | | | | | | | | | | 0 |
| *Jassa marmorata* | P | M | | 1 | | | | | | | | 1 |
| *Melita nitida* | P | M | | | | | | | | | | 0 |
| *Microdeutopus gryllotalpa* | A; P | M | 1 | | | | | | | | | 1 |
| *Monocorophium acherusicum* | P (Cr) | M | 1 | 1 | | | 1 | | | | C | 3 |
| *Monocorophium insidiosum* | P (Cr) | M | | | | | | | | | | 0 |
| *Monocorophium uenoi* | P | M | | | | | | | | | | 0 |
| *Paracorophium lucasi* | P | M | | | | | | | | | | 0 |
| *Paradexamine* sp. | P | M | | | | | | | | | | 0 |
| *Corophium alienense* | P | M | | | | | | | | | | 0 |
| *Corophium heteroceratum* | P | M | | | | | | | | | | 0 |
| *Stenothoe valida* | P | M | | | | | | | | | | 0 |
| *Transorchestia enigmatica* | P | M | | | | | | | | | | 0 |
| Amphipoda-Caprellidea | | | | | | | | | | | | |
| *Caprella drepanochir* | P* | M | | | | | | | | | | 0 |
| *Caprella mutica* | A; P | M | | | | | | | | | C | 0 |
| *Caprella scaura* | A; G; P | M | | | | | | | | | | 0 |
| *Caprella simia* | P | M | | | | | | | | | | 0 |
| Decapoda-Anomura | | | | | | | | | | | | |
| *Petrolisthes armatus* | A* | M | | 1 | | 1 | 1 | | | | | 3 |
| *Upogebia affinis* | A* | M | | | | | | | | | | 0 |

(continued)

| Taxonomic group and species | Coast | Salinity range | Impact type | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | North America | | | | | | | | | |
| | | | Marine and estuarine | | | | | | | Fresh | Other global regions | Sum |
| | | | P | C | X | F | H | T | E | | | |
| Decapoda-Astacoidea | | | | | | | | | | | | |
| *Orconectes virilis* | A; P | F | | | | | | | | C,E | | 0 |
| *Pacifastacus leniusculus* | P* | F | | | | | | | | C,T,E | | 0 |
| *Procambarus clarkii* | A; G*; P | F | | | | | | | | H,E | | 0 |
| Decapoda-Caridea | | | | | | | | | | | | |
| *Exopalaemon modestus* | P | F | | 1 | | | | | | | | 1 |
| *Macrobrachium olfersii* | A; G | C | | | | | | | | | | 0 |
| *Palaemon macrodactylus* | P | M | | | | | | | | | | 0 |
| Decapoda-Brachyura | | | | | | | | | | | | |
| *Carcinus maenas* | A; P | M | 1 | 1 | | | | | 1 | | P,C,E | 3 |
| *Charybdis hellerii* | A; G | M | | | | | | | | | | 0 |
| *Eriocheir sinensis* | P; A | C | | | | | 1 | 1 | 1 | | H,E | 3 |
| *Eurypanopeus depressus* | A* | M | | | | | | | | | | 0 |
| *Hemigrapsus sanguineus* | A | M | 1 | 1 | | | | | | | | 2 |
| *Platychirograpsus spectabilis* | G | C | | | | | | | | | | 0 |
| *Rhithropanopeus harrisii* | P | B | | | | | | | | | | 0 |

## Appendix 2

Classification of information type and effect magnitude for non-native species of crustaceans considered established in tidal (marine and estuarine) waters of North America. Information included is as follows:

(a) **Taxonomic Group and Species** is provided for each crustacean classified as non-native and established in North America.

(b) **Information Type** indicates the quality of information source that reported an impact. Information type was classified as one of the following: 1 = qualitative information (including best professional judgment); 2 = presence/absence data that indicate a measureable change associated with the occurrence of the non-native species; 3 = mechanistic or autoecological data that infer impact has occurred; 4 = correlative data that demonstrates a quantitative relationship between the invader (presence or abundance) and an effect; 5 = controlled laboratory experiment(s); 6 = controlled field experiment(s). Information type is shown for the same categories and format as outlined above (see Impact Type); MAX indicates the highest numerical value recorded for Information Type for North America.

(continued on page xx)

| Taxonomic group & species | Information type | | | | | | | | | | Effect magnitude | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | North America | | | | | | | | Other global regions | Max |
| | Marine and estuarine | | | | | | | Fresh | | | Marine and estuarine | | | | | | | Fresh | | |
| | P | C | X | F | H | T | E | | | | P | C | X | F | H | T | E | | | |
| Cladocera | | | | | | | | | | | | | | | | | | | | |
| *Daphnia lumholtzi* | | | | | | | | 4,5 | | 0 | | | | | | | | | | 0 |
| *Ilyocryptus agilis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Copepoda-Harpacticoida | | | | | | | | | | | | | | | | | | | | |
| *Harpacticella paradoxa* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Copepoda-Calanoidea | | | | | | | | | | | | | | | | | | | | |
| *Acartiella sinensis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Sinocalanus doerrii* | | 4 | | 3,4 | | | | | | 4 | | 4 | | 3 | | | | | | 4 |
| *Pseudodiaptomus forbesi* | | 4 | | 3,4 | | 4 | | | | 4 | | 4 | | 3 | | 4 | | | | 4 |
| *Pseudodiaptomus inopinus* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Pseudodiaptomus marinus* | | 2 | | | | | | | | 2 | | 4 | | | | | | | | 4 |
| *Eurytemora affinis* (A subclade) | 3 | | | 3 | | 3 | | | | 3 | 0 | | | 0 | | 0 | | | | 0 |
| *Tortanus dextrilobatus* | 3,5 | | | | | | | | | 5 | 3 | | | | | | | | | 3 |
| Copepoda-Cyclopoida | | | | | | | | | | | | | | | | | | | | |
| *Lernaea cyprinacea* | | | 2 | | | | | | | 2 | | | 0 | | | | | | | 0 |
| *Mytilicola orientalis* | | | 2 | | | | | | 2 | 2 | | | 2 | | | | | | 2 | 2 |
| *Pseudomyicola ostreae* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Limnoithona sinensis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Limnoithona tetraspina* | | 4 | | | | | | | | 4 | | 4 | | | | | | | | 4 |
| *Oithona davisae* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Cirripedia-Rhizocephala | | | | | | | | | | | | | | | | | | | | |
| *Loxothylacus panopaei* | | 3,5 | | | | | | | | 5 | | 0 | | | | | | | | 0 |
| Cirripedia-Thoracica | | | | | | | | | | | | | | | | | | | | |
| *Amphibalanus amphitrite* | | 4 | | | | | 2,3,4 | | 2 | 4 | | 0 | | | | | 0 | | 4 | 0 |
| *Amphibalanus eburneus* | | | | | | | 2,3 | | 2,3 | 3 | | | | | | | 0 | | 0 | 0 |
| *Amphibalanus improvisus* | | | | | | | 2,3 | | 2,3,6 | 3 | | | | | | | 0 | | 0–3 | 0 |
| *Amphibalanus reticulatus* | | | | | | | 2,3 | | 2,3 | 3 | | | | | | | 0 | | 0 | 0 |
| *Balanus trigonus* | | | | | | | 2,3 | | 2,3 | 3 | | | | | | | 0 | | 0 | 0 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chthamalus fragilis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Megabalanus coccopoma* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Ostracoda | | | | | | | | | | | | | | | | | | | | |
| *Eusarsiella zostericola* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Aspidoconcha limnoriae* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Redekea californica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Spinileberis quadriaculeata* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Kotoracythere inconspicua* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Leptostraca | | | | | | | | | | | | | | | | | | | | |
| *Epinebalia* sp A. | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Mysidacea | | | | | | | | | | | | | | | | | | | | |
| *Deltamysis holmquistae* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Hyperacanthomysis longirostris* | | 4 | | 3,4 | | | | | | 4 | | 4 | | 4 | | | | | | 4 |
| *Neomysis japonica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Orientomysis aspera* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Orientomysis hwanhaiensis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Praunus flexuosus* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Cumacea | | | | | | | | | | | | | | | | | | | | |
| *Nippoleucon hinumensis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Isopoda | | | | | | | | | | | | | | | | | | | | |
| *Asellus hilgendorfi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Caecidotea racovitzai* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Caecijaera horvathi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Dynoides dentisinus* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Eurylana arcuata* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Gnorimosphaeroma rayi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Iais californica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Iais floridana* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Ianiropsis* sp. | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Ligia exotica* | | | | | | | | | | 0 | | | | | | | | | | 0 |

(continued)

| Taxonomic group & species | Information type | | | | | | | | | | Effect magnitude | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | North America | | | | | | | | Other global regions | Max |
| | Marine and estuarine | | | | | | | Fresh | | | Marine and estuarine | | | | | | | Fresh | | |
| | P | C | X | F | H | T | E | | | | P | C | X | F | H | T | E | | | |
| *Ligia oceanica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Limnoria pfefferi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Limnoria quadripunctata* | | | | | | | 2,3 | | 2,3 | 3 | | | | | | | 4 | | 4 | 4 |
| *Limnoria tripunctata* | | | | | | | 2,3 | | 2,3 | 3 | | | | | | | 4 | | 4 | 4 |
| *Paracerceis sculpta* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Paradella dianae* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Paranthura japonica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Pseudosphaeroma campbellensis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Sphaeroma quoianum* | | | | | 3,5,6 | | 3,5,6 | | | 6 | | | | | 4 | | 4 | | | 4 |
| *Sphaeroma terebrans* | | | | | 3 | | 3 | | | 3 | | | | | 0 | | 1 | | | 1 |
| *Sphaeroma walkeri* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Synidotea laevidorsalis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Uromunna sp. A* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Tanaidacea | | | | | | | | | | | | | | | | | | | | |
| *Sinelobus cf. stanfordi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Amphipoda-Gammaridea | | | | | | | | | | | | | | | | | | | | |
| *Abludomelita rylovae* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Ampelisca abdita* | 4 | 4 | | | | | | | | 4 | 2 | 2 | | | | | | | | 2 |
| *Ampithoe longimana* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Ampithoe valida* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Aoroides secunda* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Chelura terebrans* | | | | | | | 3 | | | 3 | | | | | | | 1 | | | 1 |
| *Crangonyx floridanus* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Crangonyx pseudogracilis* | | | | | | | | | 4 | 0 | | | | | | | | | 2 | 0 |
| *Echinogammarus ischnus* | | | | | | | | 5,6 | 5,6 | 0 | | | | | | | | 2 | 2 | 0 |
| *Eochelidium miraculum* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Eochelidium* sp. A | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Gammarus daiberi* | | | | 1 | | | | | | 1 | | | | 0 | | | | | | 0 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gammarus tigrinus* | | | | | | | | | 5 | 0 | | | | | | | | | 4 | 0 |
| *Gitanopsis* sp. | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Grandidierella japonica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Incisocalliope derzhavini* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Jassa marmorata* | | 1 | | | | | | | | 1 | | 0 | | | | | | | | 0 |
| *Melita nitida* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Microdeutopus gryllotalpa* | 6 | | | | | | | | | 6 | 3 | | | | | | | | | 3 |
| *Monocorophium acherusicum* | 4 | 1 | | | 1 | | | | 1 | 4 | 2 | 0 | | | 0 | | | | 0 | 2 |
| *Monocorophium insidiosum* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Monocorophium uenoi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Paracorophium lucasi* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Paradexamine* sp. | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Corophium alienense* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Corophium heteroceratum* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Stenothoe valida* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Transorchestia enigmatica* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Amphipoda-Caprellidea | | | | | | | | | | | | | | | | | | | | |
| *Caprella drepanochir* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Caprella mutica* | | | | | | | | | 5 | 0 | | | | | | | | | 4 | 0 |
| *Caprella scaura* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Caprella simia* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Decapoda-Anomura | | | | | | | | | | | | | | | | | | | | |
| *Petrolisthes armatus* | | 6 | | 5 | 6 | | | | | 6 | | 2 | | 2 | 2 | | | | | 2 |
| *Upogebia affinis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| Decapoda-Astacoidea | | | | | | | | | | | | | | | | | | | | |
| *Orconectes virilis* | | | | | | | | 4 | | 0 | | | | | | | | 3 | | 0 |
| *Pacifastacus leniusculus* | | | | | | | | 1 | | 0 | | | | | | | | 1 | | 0 |
| *Procambarus clarkii* | | | | | | | | 1 | | 0 | | | | | | | | 1 | | 0 |
| Decapoda-Caridea | | | | | | | | | | | | | | | | | | | | |
| *Exopalaemon modestus* | | 4 | | | | | | | | 4 | | 4 | | | | | | | | 4 |
| *Macrobrachium olfersii* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Palaemon macrodactylus* | | | | | | | | | | 0 | | | | | | | | | | 0 |

(continued)

| Taxonomic group & species | Information type | | | | | | | | | | Effect magnitude | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | North America | | | | | | | | Other global regions | Max |
| | Marine and estuarine | | | | | | | Fresh | | | Marine and estuarine | | | | | | | Fresh | | |
| | P | C | X | F | H | T | E | | | | P | C | X | F | H | T | E | | | |
| Decapoda-Brachyura | | | | | | | | | | | | | | | | | | | | |
| *Carcinus maenas* | 1–6 | 1–6 | | | | | 3 | | 1–6 | 6 | 3 | 3 | | | | | 2 | | 1–3 | 3 |
| *Charybdis hellerii* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Eriocheir sinensis* | | | | | 1–3 | 1–3 | 1–3 | | 1–3 | 3 | | | | | 1 | 0 | 4 | | 1–4 | 4 |
| *Eurypanopeus depressus* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Hemigrapsus sanguineus* | 1–6 | 1–6 | | | | | | | | 6 | 4 | 4 | | | | | | | | 4 |
| *Platychirograpsus spectabilis* | | | | | | | | | | 0 | | | | | | | | | | 0 |
| *Rhithropanopeus harrisii* | | | | | | | | | | 0 | | | | | | | | | | 0 |

(c) **Effect Magnitude** indicates an estimate of the reported effect size or magnitude. The magnitude was estimated from the original source(s) for each Impact Type and classified as one of the following: 0 = undescribed or unassessed (in cases where a significant impact is reported); 1 = an effect of <10% change; 2 = an effect of 10–50% change; 3 = an effect of 50–75% change; 4 = an effect of >75% change. Information type is shown for the same categories and format as outlined above (see Impact Type); MAX indicates the highest numerical value recorded for Effect Magnitude for North America.

For references associated with impact characteristics of each species, see Appendix 3. Note that impact references are not an exhaustive list for all species; in cases where multiple sources demonstrated the same type of impact, a subset was selected that included quantitative measures with highest levels for effect magnitude and certainty (see text and Appendices 2 and 3). Additional references are available in NEMESIS (2009) and upon request.

## Appendix 3

Classification of certainty that observed effects were caused by the respective non-native species of crustaceans considered established in tidal (marine and estuarine) waters of North America. Information included is as follows:

(a) **Taxonomic Group and Species** is provided for each crustacean classified as non-native and established in North America.
(b) **Certainty** provides a qualitative and categorical index of the strength of inference about impact magnitude reported. This is derived from the information type, where certainty or confidence in available impact estimates is considered low in the absence of quantitative estimates or the ability to partition effects among multiple (confounding) factors. Values are: 1 = low, 2 = medium, 3 = high. Information type is shown for the same categories and format as outlined above (see Impact Type); MAX indicates the highest numerical value recorded for Certainty for North America.
(c) **Impact References** shows the source(s) of information used to generate the above information matrix. Note that impact references are not an exhaustive list for all species; in cases where multiple sources demonstrated the same type of impact, a subset was selected that included quantitative measures with highest levels for effect magnitude and certainty (see text and Appendices 2 and 3). Additional references are available in NEMESIS (2009) and upon request.

| Taxonomic group & species | Certainty | | | | | | | | | | Impact references (N. American marine-estuarine in bold) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | |
| | Marine and estuarine | | | | | | | Fresh | | | |
| | P | C | X | F | H | T | E | | | | |
| Cladocera | | | | | | | | | | | |
| *Daphnia lumholtzi* | | | | | | | | | | 0 | Swaffar and O'Brien 1996; Kolar and Wahl 1998; Johnson and Havel 2001 |
| *Ilyocryptus agilis* | | | | | | | | | | 0 | |
| Copepoda-Harpacticoida | | | | | | | | | | | |
| *Harpacticella paradoxa* | | | | | | | | | | 0 | |
| Copepoda-Calanoidea | | | | | | | | | | | |
| *Acartiella sinensis* | | | | | | | | | | 0 | |
| *Sinocalanus doerrii* | | 1 | | 1 | | | | | | 1 | **Meng and Orsi** 1991 |
| *Pseudodiaptomus forbesi* | | 1 | | 1 | | 1 | | | | 1 | **Meng and Orsi** 1991**; Orsi and Walter** 1991**; Baxter et al.** 2008**; Sytsma et al.** 2004**; Cordell et al.** 2008 |
| *Pseudodiaptomus inopinus* | | | | | | | | | | 0 | |
| *Pseudodiaptomus marinus* | | 1 | | | | | | | | 1 | **Fleminger and Kramer** 1988 |
| *Eurytemora affinis* (A subclade) | 1 | | | 1 | | 1 | | | | 1 | **Ambler et al.** 1985**; Meng and Orsi** 1991**; Bryant and Arnold** 2007 |
| *Tortanus dextrilobatus* | 3 | | | | | | | | | 3 | **Hooff and Bollens** 2004 |
| Copepoda-Cyclopoida | | | | | | | | | | | |
| *Lernaea cyprinacea* | | | 1 | | | | | | | 1 | Haley and Winn 1959; Tidd and Shields 1963, Hoffman 1967; Khalifa and Post 1976 |
| *Mytilicola orientalis* | | | 1 | | | | | | 1 | 1 | **Odlaug** 1946**; Katkansky et al.** 1967; Steele and Mulcahy 2006 |
| *Pseudomyicola ostreae* | | | | | | | | | | 0 | |
| *Limnoithona sinensis* | | | | | | | | | | 0 | |
| *Limnoithona tetraspina* | | | 1 | | | | | | | 1 | **Bouley and Kimmerer** 2006**; Cordell et al.** 2008 |
| *Oithona davisae* | | | | | | | | | | 0 | |

(continued)

| | Certainty | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | | Impact references (N. American marine-estuarine in bold) |
| | Marine and estuarine | | | | | | | | | | |
| Taxonomic group & species | P | C | X | F | H | T | E | Fresh | | Max | |
| Cirripedia-Rhizocephala | | | | | | | | | | | |
| *Loxothylacus panopaei* | | | 1 | | | | | | | 1 | **Alvarez et al.** 1995**; Hines et al.** 1997**; Kruse and Hare** 2007 |
| Cirripedia-Thoracica | | | | | | | | | | | |
| *Amphibalanus amphitrite* | | 1 | | | | | 1 | | 1 | 1 | **Visscher** 1927**; Moore and Frue** 1959**; Sutherland and Karlson** 1977**; Bros** 1987**;** Zvyagintsev 2003; Boudreaux et al. 2009**;** |
| *Amphibalanus eburneus* | | | | | | | 1 | | 1 | 1 | **Visscher** 1927**; Moore and Frue** 1959**;** |
| *Amphibalanus improvisus* | | | | | | | 1 | | 1–3 | 1 | Vuorinen et al. 1986; Zvyagintsev 2003; Dürr and Wahl 2004; Kotta et al. 2007 |
| *Amphibalanus reticulatus* | | | | | | | 1 | | 1 | 1 | Utinomi 1970; **Moore et al.** 1974 |
| *Balanus trigonus* | | | | | | | 1 | | 1 | 1 | Zevina 1988 |
| *Chthamalus fragilis* | | | | | | | | | | 0 | |
| *Megabalanus coccopoma* | | | | | | | | | | 0 | |
| Ostracoda | | | | | | | | | | | |
| *Eusarsiella zostericola* | | | | | | | | | | 0 | |
| *Aspidoconcha limnoriae* | | | | | | | | | | 0 | |
| *Redekea californica* | | | | | | | | | | 0 | |
| *Spinileberis quadriaculeata* | | | | | | | | | | 0 | |
| *Kotoracythere inconspicua* | | | | | | | | | | 0 | |
| Leptostraca | | | | | | | | | | | |
| *Epinebalia* sp A. | | | | | | | | | | 0 | |
| Mysidacea | | | | | | | | | | | |
| *Deltamysis holmquistae* | | | | | | | | | | 0 | |
| *Hyperacanthomysis longirostris* | | 1 | | 1 | | | | | | 1 | **Feyrer et al.** 2003**; Nobriga and Feyrer** 2008 |
| *Neomysis japonica* | | | | | | | | | | 0 | |
| *Orientomysis aspera* | | | | | | | | | | 0 | **Nobriga and Feyrer** 2008 |

(continued)

| Taxonomic group & species | Certainty | | | | | | | | | | Impact references (N. American marine-estuarine in bold) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | |
| | Marine and estuarine | | | | | | | Fresh | | | |
| | P | C | X | F | H | T | E | | | | |
| *Orientomysis hwanhaiensis* | | | | | | | | | | 0 | |
| *Praunus flexuosus* | | | | | | | | | | 0 | |
| Cumacea | | | | | | | | | | | |
| *Nippoleucon hinumensis* | | | | | | | | | | 0 | |
| Isopoda | | | | | | | | | | | |
| *Asellus hilgendorfi* | | | | | | | | | | 0 | |
| *Caecidotea racovitzai* | | | | | | | | | | 0 | |
| *Caecijaera horvathi* | | | | | | | | | | 0 | |
| *Dynoides dentisinus* | | | | | | | | | | 0 | |
| *Eurylana arcuata* | | | | | | | | | | 0 | |
| *Gnorimosphaeroma rayi* | | | | | | | | | | 0 | |
| *Iais californica* | | | | | | | | | | 0 | |
| *Iais floridana* | | | | | | | | | | 0 | |
| *Ianiropsis* sp. | | | | | | | | | | 0 | |
| *Ligia exotica* | | | | | | | | | | 0 | |
| *Ligia oceanica* | | | | | | | | | | 0 | |
| *Limnoria pfefferi* | | | | | | | | | | 0 | |
| *Limnoria quadripunctata* | | | | | | | 3 | | 3 | 3 | Eltringham and Hockley 1967; Coughlan 1977; **Carlton** 1979**; Cohen and Carlton** 1995 |
| *Limnoria tripunctata* | | | | | | | 3 | | 3 | 3 | Eltringham and Hockley 1967; Coughlan 1977; **Carlton** 1979**; Quayle** 1992**; Cohen and Carlton** 1995 |
| *Paracerceis sculpta* | | | | | | | | | | 0 | |
| *Paradella dianae* | | | | | | | | | | 0 | |
| *Paranthura japonica* | | | | | | | | | | 0 | |
| *Pseudosphaeroma campbellensis* | | | | | | | | | | 0 | |
| *Sphaeroma quoianum* | | | | | 3 | | 3 | | | 3 | **Talley et al.** 2001**; Higgins (cited by Davidson** 2006**); Davidson** 2006 |
| *Sphaeroma terebrans* | | | | | 1 | | 1 | | | 1 | **Rehm and Humm** 1973**; Conover and Reid** 1975**; Simberloff et al.** 1978**; Ribi** 1982; Villalobos 1985; **Estevez** 1994 |
| *Sphaeroma walkeri* | | | | | | | | | | 0 | |

(continued)

| Taxonomic group & species | Certainty | | | | | | | | | | Impact references (N. American marine-estuarine in bold) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | |
| | Marine and estuarine | | | | | | | | | | |
| | P | C | X | F | H | T | E | Fresh | | | |
| *Synidotea laevidorsalis* | | | | | | | | | | 0 | |
| *Uromunna sp. A* | | | | | | | | | | 0 | |
| Tanaidacea | | | | | | | | | | | |
| *Sinelobus cf. stanfordi* | | | | | | | | | | 0 | |
| Amphipoda-Gammaridea | | | | | | | | | | | |
| *Abludomelita rylovae* | | | | | | | | | | 0 | |
| *Ampelisca abdita* | 1 | 1 | | | | | | | | 1 | **Nichols and Thompson** 1985 |
| *Ampithoe longimana* | | | | | | | | | | 0 | |
| *Ampithoe valida* | | | | | | | | | | 0 | |
| *Aoroides secunda* | | | | | | | | | | 0 | |
| *Chelura terebrans* | | | | | | | 1 | | | 1 | **Barnard** 1950**;** **Barnard** 1955; **Wallour** 1960**;** Kuhne and Becker 1964 |
| *Crangonyx floridanus* | | | | | | | | | | 0 | |
| *Crangonyx pseudogracilis* | | | | | | | | | 1 | 0 | |
| *Echinogammarus ischnus* | | | | | | | | | 3 | 0 | |
| *Eochelidium miraculum* | | | | | | | | | | 0 | |
| *Eochelidium* sp. A | | | | | | | | | | 0 | |
| *Gammarus daiberi* | | | | 1 | | | | | | 1 | **Nobriga and Feyrer** 2008**; Grimaldo et al.** 2009 |
| *Gammarus tigrinus* | | | | | | | | | 3 | 0 | **Van Riel et al.** 2007 |
| *Gitanopsis* sp. | | | | | | | | | | 0 | |
| *Grandidierella japonica* | | | | | | | | | | 0 | **West et al.** 2003**; Whitcraft et al.** 2008 |
| *Incisocalliope derzhavini* | | | | | | | | | | 0 | |
| *Jassa marmorata* | | 1 | | | | | | | | 1 | |
| *Melita nitida* | | | | | | | | | | 0 | |
| *Microdeutopus gryllotalpa* | 3 | | | | | | | | | 3 | **Hauxwell et al.** 1998 |
| *Monocorophium acherusicum* | 1 | 1 | | | 1 | | | | 1 | 1 | **Barnard** 1958; Onbe 1966; Talman et al. 1999 |
| *Monocorophium insidiosum* | | | | | | | | | | 0 | |
| *Monocorophium uenoi* | | | | | | | | | | 0 | |
| *Paracorophium lucasi* | | | | | | | | | | 0 | |
| *Paradexamine* sp. | | | | | | | | | | 0 | |
| *Corophium alienense* | | | | | | | | | | 0 | |
| *Corophium heteroceratum* | | | | | | | | | | 0 | |

(continued)

| Taxonomic group & species | Certainty | | | | | | | | | | Impact references (N. American marine-estuarine in bold) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | Max | |
| | Marine and estuarine | | | | | | | Fresh | | | |
| | P | C | X | F | H | T | E | | | | |
| *Stenothoe valida* | | | | | | | | | | 0 | |
| *Transorchestia enigmatica* | | | | | | | | | | 0 | |
| Amphipoda-Caprellidea | | | | | | | | | | | |
| *Caprella drepanochir* | | | | | | | | | | 0 | |
| *Caprella mutica* | | | | | | | | | 2 | 0 | **Page et al.** 2007; Shucksmith et al. 2009 |
| *Caprella scaura* | | | | | | | | | | 0 | |
| *Caprella simia* | | | | | | | | | | 0 | |
| Decapoda-Anomura | | | | | | | | | | | |
| *Petrolisthes armatus* | | 3 | | 3 | 3 | | | | | 3 | **Hollebone and Hay** 2008 |
| *Upogebia affinis* | | | | | | | | | | 0 | |
| Decapoda-Astacoidea | | | | | | | | | | | |
| *Orconectes virilis* | | | | | | | | 1 | | 0 | Schwartz et al. 1963 |
| *Pacifastacus leniusculus* | | | | | | | | 1 | | 0 | Cohen and Carlton 1995; Taugbøl and Johnsen 2006 |
| *Procambarus clarkii* | | | | | | | | 1 | | 0 | Cohen and Carlton 1995 |
| Decapoda-Caridea | | | | | | | | | | | |
| *Exopalaemon modestus* | | 1 | | | | | | | | 1 | **Hieb** 2006**; Nobriga and Feyrer** 2008 |
| *Macrobrachium olfersii* | | | | | | | | | | 0 | |
| *Palaemon macrodactylus* | | | | | | | | | | 0 | |
| Decapoda-Brachyura | | | | | | | | | | | |
| *Carcinus maenas* | 3 | 2 | | | | | 2 | | 1–3 | 3 | **Vermeij** 1982**; Grosholz et al.** 2000**; Jensen et al.** 2002**;** Walton et al. 2002; **Trussell et al.** 2004**; Floyd and Williams** 2004**; Griffen and Byers** 2006**;** Grosholz et al (in review) |
| *Charybdis hellerii* | | | | | | | | | | 0 | |
| *Eriocheir sinensis* | | | | | 1 | 1 | 3 | | 1–3 | 3 | Panning 1939; **Rudnick et al.** 2003**; Chinese mitten crab Working Group** 2003**; Rudnick et al.** 2005 |
| *Eurypanopeus depressus* | | | | | | | | | | 0 | |

(continued)

| | Certainty | | | | | | | | | | Impact references (N. American marine-estuarine in bold) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | North America | | | | | | | | Other global regions | | |
| | Marine and estuarine | | | | | | | | | | |
| Taxonomic group & species | P | C | X | F | H | T | E | Fresh | | Max | |
| *Hemigrapsus sanguineus* | 3 | 3 | | | | | | | | 3 | **Jensen et al.** 2002; **Lohrer and Whitlatch** 2002; **Griffen and Byers** 2006; **Tyrrell et al.** 2006; **Griffen and Delaney** 2007; **Griffen et al.** 2008 |
| *Platychirograpsus spectabilis* | | | | | | | | | | 0 | |
| *Rhithropanopeus harrisii* | | | | | | | | | | 0 | **Cohen and Carlton** 1995; Zaitsev and Öztürk 2001, cited by Roche and Torchin 2007 |

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# Alien Decapod Crustaceans in the Southwestern Atlantic Ocean

**Marcos Tavares**

**Abstract** Thirteen marine alien species of decapod crustaceans have been recorded from the Southwestern Atlantic. Five species of alien decapods have established local populations: *Charybdis hellerii* (Brazil), *Eurypanopeus depressus* (Uruguay and Argentina), *Palaemon macrodactylus* (Argentina), *Pyromaia tuberculata* (Brazil and Argentina) and *Rhithropanopeus harrisii* (Brazil). The history and distribution of these species is reviewed. Also discussed is the local penaeid shrimp culture, entirely based on introduced species. The early warning detection system for alien marine species in the Southwestern Atlantic is largely informal and is mainly the by-product of ecological studies and local faunal inventories. Poor taxonomic resolution and misinterpretation of disjunct ranges (or even continuous ranges) as "natural" patterns, may be the reason so few decapods are considered alien in the region. This may well apply to other marine invertebrates in the Southwestern Atlantic.

## 1 Introduction

Although the Southwestern Atlantic coast harbours a diverse array of alien marine invertebrates (Orensanz et al. 2002; Tavares and Mendonca 2004; Lopes 2009), only five of these are decapod crustaceans. Reviewed here is the history and distribution of these five species. Also discussed is the current state of penaeid shrimp culture, which is based upon alien species. An Appendix summarizes additional records of alien decapods based upon single specimens (Table 1; Figs. 1c, d and 2b, d). For the purposes of the present contribution the Southwestern Atlantic

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**Table 1** Alien marine decapod crustaceans recorded to the Southwestern Atlantic based upon single specimens (SWA). Note that *Acidops cessacii* (A. Milne-Edwards, 1878) suspected to be introduced in Brazil (Tavares and Mendonca 2004) actually has long been overlooked and is common in the San Peter and San Paul Archipelago (00°55′ e 29°21”W) (Tavares, unpublished data). IWP, Indo-West Pacific. EA, Eastern Atlantic. EP, Eastern Pacific. AR, Argentina. BR, Brazil. CSR, circum-subantarctic region. UR, Uruguay

| Species | Significant references | Natural range | Occurrence in SWA | Vector |
|---|---|---|---|---|
| *Bellia picta* H. Milne Edwards, 1848 | Melo 1989; Tavares and Mendonca 2004 | EP | BR | Shipping |
| *Cancer pagurus* Linnaeus, 1758 | Tavares and Mendonca 2004 | EA | BR | Shipping |
| *Halicarcinus planatus* (Fabricius, 1775) | Tavares 2003 | EP, AR, CSR, UR | BR | Shellfish culture |
| *Liocarcinus navigator* (Herbst, 1794) | Melo and Crivelaro 2002 | EA | BR | Shipping |
| *Metapenaeus monoceros* (Fabricius, 1798) | D'Incao 1995 | IWP | BR | Shipping |
| *Pilumnoides perlatus* (Poeppig, 1836) | Melo et al. 2000 | EP | BR | Shipping |
| *Scylla serrata* (Forskål, 1775) | Melo 1983; Tavares and Mendonca 2004 | IWP | BR | Shipping |
| *Taliepus dentatus* (H. Milne Edwards, 1834) | Melo 1996; Tavares and Mendonca 2004 | EP | BR | Shipping |

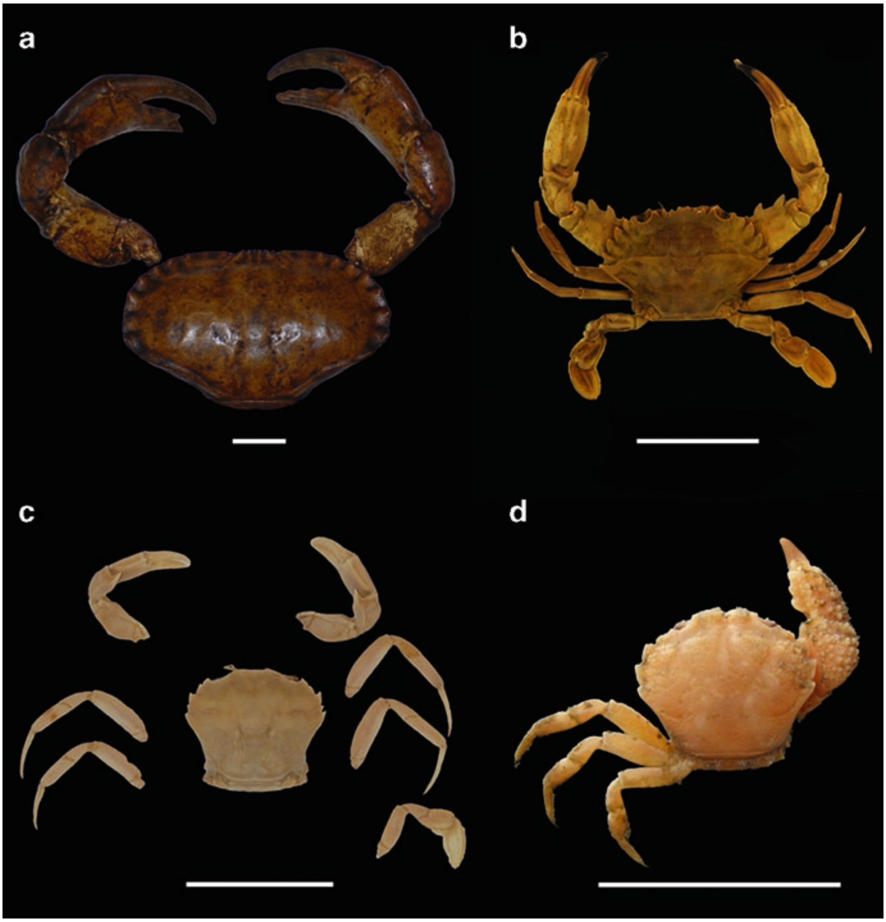

**Fig. 1** Alien marine brachyuran crabs either successfully established on or recorded to the Southwestern Atlantic. (**a**) *Cancer pagurus* Linnaeus, 1758, Santos, SP (MZUSP 948). (**b**), *Charybdis hellerii* (A. Milne-Edwards, 1867), Rio de Janeiro, RJ (MZUSP 20361). (**c**) *Liocarcinus navigator* (Herbst, 1794), Ilha Grande, RJ (MZUSP 13110). (**d**) *Pilumnoides perlatus* (Poeppig, 1836), Ubatuba, SP (13477). Scale bars: **a**–**c**, 50 mm. **d**, 5 mm

encompasses the coasts of Brazil (south of the equator), Uruguay, and Argentina. Neither cryptogenic nor freshwater species have been included.

Possibly the oldest record of an alien decapod species from the Southwestern Atlantic (but which shall not be further mentioned), was the inadvertent description as a new species of a dead specimen of the common edible European crab *Cancer pagurus* found sometime before 1930 in Brazil (Rathbun 1930a). That was a large (25 cm CW) "dead and dismembered" specimen of *Cancer pagurus* found (presumably washed ashore) in Santos by the naturalist Hermann H. Lüderwaldt of the Museum of Zoology in São Paulo (Rathbun 1930a). Only the carapace and

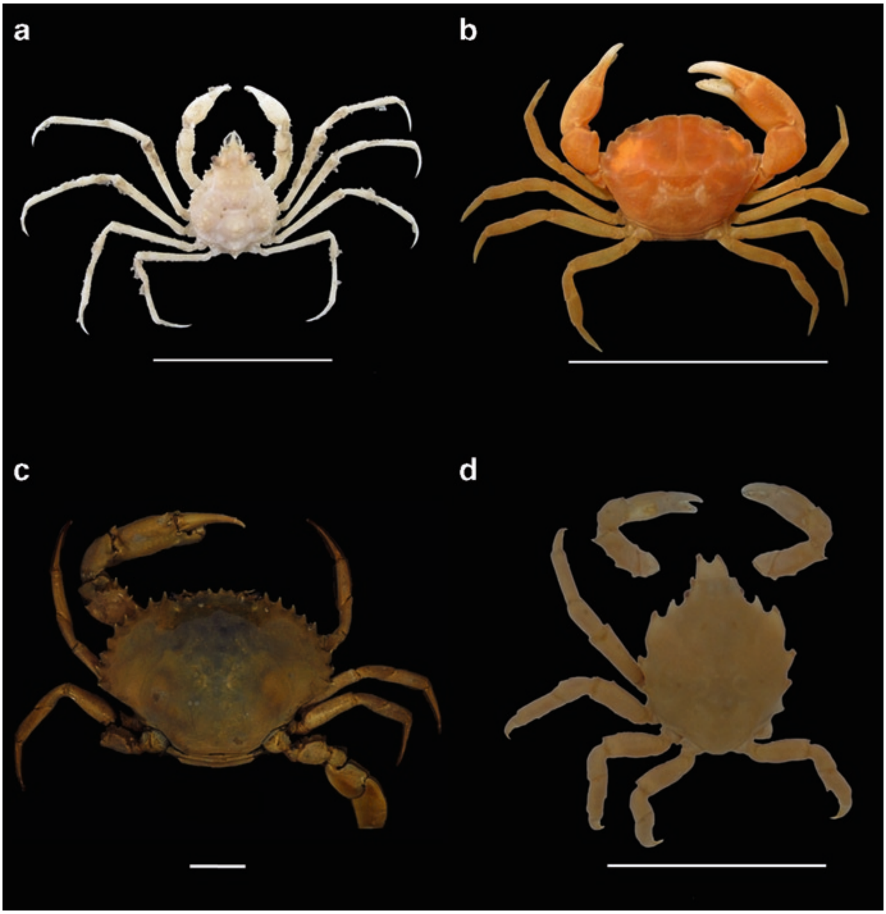

**Fig. 2** Alien marine brachyuran crabs either successfully established on or recorded to the Southwestern Atlantic. (**a**) *Pyromaia tuberculata* (Lockington, 1877), northern coast of São Paulo (MZUSP 14204). (**b**) *Rhithropanopeus harrisii* (Gould, 1841), Lagoa dos Patos, RS (MZUSP 15240). (**c**) *Scylla serrata* (Forskål, 1775), Peruíbe, SP (MZUSP 5310). (**d**) *Taliepus dentatus* (H. Milne Edwards, 1834), Angra dos Reis, RJ (MZUSP 9582). Scale bars: **a**–**b**, **d**, 20 mm **c**, 50 mm

chelipeds were kept, and photographs of these (but not the material) were sent to Mary Jane Rathbun at the Smithsonian Institution, who was so taken by the "striking ... discovery of a giant *Cancer* on the Atlantic coast of South America" that she described it the spring of 1930a as a new species, *Cancer luederwaldti* Rathbun 1930 (Fig. 1a). Within a few months W. T. Calman of the Natural History Museum (British Museum) wrote to Rathbun, pointing out that *C. luederwaldti* was in fact a specimen of the well-known *C. pagurus*. In November 1930 Rathbun corrected her mistake, writing that her "error but emphasizes the desirability of world monographs rather than local faunas" (Rathbun 1930b).

## 2 Established Alien Decapods

Five species of alien decapods have become successfully established on the Atlantic coast of South America: *Charybdis hellerii* from the Indo-West Pacific (Brazil), *Eurypanopeus depressus* (Uruguay and Argentina) and *Rhithropanopeus harrisii* (Brazil) both from the Northwestern Atlantic, *Palaemon macrodactylus* (Argentina), and *Pyromaia tuberculata* (Brazil and Argentina) from the Eastern Pacific.

### 2.1 *Charybdis hellerii (A. Milne-Edwards, 1867) (Fig. 1b)*

The portunid crab *Charybdis hellerii* is native to the Indo-West Pacific Ocean (Davie 2002). Its geographical range has been expanded westward as a result of recent human activities: invasion of the Eastern Mediterranean Sea through the Suez Canal (Galil et al. 2002), and ballast-mediated invasion of the Western Atlantic, probably loaded at an Israeli port (Campos and Türkay1989). In the New World the first specimens of *C. hellerii* were reported between 1987 and 1988 (Cuba, Gómez and Martínez-Iglesias 1990; northeastern Venezuela, Hernández and Bolagños 1995; Caribbean coast of Colombia, Campos and Türkay 1989). *Charybdis hellerii* spread extremely fast: in April 1995 it was captured in the Indian River lagoon system of Florida, around 27°N (Lemaitre 1995) and as far south as Rio de Janeiro (22°54′S) and Ubatuba (23°26′S) (Negreiros-Frazoso 1996; Tavares and Mendonça 1996). *Charybdis hellerii* has also been recorded from French Guiana (Tavares and Amouroux 2003). Males, ovigerous females, and juveniles have been caught in numerous localities along the Brazilian coast (approximately from 5°S to 27°S).

*Charybdis hellerii* inhabits a variety of biotopes from intertidal to beyond 30 m depth, including coral reefs and mangroves (d’Udekem d’Acoz 1999). In the Southwestern Atlantic, *C. hellerii* has been found mostly in bays and estuaries in rocky shores and breakwaters (Tavares and Mendonca 2004; Junqueira et al. 2009).

A number of biological traits favour *C. hellerii* invasions of new areas (Dineen et al. 2001): (i) long larval life; (ii) rapid growth and short generation time; (iii) ability to store sperm and produce multiple broods of high fecundity and rapid succession; (iv) generalized carnivorous diet; and (v) ability to use diversity of habitats. Mantelatto and Garcia (2001) found that *C. hellerii* attains sexual maturity at a small size (35 mm of carapace width). The fecundity of *C. hellerii* at 59 mm of carapace width can be of as much as 47,000 larvae (zoea I).

Self-maintaining populations of *C. hellerii* have been established along the Southwestern Atlantic (Tavares and Mendonca 2004; Junqueira et al. 2009). In Ubatuba, southwestern Brazil *C. hellerii* is not as abundant as the native portunid species (Fransozo et al. 1992; Mantelatto and Fransozo 2000). However, that seems not be the case elsewhere (Carqueija 2000). In Northeastern Brazil (Baía de Todos os Santos) *C. hellerii* was shown to be more abundant than

*Callinectes marginatus* (A. Milne Edwards, 1861). *Charybdis hellerii* is neither marketed nor consumed in any form by local populations. As a result only the native portunids are subject to fishery pressure. Most populations of *C. hellerii* have been reported from bays and estuaries, but there is a risk that it may enter sensitive habitats such as coral reefs and mangroves. In November 2009 a carapace of *C. hellerii* was found among prey remains in middens of *Octopus* sp. in sandstone reefs along the Northeastern Brazilian coast of Rio Grande do Norte, Brazil (Tavares, unpublished data).

*Charybdis hellerii* is a potential host for the White Spot Syndrome Virus (WSSV), which naturally infects several species of *Charybdis*, as well as other species of decapods (Chang et al. 2001; Chakraborty et al. 2002). There are several ways in which viruses may move from natural environments to aquaculture facilities and vice versa, and lethal outbreaks of WSSV and another viruses have been reported to decimate crops of penaeid shrimps (JSA 1997).

## 2.2 *Eurypanopeus depressus* (Smith, 1869)

*Eurypanopeus depressus* is native to the Northwest Atlantic, where it occurs from Massachussetts Bay to Texas and the West Indies (Rathbun 1930a; Williams 1965, 1984). It has been reported from estuarine ponds, oyster bars, and artificial reefs, from shore to 48 m depth (Ryan 1956; Williams 1984). Juanicó (1978) reported a total of five males from Montevideo and Maldonado (Uruguay), collected in 1954, 1968, and 1975. In 2000 and 2003, 31 males and 37 females were collected in the intertidal in Montevideo and Balneario Costa Azul (Uruguay), and four males and 13 females in Mar Chiquita Lagoon (Argentina) (Spivak and Luppi 2005). Both Juanicó (1978) and Spivak and Luppi (2005) considered these isolated populations in Uruguay and Argentina a natural extension of the species' range, probably resulting from changes in hydrographic or climatic conditions. Although Mar Chiquita Lagoon has been continuously and intensely studied, the presence of *E. depressus* was only recently detected (Spivak and Luppi 2005). The species has not been found previously south of the West Indies. These disjunct distributions suggest the presence of *E. depressus* may be anthropogenic. The species is commonly associated with oyster and artificial reefs (Williams 1984), but it is unlikely it was introduced with shellfish culture, as Uruguay and Argentina imported their breeding stock from Chile. It may have been introduced with ship fouling to the port of Montevideo.

## 2.3 *Palaemon macrodactylus* Rathbun, 1902

*Palaemon macrodactylus* is native to the Northwest Pacific: Japan (Rathbun 1902), Korea and northern China (Newman 1963). It was first introduced to the USA (prior to 1957) and then to Australia (late 1970s). It is nowadays known from Spain

(1997–1999), Argentina (2000), Atlantic Coast of the United States (2001–2002 and again in 2008), United Kingdom (2001), Belgium and The Netherlands (2004), Germany (2004), France (2006), and the Black Sea (2009) (Newman 1963; Buckworth 1979; Holthuis 1980; Ashelby et al. 2004; Cuesta et al. 2004; Spivak et al. 2006; González-Ortegón et al. 2007; Worsfold and Ashelby 2006; Beguer et al. 2007; Micu and Niță 2009; Warkentine and Rachlin 2010).

Ten males and six females (three ovigerous) were caught using hand nets, subtidally in the Mar del Plata Harbour in March 2000, December 2003, and March 2004 (Spivak et al. 2006). It was suggested that *P. macrodactylus* arrived at the harbor with discharged ballast water. The species is at present restricted to the harbour area but it may spread to Mar Chiquita Lagoon, the nearest estuarine habitat, about 35 Km north of Mar del Plata (Spivak et al. 2006).

## 2.4 *Pyromaia tuberculata (Lockington, 1877) (Fig. 2a)*

*Pyromaia tuberculata* is native to the Northeastern Pacific Ocean, where it ranges from San Francisco Bay, California to Chile (Garth 1958). It has a long history of successfully establishing self-sustaining populations in distant new regions (Sakai 1976; Webber and Wear 1981; Williams 1984; Kim 1985; Morgan 1990; Furota 1996a, b; Furota and Furuse 1988; Furota and Kinoshita 2004; Ahyong 2005): Japan (before 1970); Korea (1970s), Australia (1978) and New Zealand (1978). It was probably carried across the world in ballast tanks of ships or hidden amongst fouling organisms.

*Pyromaia tuberculata* was first recorded from the Southwestern Atlantic by Melo et al. (1989) based a female caught in 1988 in Paraná (Brazil). The collections of the Museum of Zoology in São Paulo contain additional specimens from Paraná (collected in 1987), São Paulo (Ubatuba, 1985, 1986, 1988) and Rio de Janeiro (Cabo Frio 1986). Since, it has spread to the southeastern Brazilian coast (Santa Catarina and Rio Grande do Sul), Uruguay (zoeae and megalopae collected in 2000) and Argentina (adult males and females collected in 2000) (Tavares and Mendonça 1996, 2004; Schejter et al. 2002). There is a doubtful record from northern Brazil (Piauí) (Lima et al. 2008). The occurrence of *P. tuberculata* in the Southwestern Atlantic was considered as a natural distribution pattern (Melo et al. 1989; Melo 1996), only lately it was recognized as an alien to the Southwestern Atlantic (Tavares and Mendonça 1996, 2004).

In its native range, it is usually hidden under stones or amongst fouling organisms; it also occurs on mud and sandy-mud bottoms down to 412 m depth (Rathbun 1925; Garth 1957, 1958; Hendrickx 1999). *Pyromaia tuberculata* is eurythermic and resistant to quasi-anoxic conditions (Hendrickx 1999). It is abundant in organically polluted bays, such as Tokyo Bay, Japan, and Guanabara Bay, Brazil. In the Southwestern Atlantic it is abundant locally (Bertini et al. 2004), and has been reported from sandy- and muddy-bottoms, and from rocky bottoms covered with algae and under stones, from the intertidal to 130 m (Junqueira et al. 2009).

### 2.5 *Rhithropanopeus harrisii* (Gould, 1841) (Fig. 2b)

*Rhithropanopeus harrisii* is native to the Northwest Atlantic, where it occurs from Canada to Mexico (Williams 1984). It has been introduced to Japan, the Pacific coast of the United States, the Panama Canal, and Europe (Galil et al. 2002; Iseda et al. 2007; Roche and Torchin 2007). Between 1982 and 1985 D'Incao and Martins (1998) obtained 92 males and 61 females from Southwestern Brazil (Lagoa dos Patos, RS), where *R. harrisii* has established self-sustaining populations. Additional surveys made between July 1995 and December 1997 yielded ovigerous females. Otter-trawl and renfro nets surveys carried out in soft bottoms from February to November 1999 obtained 295 males and 299 females (4.34% were ovigerous), the largest catches were taken in autumn and spring (Rodrigues and D'Incao 2002). The species has not been caught in other parts of Brazil. The record by Christiansen (1969) from the northeastern coast of Brazil is erroneous (see also Roche and Torchin 2007). *Rhithropanopeus harrisii* prospers in a wide range of salinities (Williams 1984) and is likely to expand its geographical range southward, towards the temperate waters of the Uruguayan and Argentinean estuaries.

D'Incao and Martins (1998) suggested that *R. harrisii* arrived on the Brazilian coast via in ballast water. However, *R. harrisii* is commonly associated with some kind of shelter, whether it be oyster beds, stones, vegetation, or artificial refuges (Ryan 1956). In the Patos lagoon it has also been found under stones and on foreshore debris (D'Incao 2010, pers. comm.). Since it is usually hidden among fouling organisms perhaps it had been transported to Brazil in ship fouling rather than in ballast.

In its native range, the euryhaline *R. harrisii* is found from the intertidal to depth of 9 m. It can reach very high densities (Odum and Heald 1972), foul water intake pipes and cause economic loss to fishermen by spoiling fishes in gill nets (Zaitsev and Öztürk B 2001). In Texas it has been reported to have fouled PVC intakes in lakeside homes (Roche and Torchin 2007).

## 3 Penaeid Shrimp Farming

Five species of penaeids (Table 2) have been cultured along the South American coast.

**Table 2** Alien penaeid shrimps brought to the Southwestern Atlantic for farming purposes. IWP, Indo-West Pacific. EP, Eastern Pacific

| Species | Source region | Currently farmed | Escapees in the wild |
|---|---|---|---|
| *Marsupenaeus japonicus* | IWP | No | Yes |
| *Penaeus monodon* | IWP | No | Yes |
| *Fenneropenaeus penicillatus* | IWP | No | No |
| *Litopenaeus stylirostris* | EP | No | No |
| *Litopenaeus vannamei* | EP | Yes | Yes |

## 3.1 Marsupenaeus japonicus (Bate, 1888)

*Marsupenaeus japonicus* is native to the Indo-West Pacific (Galil et al. 2002). In 1978 shrimp farmers brought *M. japonicus* to Natal, Brazil along with four other alien penaeid species (Tavares and Mendonça 1996). The aquaculture experiments with *M. japonicus* were resumed in the 1980s (Tavares and Mendonça 1996, 2004; Cavalli et al. 2008). Escapees have been captured on the Northeastern Brazilian coast (Fausto-Filho 1987).

## 3.2 Penaeus monodon (Fabricius, 1798)

*Penaeus monodon* is native to the Indo-West Pacific Ocean (D'Udekem D'Acoz 1999). It was brought to Brazil (Natal in 1981 and Bahia in 1985) for aquaculture experiments (Tavares and Mendonça 1996, 2004). Fausto-Filho (1987) reported an escapee from Maranhão (Tutóia). Although the culturing of *P. monodon* ended in the 1980s, several adult and immature specimens have been collected off Pernambuco, Alagoas and Santos (Severino-Rodrigues et al. 2000; Coelho et al. 2001). These findings led Coelho et al. (2001) to suggest that *P. monodon* established self-sustaining populations in Brazil. Severino-Rodrigues et al. (2000) hypothesized that the source of *P. monodon* in the Southwestern Atlantic was ballast-transported specimens from the self-sustaining populations in the Mediterranean. In 1988 about 200,000 post-larval *P. monodon* from Hawaii escaped from the Waddell Mariculture Center in South Carolina (McCann et al. 1996). Subsequently, about 1,000 adults were caught by commercial shrimpers as far south as Florida. It is likely that the source of the Brazilian feral populations are escaped and released specimens from farms.

## 3.3 Fenneropenaeus penicillatus (Alcock, 1905)

In 1985 the Indo-West Pacific *Fenneropenaeus penicillatus* was transported to Brazil (Valença, Bahia) to be farmed. Although shrimp farming in Brazil has been mostly restricted to *Litopenaeus vannamei*, *F. penicillatus* continued to be cultured in Bahia (Acupe, Santo Amaro da Purificação) until recently (Oliveira and Corrêa 1999). No escapees have been reported from the area (Tavares and Mendonça 1996, 2004).

## 3.4 Litopenaeus stylirostris (Stimpson, 1874)

*Litopenaeus stylirostris* is native to the Eastern Pacific (Dore and Frimodt 1987). The species was imported to Brazil by shrimp farmers in 1983 for aquaculture experiments (Tavares and Mendonça 1996). A few years later most shrimp farmers shifted to *Litopenaeus vannamei*, but at least until 2003 *L. stylirostris* was farmed in Brazil (Rio Grande do Norte). No escapees have been reported.

### 3.5 *Litopenaeus vannamei (Boone, 1931)*

*Litopenaeus vannamei* is of Eastern Pacific origin, ranging from Mexico to Peru (Holthuis 1980). In 1981 it was introduced to Rio Grande do Norte, Brazil, along with *L. stylirostris*, *Marsupenaeus japonicus*, *Penaeus monodon*, and *Fenneropenaeus penicillatus* (Tavares and Mendonça 1996, 2004; Junqueira et al. 2009). Adaptation to culture conditions, good market acceptance, and the development of culture technologies made *L. vannamei* the species preferred by Brazilian shrimp farmers in Pará, Maranhão, Piauí, Ceará, Rio grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina. It was first introduced into the USA (South Carolina) as postlarvae from Panama in 1985 and became the main species of shrimp farmed in North America (Briggs et al. 2004).

The social, economic, and environmental impacts of *L. vannamei* farming in Asia and Brazil have been discussed in detail by Briggs et al. (2004) and Junqueira et al. (2009), respectively. Escapees of *L. vannamei* are now common in many areas worldwide, and have been found in several locations in Brazil (Santos and Coelho 2002; Junqueira et al. 2009; Tavares, unpublished data). Escapees have the potential to interbreed with *Litopenaeus schmitti* (Burkenroad, 1936), native to the Southwestern Atlantic, and to transmit several viral diseases (Briggs et al. 2004). The World Organization for Animal Health (OIE) recognizes seven viral diseases of shrimp of significant socio-economic and/or public health importance (OIE 2003). Since *L. vannamei* is euryhaline and tolerant to very low salinity, it is cultured both inland and in coastal areas, impacting natural and agricultural habitats and water quality (Junqueira et al. 2009). Shrimp farming has been responsible for substantial environmental damages in Northeastern Brazil (Junqueira et al. 2009).

## 4 Discussion

### 4.1 *Taxonomic Resolution and Patterns of Diversity and Geographic Distribution*

That marine biodiversity is greatly underestimated has become a cliché in recent years, especially with regards to the tropics. No one would dispute that without basic taxonomic information no inventories of threatened areas, alien species assessment, risk assessment projections, or programs for rational planning are possible. The study of the crustacean fauna of the Southwestern Atlantic started 500 years ago (Almaça 1993; Rodriguez 1993; Tavares 1993b), yet we remain ignorant of much of its diversity. About 400 species of marine brachyurans are known from the Southwestern Atlantic (Melo 1996; Boschi

2000; Boschi et al. 1992), yet it is widely acknowledged that the inventory is far from complete. A large number of the brachyurans recorded from the Southwestern Atlantic occur off the Atlantic coast of the United States (mostly south of the Carolinas), Gulf of Mexico, and the Caribbean Sea. Although commonly accepted (Coelho and Ramos 1972; Melo 1996; and references therein), the assumption of a widely distributed Western Atlantic crab fauna remains largely untested.

Between 1917 and 1937 Rathbun published four seminal monographs on the crab fauna of America (Rathbun 1917, 1925, 1930a, 1937). Few collections from the Southwestern Atlantic were available for her studies, mainly of brackish and marine intertidal species obtained during the United States Exploring Expedition (1838–1842), the Hartt Explorations (1865–1878), the Branner-Agassiz Expedition (1899), the Thayer Expedition (1865–1866), and the collections amassed by a number of travelling zoologists including Herbert Smith, Fritz Müller, Hermann von Ihering, Hermann Lüderwaldt, and Waldo Schmidt. Also available were some deep-water samples obtained by the HMS “Challenger” (1873) and the Steamers “Hassler” (US Coast and Geodesic Survey, 1872) and “Albatross” (the US Fish Commission Albatross 1887) (Rodriguez 1993; Freitas 2001; Tavares, unpublished data). As a result, comparatively few specimens from the Southwestern Atlantic were studied by Rathbun and compared with those collected further north. The best existing crab collections from the Southwestern Atlantic are in Brazilian, Uruguayan, and Argentinean institutions, but the bulk of these collections were assembled after 1950. But more than 7 decades after Rathbun’s landmark publications, this situation remains very much unchanged, and today, most of what we know about the diversity of Brachyura in the Southwestern Atlantic derives from identifications based on literature alone, largely Rathbun’s monographs (and Williams 1965, 1984).

Therefore it does not come as a surprise to learn that the number of species recorded from the Southwestern Atlantic increases fast. Indeed, more than 50 species have been added to the Brazilian crab fauna since the last inventory was published in 1996 (Melo 1996). Most (if not all) of these species have been identified without recourse to comparative material. However, on several occasions individuals from the Southwestern Atlantic previously identified as northern species proved to be new to science after comparison with northern individuals (Manning and Holthuis 1989; Manning et al. 1989; Tavares 1991, 1993a; Tavares and Melo 2005, 2010). Molecular techniques have also helped separate species previously considered to be widely distributed in the Western Atlantic (Gusmão et al. 2000, 2006). As quality training in systematics is essential, availability and accessibility of extensive comparative collections is necessary to properly evaluate marine biodiversity and the rapid temporal changes in the marine biota. Thirteen marine alien species of decapod crustaceans have been recorded from the Southwestern Atlantic, most are known from a single record. Surprisingly, given the centuries of extensive shipping, few alien crab species are known to have established populations in Brazil, Uruguay, and Argentina. However, about 200 crab species have shown disjunct geographic distribution between the southern and northern western Atlantic coasts (South Carolinas through Florida, Gulf of Mexico or the Caribbean Sea). One wonders how many are artifacts of poor taxonomic resolution, and to which extent have we missed invasions by misinterpreting disjunct ranges (or even the continuous ranges) as “natural” patterns. The distribution pattern of *Eurypanopeus depressus* is but a recent example (see above). Although the examples given concern brachyuran crustaceans, it may well be they apply to other groups of marine Southwestern Atlantic invertebrates.

## 4.2 Detection, Regulations and Management

The role played by human activities in transferring alien marine and estuarine species into new areas is widely recognized as a critical element of ecosystem change by both the scientific community and government agencies. Although guidance to help in the detection and control of alien marine species is available to decision-makers (Bax et al. 2001; Hewitt CL Martin 2001), control capabilities vary widely among countries. It is far beyond the scope of this paper to discuss in detail the control capabilities and the existing laws in Brazil and adjacent countries. The considerations below refer to Brazil, but many the same also apply to Uruguay and Argentina. Vectors of introduction and current applicable laws referring to alien marine species in Brazil are summarized in Table 3.

**Table 3** Vectors of introduction and current applicable laws referring to alien marine species in Brazil (Adapted from Fernandes et al. 2009)

| Vectors of introduction | Current applicable laws |
|---|---|
| Ballast water and sediment from ballast tanks | NORMAM/20; Law 6938/81 Resolution RDC 217/ANVISA; Federal Law N$^{0}$ 8630/93; Decret N$^{0}$ 1265/94 |
| Fouling on ship hulls, oil platforms, sport boats, and navigation buoys | Decret N$^{0}$ 1265/94; Lei: 9638 |
| Floating debris fouling | LESTA/AM N$^{0}$ 9537/97; MARPOL (annex 5), Decret: 2508. Law 6938/81 |
| Importation of specimens for ornamental purposes | Decret N$^{0}$ 3179/99; Federal Law N$^{0}$ 5197/67; Federal Law N$^{0}$ 9605/98 Art 61; Law of the Sea/93 |
| Importation of specimens for farming purposes | Federal Law N$^{0}$ 5197/67; Federal Law N$^{0}$ 9605/98 Art 61; Law of the Sea/93; Decret N$^{0}$ 3179/99 |
| Inappropriate release of specimens | Federal Law N$^{0}$ 9605/98 Art 54 |
| Inappropriate handling of specimens; pond water leaking; release of cysts, spores, eggs, larvae, and juveniles into the marine environment | Federal Law N$^{0}$ 9605/98 Art 54 e 61; Federal Law N$^{0}$ 6938/81 (pollution) |
| Biopiracy (biological resources) | Federal Law N$^{0}$ 5197/67; Decret N$^{0}$ 4339/02 |
| Introduction of species for scientific purposes | Decret N$^{0}$ 3179/99; Federal Law N$^{0}$ 6938/81; CITIES/79 |

The recognition of an alien species as such is central to its management. Brazil has neither a facility primarily devoted to early detection of alien marine species, nor a long-term monitoring program of marine invasions (Fernandes et al. 2009). Collection and identification of alien marine species is the by-product of ecological studies and local faunal inventories produced by research teams from different Brazilian universities and research institutes, which rarely target marine invasions. Thus surveillance is largely informal and databases small in number and irregularly updated, with the exception of the comprehensive database of the Hórus Institute for Development and Environmental Conservation (Hórus 2010). Port surveys devoted to the early detection of alien marine species were restricted to two ports in Southeastern Brazil, Itaguaí (Sepetiba Bay, Rio de Janeiro) and Paranaguá (Paraná). Both port surveys were conducted as part of a plan to reduce the transfer of aquatic organisms in ballast water (Leal Neto and Jablonski 2004).

Brazil has a plethora of regulations for the importation of alien marine species for farming and ornamental purposes (Table 3), but no quarantine systems in place (Tavares 2003; Fernandes et al. 2009). A few years ago, the Brazilian Ministry of the Environment sponsored a National Report, in order to assemble a comprehensive view of invasive marine species in the country (Lopes 2009). In 2009 the federal government published a national strategy for invasive exotic species which should provide a framework for future actions (Brazil 2009).

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# The Alien and Cryptogenic Marine Crustaceans of South Africa

**Charles Griffiths, Tamara Robinson, and Angela Mead**

**Abstract** Some 33 marine crustaceans are currently known or suspected to have been introduced to South Africa, with additional species regularly being discovered. The current list, including cryptogenic forms, comprises two barnacles, one copepod, 11 isopods, 17 amphipods and two crabs. We tabulate these species and examine their temporal patterns of discovery and current spatial distributions. The earliest introductions are thought to have arrived in dry ballast, or on wooden vessels, either boring into the wood itself, or as fouling. More recent introductions include species suspected to have arrived via ballast water, or along with farmed oysters. Most introduced crustaceans are confined to the few harbours and sheltered sites along this linear and wave-exposed coastline. Only two are known to cause significant ecological or economic impacts. The Pacific barnacle *Balanus glandula* has invaded over 400 km of open coast and altered community structure there, while the European shore crab *Carcinus maenas* has caused significant ecological disruption in the limited sites where it is now abundant. Future risks include the almost inevitable spread of *C. maenas* to additional sheltered sites, and introductions of additional species, especially via ballast water. Ballast water treatment and replacement of imported oyster spat by locally-cultured stock are among measures recommended to limit further introductions.

## 1 Introduction

Numerous marine species, including a variety of crustaceans, have been transported, both intentionally and accidentally, around the globe ever since people began navigating the open ocean. Since the late Fifteenth century, when European explorers first landed in South Africa, this region has been an important port of call

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along major sea routes, notably those linking Europe to Asia, the Persian Gulf and Australasia. Centuries of consistent, high-volume shipping have inevitably resulted in regular introductions of marine species, including crustaceans. During the twentieth century an additional vector has opened up as a result of the growing international trade of marine species for aquaculture.

Most early researchers failed to recognize the significance of marine introductions and simply recorded such species as “cosmopolitan” or “widespread”. The first paper specifically attempting to identify and list introduced marine species from South Africa was published as recently as 1992 (Griffiths et al. 1992) and recorded just 15 species (two of which were crustaceans), but several of these have been removed from later lists, as they either no longer support extant populations, or were based on misidentifications. Several additional reviews have been published in the last 20 years. Griffiths (2000) provided a list of 17 naturalised and five farmed species and Awad (2002) reproduced an almost identical list. Robinson et al. (2005) first distinguished between confirmed introductions and cryptogenic species (for a definition of cryptogenic see Carlton 2009), listing 10 introductions and 22 cryptogenic species, while Griffiths et al. (2009) listed 22 confirmed introductions and 18 cryptogenic species (some earlier species having been “promoted” onto the confirmed list of introductions). Ongoing work has, however, rapidly augmented these numbers, to the point that 86 introductions and 39 cryptogenic species are presently recognized (Mead et al. submitted), among which are 33 crustaceans. No similar listings of introduced marine species exist for other African countries, although many of the species recorded in South Africa have ranges that extend at least into Namibia or Mozambique. In the following account we discuss the taxonomic composition, origins, distribution patterns and ecological impacts of the South African alien and cryptogenic marine crustacean fauna.

## 2 Inventory

Crustaceans currently recorded as introduced to South African waters include representatives of the Copepoda, Cirripedia, Isopoda, Amphipoda and Decapoda. The species, their region of origin, date of first record, and a key reference to each are given in Table 1.

Copepoda are represented by just one species, *Acartia spinicauda*, which is thought to have been introduced via ballast water. It should be noted, however, that taxa with small body sizes, such as copepods and ostracods have received relatively little attention, both in terms of sampling coverage and taxonomic expertise in South Africa. It is thus likely that the actual numbers of introductions in these groups are significantly higher than reported.

Two introduced barnacles are known from South African shores; both of which are suspected to have been introduced via ship fouling (Mead et al. submitted). *Amphibalanus venustus* occurs at low densities on the warm south and east coasts and was first recorded in the early twentieth century (Henry and McLaughlin 1975).

**Table 1** Crustaceans introduced to South African waters

| Class/Order | Species | Status | Date of first collection | Region of origin | Vector | Reference |
|---|---|---|---|---|---|---|
| **Cirripedia** | | | | | | |
| | *Amphibalanus venustus* | I | 1938 | Western North Atlantic | SF | Mead et al. submitted |
| | *Balanus glandula* | I | 1992 | North American Pacific | SF | Simon-Blecher et al. 2008 |
| **Copepoda** | | | | | | |
| | *Acartia spinicauda* | I | 2003 | Southeast Asia | BW | Mead et al. submitted |
| **Isopoda** | | | | | | |
| | *Dynamene bidentata* | I | 2006 | Europe | SF/BW | Mead et al. submitted |
| | *Ligia exotica* | C | Before 1932 | Unknown | SB | K.H. Barnard 1932 |
| | *Limnoria quadripunctata* | I | Before 1897 | Unknown | SB | Hammersley-Heenan 1897 |
| | *Limnoria tripunctata* | I | 2007 | Unknown | SB | Hammersley-Heenan 1897 |
| | *Paracerceis sculpta* | I | 2007 | Northeast Pacific | SF/BW | Mead et al. submitted |
| | *Sphaeroma annandalei* | C | 1926 | Unknown | SF/BW | Mead et al. submitted |
| | *Sphaeroma serratum* | I | 1950 | Europe | SF/BW | K.H. Barnard 1951 |
| | *Sphaeroma terebrans* | C | 1908 | Northern Indian Ocean | SF/BW | Mead et al. submitted |
| | *Sphaeroma walkeri* | I | 1915 | Northern Indian Ocean | SF/BW | Mead et al. submitted |
| | *Synidotea hirtipes* | C | 1897 | Unknown | SF/BW | Mead et al. submitted |
| | *Synidotea variegata* | C | 1940 | Indo-Pacific | SF/BW | Mead et al. submitted |
| **Amphipoda** | | | | | | |
| | *Apocorophium acutum* | I | 1915 | North Atlantic | SF/BW | K.H. Barnard 1916 |
| | *Caprella equilibra* | C | 1888 | Unknown | SF/BW | Stebbing 1888 |
| | *Caprella penantis* | C | 1903 | Unknown | SF/BW | Mayer 1903 |
| | *Cerapus tubularis* | I | 1901 | North America | BS | K.H. Barnard 1916 |
| | *Chelura terebrans* | I | 1888 | Pacific Ocean | SF | Stebbing 1910 |
| | *Corophium triaenonyx* | C | 1931 | Asia | SF/BW | Mead et al. submitted |

(continued)

**Table 1** (continued)

| Class/Order | Species | Status | Date of first collection | Region of origin | Vector | Reference |
|---|---|---|---|---|---|---|
| | *Cymadusa filosa* | C | 1913 | Unknown | BS | Mead et al. submitted |
| | *Erichthonius brasiliensis* | I | 1910 | North Atlantic | SF | Stebbing 1910 |
| | *Ischyrocerus anguipes* | I | 1916 | North Atlantic | SF/BW | K.H. Barnard 1916 |
| | *Jassa marmorata* | I | Before 1948 | North Atlantic | SF/BW | Conlan 1990 |
| | *Jassa morinoi* | I | Before 1952 | North Pacific | SF/BW | Conlan 1991 |
| | *Jassa slatteryi* | I | Before 1950 | North Pacific | SF/BW | Conlan 1992 |
| | *Melita zeylanica* | C | Before 1940 | Indian Ocean/Australia | SF/BW | K.H Barnard 1940 |
| | *Monocorophium acherusicum* | I | 1915 | North Atlantic | SF/BW | K.H. Barnard 1916 |
| | *Orchestia gammarella* | I | 1949 | Europe | BS | K.H. Barnard 1951 |
| | *Paracaprella pusilla* | C | 1955 | Unknown | SF/BW | Mead et al. submitted |
| | *Platorchestia platensis* | I | 1904 | Unknown | BS | Griffiths 1975 |
| **Decapoda** | | | | | | |
| | *Carcinus maenas* | I | 1983 | Europe | SF/BW/OR | Joska & Branch 1986 |
| | *Xantho incisus* | I | 2008 | Europe | M | Haupt et al. 2010 |

Status: *I* introduced, *C* cryptogenic. Vector: *SB* ship boring, *SF* ship fouling, *BW* ballast water, *BS* solid ballast, *M* mariculture, *OR* oil rigs

In contrast, *Balanus glandula* is the most common barnacle along the cool-temperate west coast. This species was first recorded only in 2008 (Simon-Blecher et al. 2008) although photographic evidence suggests that it had in reality been common there for at least the previous 15 years, but had been misidentified as the local *Chthamalus dentatus* (Laird and Griffiths 2008). The high densities of intertidal *B. glandula* suggest that it has significant ecological impacts on the local biota (see below).

Of the 11 introduced Isopoda, the earliest introductions are thought to be *Ligia exotica*, *Limnoria quadripunctata* and *Limnoria tripunctata. Ligia exotica* is assumed to have been introduced with solid ballast, while both *Limnoria* species are wood-borers and are likely to have arrived on infested wooden ships. The remaining eight species are most likely to have arrived via ballast water and/or ship fouling. All four non-indigenous *Sphaeroma* species known from South Africa are estuarine wood-borers. Two, *S. annandalei* and *S. terebrans,* are considered cryptogenic, while *S. serratum* and *S. walkeri* are confirmed introductions. *S. walkeri*, considered a marine species, is found in South African estuaries to depths of 5 m. Its has also been introduced to California, Florida, East Africa, Hong Kong and the Mediterranean, to name but a few regions, and is considered one of the most widely distributed ship-transported isopods in the world (Mead et al. submitted).

The Amphipoda are the most diverse group of introduced crustaceans in the region, with 17 listed species, of which seven are considered cryptogenic. The species fall into three main functional groups. One species, *Chelura terebrans* is a wood-borer (it in fact enlarges and colonizes existing burrows of gribbles of the genus *Limnoria*, J. L. Barnard 1955), and would have been introduced in the days of wooden sailing vessels. A second functional group includes two air-breathing drift-line species, or "beach-hoppers", *Orchestia gammarella* and *Platorchestia platensis*, which would have been introduced with dry ballast, probably centuries ago. The former has an interesting taxonomic history, since it was described as a supposedly indigenous littoral amphipod *Talorchestia inaequalipes* by Barnard (1951), and only later recognised as being conspecific with North Atlantic *O. gammarella* (Griffiths 1975). Most of the remaining species comprise a cluster of clinging caprellid and tube-dwelling corophiid species. These are associated with fouling communities and were no doubt introduced with shipping. Notable among these are three species of *Jassa* that were long identified under the name *J. falcata* until Conlan (1990) revised the genus and revealed that the South African species in fact represented three introduced species, *J. marmorata*, *J. morinoi* and *J. slatteri.* The remaining species comprise one estuarine form, *Melita zeylanica*, which is particularly abundant within reefs of the introduced reef worm *Ficopomatus enigmaticus*, along with which it may have been imported, and *Cymadusa filosa*, which weaves nests from the fronds of algae and sea grasses in sheltered sites.

Only two introduced Decapoda have been recorded from South Africa. The shore, or green, crab *Carcinus maenas* is a well-known European introduction on both the Atlantic and Pacific coasts of North America, in Australia, Argentina, Japan and South Africa (Carlton and Cohen 2003). Interestingly, this species is almost entirely restricted to sheltered sites and appears unable to establish significant populations on the open, wave-swept coastline of South Africa (Hampton and

Griffiths 2007). It was first collected from Table Bay Docks (Cape Town) in 1983, where it has established dense populations and has decimated shellfish populations (Robinson et al. 2005). *Carcinus maenas* was probably introduced by ship fouling, ballast water or oilrigs. The second introduced crab, *Xantho incisus*, also originates from Europe, but was first collected only in 2008, from an oyster farm on the South African west coast (Haupt et al. 2010). This species has not been previously reported as introduced in any other region and no ecological impacts are currently known. *Xantho incisus* is thought to have been accidentally introduced with oyster spat imported from France.

## 3 Temporal Trends

The accumulative historic pattern of discovery of marine crustacean invasions into South Africa (Fig. 1) indicates the roles of the various likely vectors. It is important to note that this analysis is based on the first collection date of each species (Mead et al. submitted) and not the publication date, as is given in earlier papers. Even these dates, of course, inevitably postdate true dates of introduction, since

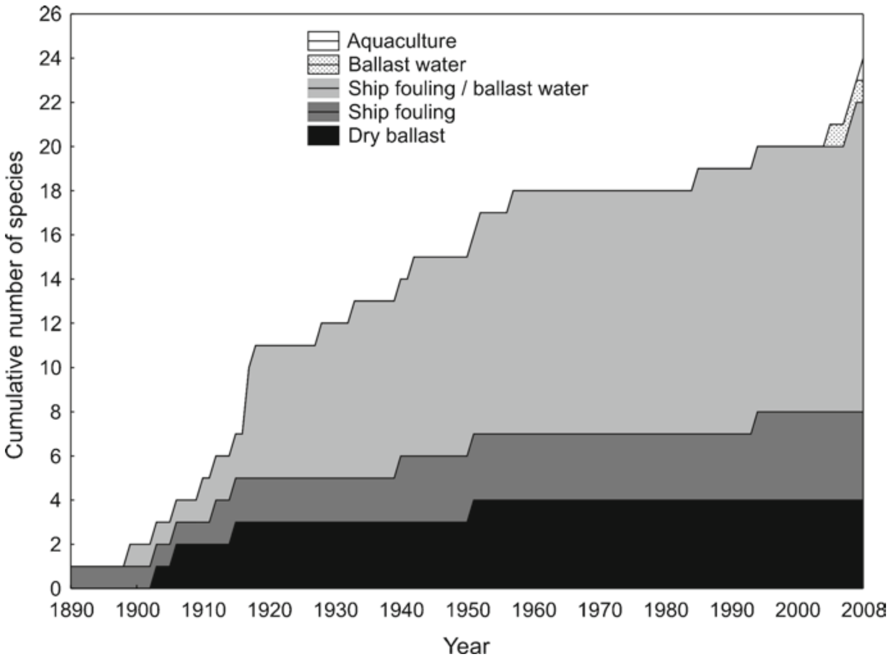

**Fig. 1** Cumulative discovery rate of known or suspected alien crustaceans in South Africa, plotted according to most likely vector

few invasions would have been detected as soon as they occurred, while others certainly lay undetected for decades, perhaps centuries.

Interestingly, several species now recognized as introduced were first detected by the late 1800s; the early days of marine taxonomic research in South Africa (Griffiths 1999). In all probability these species would have been present since the early years of European settlement, but no surveys were undertaken, nor were taxonomists present, to document their arrival. The rate of discovery has continued to increase since then, with two eras of particularly rapid increase. The first of these took place between 1913 and 1916 and reflects the work done by the prolific crustacean taxonomist K. H. Barnard, of the South African Museum. The second recent acceleration of discovery has been driven by directed research into marine bio-invasions, largely funded by the National Research Foundation-Department of Science and Technology Centre of Excellence for Invasion Biology, with which the authors are associated.

In terms of the roles of the various vectors, Fig. 1 clearly shows that shipping, either in the form of dry ballast, hull fouling, or ballast water, has been, and continues to be, the dominant means of invasion, with dry ballast occurring early in the sequence and ballast water being a more recent (and probably still largely unrecognized) vector. Only one crustacean introduction can be attributed to aquaculture and this occurred recently.

Another notable feature of these introductions is that almost all were introduced accidentally, whereas in freshwater and terrestrial ecosystems a large proportion of introductions have been intentional; for either ornamental or culture purposes, or as bio-control agents.

## 4 Biogeographic Patterns

In terms of spatial coverage, most marine crustacean introductions in South Africa remain restricted to sheltered harbours and estuaries, probably because conditions there most closely resemble their areas of origin, which are most often the sheltered ports and estuaries of the Northern Hemisphere. Only one introduced crustacean, the Pacific barnacle *Balanus glandula*, has become abundant and widely dispersed along the open wave-swept coastline. About half of all introduced crustaceans have warm water origins, while the other half have natural ranges in temperate regions. This is reflected in the relatively even distribution of species along the cold west coast of South Africa and warmer south and east coasts (Fig. 2).

Also notable is that non-coastal introductions have yet to be confirmed from the region. This is likely a reflection of the recognised sampling bias towards South African near-shore environments (Griffiths et al. 2010). It is, however, expected that scrutiny of offshore oil and gas installations in particular will reveal further introductions.

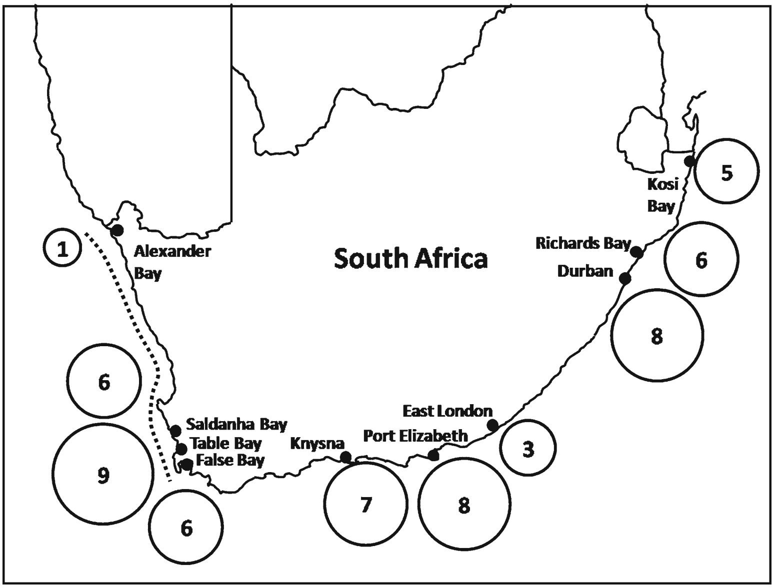

**Fig. 2** Map of South Africa showing place names mentioned in the test and numbers of introduced marine crustaceans reported from various harbours, estuaries and aquaculture sites

## 5 Main Pathways

The mechanisms or "vectors" of species importation, and hence types of species introduced and rates of introduction, have varied greatly over time and are considered in more detail below.

### *5.1 Wood Boring*

Early wooden-hulled vessels hosted a suite of specialized wood-boring species, most notably shipworms (bivalve molluscs of the family Teredinidae), gribbles (isopods of the genus *Limnoria*) and amphipods of the family Cheluridae. These species significantly damaged the vessels themselves, but also rapidly infested the wooden piers and pilings in harbours, where the infested ships docked. Because of their economic impacts wood-borers were amongst the first introduced species to be recorded. The wood boring isopod *Limnoria quadripunctata* and amphipod *Chelura terebrans* (as *L. lignorum*) were both reported by Stebbing (1910) but were almost certainly introduced well before then, while the closely related *L. tripunctata* inexplicably escaped detection until 2008 (Mead et al. submitted).

## 5.2 Dry Ballast

The use of dry ballast to adjust buoyancy and increase stability of early wooden ships was common. This solid material, usually coastal sand and rocks, was laboriously loaded into the holds by hand at the port of departure. Inter-tidal species were frequently attached to these ballast rocks, while coastal plants, seeds and insects were also accidentally loaded during the ballasting process. Many of these species survived in the damp ballast holds, only to be dumped onto a new shoreline at the port of destination (Minchin et al. 2009).

Crustaceans that are thought to have been introduced into South Africa along with dry ballast include two strand-line amphipods *O. gammarella* and *P. platensis* (formerly *O. platensis*).

## 5.3 Fouling

Early wooden vessels travelled slowly and were ideal habitats for a wide variety of fouling communities. By nature these tended to be dominated by sessile, attached forms, such as hydroids, bivalves, tubeworms, barnacles, bryozoans and ascidians. Nonetheless, other smaller, mobile species, such as amphipods and isopods, would have survived within the matrix of larger habitat-forming species. Modern steel vessels continue to carry fouling species, but as they are generally larger, travel more rapidly, and are painted with anti-fouling, the numbers and types of fouling species carried have changed over time. Shipping routes, and hence both sources and sinks of introduction, have also changed, due to the development of new harbours and industries. For example, the bulk coal and iron ore export ports of Richards Bay and Saldanha Bay, both developed in the 1970s, opened up new bulk cargo trade routes and foci of introduction in South Africa. The ongoing construction of a further new deep-water harbour at Coega, just east of Port Elizabeth, is likely to open up an additional focal point for invasion. Likely introductions via fouling include a variety of clinging and tube dwelling amphipods and isopods, including *Caprella*, *Jassa* and *Sphaeroma* spp (see Table 1 for specific details).

## 5.4 Ballast Water

Dry ballast was first replaced by water ballast in the late 1800s and had been completely phased out by the 1950s. The conversion to ballast water sparked a new wave of invasions, as this vector favours species that are either planktonic, or have a planktonic phase in their life cycle. Additionally, because ballast water is usually loaded in shallow, often turbid port areas, significant amounts of sediment can be loaded along with the water. This results in sediment layers building up on the floor of the ballast tanks, which in turn may support significant numbers of infaunal species, forms that would not be translocated via external fouling (Hewitt et al. 2009). Species introduced into South Africa by ballast water may include a significant proportion of more recent invasions, although it is often difficult to distinguish this vector from that of external hull fouling. Introductions that can confidently be attributed to ballast water include the planktonic copepod *Acartia spinicaudata*.

### *5.5 Aquaculture*

Marine aquaculture is a relatively recent development in South Africa, dating back only to the 1950s, when oyster culture was first initiated in Knysna Estuary (Korringa 1956). One crustacean species appears to have been introduced accidentally with imported oyster spat, the European crab *Xantho incisus*. The low number of crustacean introductions associated with this vector is thought to be due to the relatively short history of aquaculture, and the comparatively small number of facilities in the region.

Note that other pathways that have been reported to operate elsewhere (ICES 2005), such as naturalization of ornamental and aquarium species and release of species imported as live food, do not appear to have played a role in South Africa. There is very little trade in imported live seafood in this region and although tropical aquarium species are imported, they are unlikely to be released, due to their high commercial value, plus would have a slim chance of surviving in the subtropical to temperate waters of the region.

## 6 Economic and Ecological Impacts

Ecological impacts have been established for only two crustacean introductions along the South African coast, although it should be stressed that few species have been studied and any that are common probably influence local food chains, either by enhancing prey availability to predators (amphipods, isopods, etc), or as predators themselves (anemones, crabs).

Where it is abundant in Table Bay Harbour, the crab *Carcinus maenas* has almost totally removed shellfish populations associated with benthic wharfs and pilings (although significant populations persist on floating structures, which appear to be inaccessible to the crabs). Of more concern, however, are the potential impacts this species would have, should it expand its range to Saldanha Bay, just 100 km north of Table Bay. This sheltered bay contains large areas of suitable habitat for *C. maenas* and is both the location of the West Coast National Park and the main centre for the South African mussel and oyster culture industries. An invasion of *C. maenas* into this area has been predicted to have potentially serious impacts on the local biota (Le Roux et al. 1990). In particular, the extensive mussel stocks within the Bay (Robinson et al. 2004) would be at risk, due to spat- and juvenile-directed predation. This could destabilize the population structure of these mussel stocks; indeed an extensive invasion by *C. maenas* might even prevent the establishment of significant mussel beds, which are currently a dominant habitat type. In addition to these ecological effects, there are also potential economic impacts on cultured mussel and oyster stocks, as have been recorded elsewhere (Yamada 2001). However, the fact that South African mussel farming operations make use of the suspended rope culture system may help reduce the effect of crab predation, as these are less vulnerable to benthic predators than the bottom culture techniques used in many other regions.

The second invasive crustacean known to have ecological impacts in South Africa is the barnacle *Balanus glandula*. The abundance of the indigenous periwinkle *Afrolittorina africana*, which is the only other abundant animal species in the upper intertidal zone in this region, has been shown to be strongly positively correlated with that of *B. glandula* (Fig. 3). The reason for this is thought to be that the barnacles increase habitat complexity and provide shelter for the periwinkles (M. Van Zyl, University of Cape Town, unpublished data 2009).

Currently no formal management plan exists for the control or eradication of marine introductions in South Africa. Experience in other regions has demonstrated that regular monitoring of alien marine species is of the utmost importance, in order to track their arrival and spread, assess their impacts and predict and prevent future invasions (Bax et al. 2001; Miller et al. 2004). Despite this, monitoring is a realm of marine science that has often been neglected in South Africa. Management tools which could be useful in the South African context include regular monitoring of areas at high risk of introductions, such as harbours and aquaculture facilities, development of a "rapid response plan" to maximize the chances of eradicating newly detected introductions and strongly enforced legislative control of aquaculture ventures (particularly those wanting to import new species into South Africa).

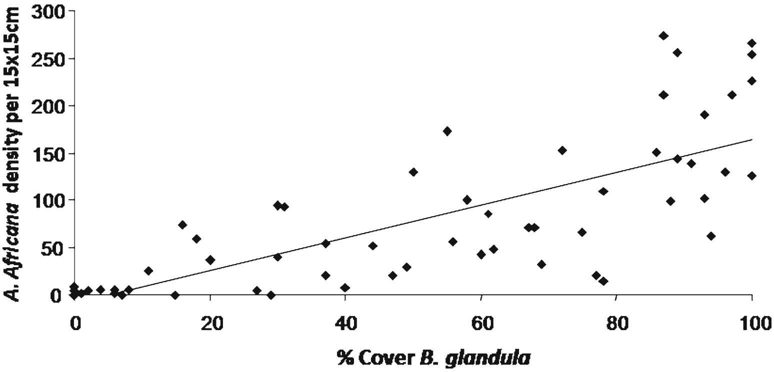

**Fig. 3** Relationship between density of introduced barnacles *Balanus glandula* and of periwinkles *Afrolittorina africana* on a rocky shore in Table Bay, South Africa

Of the introduced crustaceans present in South Africa, *C. maenas* presents the most serious problem and offers the best potential for control. The present population is concentrated in just two harbours, with a few, sparse outlying open-coast populations, which may be sustained by migration from the harbours. Thus reduction of the harbour populations would not only reduce the actual density of crabs along South African shores, but also decrease the potential for spread of the species along the open coast and to new sheltered sites. While international work has considered the possibility of biocontrol of *C. maenas* using the castrating barnacle *Sacculina carcini* (Lafferty and Kuris 1996; Thresher et al. 2000), this method carries risk of transmission to native crab species. Baited trapping, followed by diver collections, could offer a simple method of reducing population density but is unsuitable to achieve complete eradication.

## 7 Future Trends

The rapid rate of increase in the number of introduced marine species in South Africa is a clear indication that much work remains to be done, and that the current list is both taxonomically and spatially incomplete. Two main problems hinder progress. Firstly, many areas remain inadequately surveyed, not even the most obvious sites, such as Table Bay Docks, have been systematically surveyed for introduced species. There has been less survey work on the east coast than in the west. Secondly, a paucity of taxonomic expertise, particularly with regard to smaller-sized taxa, such as copepods and ostracods (among the Crustacea), makes the identification of introduced species problematic.

Considering the above, it is expected that the present number of crustacean introductions known from South Africa will continue to rise significantly, both as taxonomic research on existing marine introductions progresses and as additional species continue to be imported.

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# The Snow Crab, *Chionoecetes opilio* (Decapoda, Majoidea, Oregoniidae) in the Barents Sea

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**Abstract** The snow crab, *Chionoecetes opilio* (Fabricius, 1788), is recorded from the North Pacific, Arctic and Northwest Atlantic. In 1996 however, Russian fishing vessels captured five snow crabs in the Barents Sea and since then, fishing vessels operating in the area have occasionally reported this spider crab in the by-catch. Annual bottom-trawl surveys conducted jointly by Russia and Norway since 2004 have confirmed the presence of *C. opilio* in the northern region of the Barents Sea. Furthermore, in 2008 an increase in abundance and distribution range was found with a significant number of crabs being recorded in the central region of the Barents Sea, mainly between 180 and 350 m deep, in depths and temperatures similar to the species natural habitat in the Northwest Atlantic and North Pacific. The carapace width (CW) of the captured snow crabs typically range from 14 to 130 mm. About 40% of the crabs were juveniles (CW smaller than 50 mm), providing evidence for successful recruitment. These small-sized crabs were exclusively found on Goose Bank, identifying it as the main recruiting area. Ovigerous crabs have been collected since 2004, and the smallest female with extruded eggs measured 65 mm CW. Females larger than 80 mm CW were all egg carrying. Minimum size at maturity in male snow crab, based on presence of spermatophores, was estimated to be 43 mm CW. All males larger than 45 mm CW were mature and can potentially engage in mating. Their diet consisted of benthic organisms such as crustaceans (mainly decapods), polychaetes, molluscs, echinoderms and fish. The Barents Sea population of the snow crab seems to possess similar biological characteristic as those occurring in its natural distribution areas. *Chionoecetes opilio* was unintentionally introduced to the Barents Sea and as yet the processes that might

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limit recruitment and distribution are unknown as are its origins. Genetic methods based on new microsatellite markers have been developed and applied to several Northwestern Atlantic crab populations. It is hoped that these markers will allow identification of the origins of the snow crab population in the Barents Sea.

## 1 Introduction

Seven species (see Ng et al. 2008) are assigned to *Chionoecetes* Krøyer, 1838: *C. angulatus* Rathbun, 1924; *C. bairdi* Rathbun, 1924; *C. elongatus* Rathbun, 1924; *C. japonicus* Ratbun, 1932; *C opilio* (Fabricius, 1788); *C. pacificus* Sakai, 1978 and *C. tanneri* Ratbun, 1893. *Chionoecetes opilio* and *C. bairdi* form hybrids in the Bering Sea, with morphological characteristics derived from both parents (Jadamec et al. 1999; Merkouris et al. 1998). All are commercially exploited (Jadamec et al. 1999).

*Chionoecetes opilio*, the snow crab (Fig. 1), is a subarctic species found in the North Pacific in the Sea of Japan, the Sea of Okhotsk and Bering Sea north of the Alaska Peninsula. In the Northwestern Atlantic Ocean the snow crab is found from South Greenland, Canada to south to Casco Bay in Main USA (Jadamec et al. 1999). The crab also inhabits the Arctic Ocean, the Beaufort Sea to Cape Perry and the shelf of the Laptev Sea and the East Siberian Sea (Jadamec et al. 1999). The adult snow crab is usually found at depths from 0 to 450 m, and temperatures from 0 to 5°C (Tremblay 1997; Lovrich et al. 1995). The species is most often found on mud and sand bottoms where it buries itself during daytime (Robichaud et al. 1989).

In 1996, *C. opilio* was recorded for the first time in the northeast Atlantic when five individuals were captured by Russian commercial fishing vessels in the Barents Sea (Jørstad and Jelmert 1997; Kuzmin et al. 1999). Two more individuals were reported in 1998, and eight in 1999. Their sizes ranged from 41 to 123 mm carapace width (CW) (Kuzmin 2000, 2001). Ballast water was suggested as a possible vector. More crabs have since been reported, mainly collected as by-catch in bottom-trawl

**Fig. 1** Male snow crab (*Chionoecetes opilio*) captured in the Barents Sea 21 February 2006; 76 mm carapace width and weighted 167 g (Photo: E. Farestveit)

fishery. The Russians had collected 15 snow crabs by the end of 1999, mainly in the eastern Barents Sea. In Norwegian coastal waters fishermen caught two snow crabs off Finnmark during spring 2003, and its presence in by-catch was reported the following years. As late as 2002 the extent of the distribution and establishment of the introduced species were unknown, and no report had been made of egg-carrying females.

## 2 The Barents Sea: Short Description

The Barents Sea is a large, shallow-water shelf area located north of the mainland of Norway and Russia (Fig. 2). It is limited to the north by Franz Josef Land, westward by Svaldbard, and by the deep waters of the Norwegian and Greenland Seas. It is further limited to the east by Novaya Zemlya and the Kara Sea (Loeng and Drinkwater 2007). The total area is approximately 1.4 million km$^2$, with an average

**Fig. 2** Location of the Barents Sea in the northeast Atlantic Ocean, with surrounding seas and islands (Modified from Wikipedia)

depth of about 230 m. The maximum depth is about 500 m, but several banks are only 100 m. The Barents Sea is characterized by large annual fluctuations in physical properties such as temperature and ice coverage (Furevik 2001; Ingvaldsen 2008; Gerland et al. 2008; Sundfjord et al. 2008). The water temperatures in the southern part of the Barents Sea typically vary from 4 to 5.5°C at depths around 200 m in August/September, and can reach 7–9°C at surface (Furevik 2001). From the early 1980s there has been a steady increase in the overall temperature in the Barents Sea (Loeng H, Drinkwater K 2007). The warmest year on record was 2006 with high temperatures during both summer and winter (Ingvaldsen 2009). Approximately 40% of the Barents Sea is covered with ice during winter, but there are large seasonal and annual fluctuations in its extent and thickness (Sorteberg and Kvingedal 2006; Loeng and Drinkwater 2007). The ice reaches its maximum extent in March/April. The higher temperatures of the incoming Atlantic water masses usually lead to an increase of ice-free areas. Since 2003, the ice coverage has decreased significantly. In 2006 for the first time the Barents Sea was free of ice south of 76°N throughout the winter (Ingvaldsen 2008).

The Barents Sea forms an important fishing ground for Norway and Russia. The Barents Sea fisheries are managed in accordance with bilateral agreements. Norway and Russia conduct a long-term joint research monitoring of fishery resources in the area. The program includes annual acoustic surveys of demersal fish during summer (August–September), combined with bottom trawl recordings (e.g., Stiansen and Filin 2008). The species diversity in the Barents Sea is lower than in warmer seas (Worm et al. 2006), and thus may contribute to susceptibility to introductions. Important commercial fish species include Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus* Müller), Atlantic herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) (Loeng and Drinkwater 2007). Commercially exploited crustaceans include the northern shrimp (*Pandalus borealis*) and the intentionally introduced red king crab (*Paralithodes camtschaticus*) (see Jørgensen and Nilssen 2011).

## 3 Distribution of Snow Crab in the Barents Sea

Routine sampling of snow crabs began in 2004. These occur both during the annual winter bottom-trawl surveys run in February/March by the Institute of Marine Research in Norway, and the summer surveys in August/September run in collaboration with the Polar Research Institute of Marine Fisheries and Oceanography in Russia. The bottom-trawl surveys target cod and haddock, but records are kept of the by-catch including snow crabs. In 2007 the Russians have began monitoring specifically the snow crab, their annual surveys taking place in August–September (Pavlov 2008).

The abundance of snow crab, estimated as numbers per nautical mile trawled distance, increased from 2004 to 2009 (Fig. 3). The main concentrations were found on Goose Bank in southeastern part of the Barents Sea (Fig. 4). From 2006

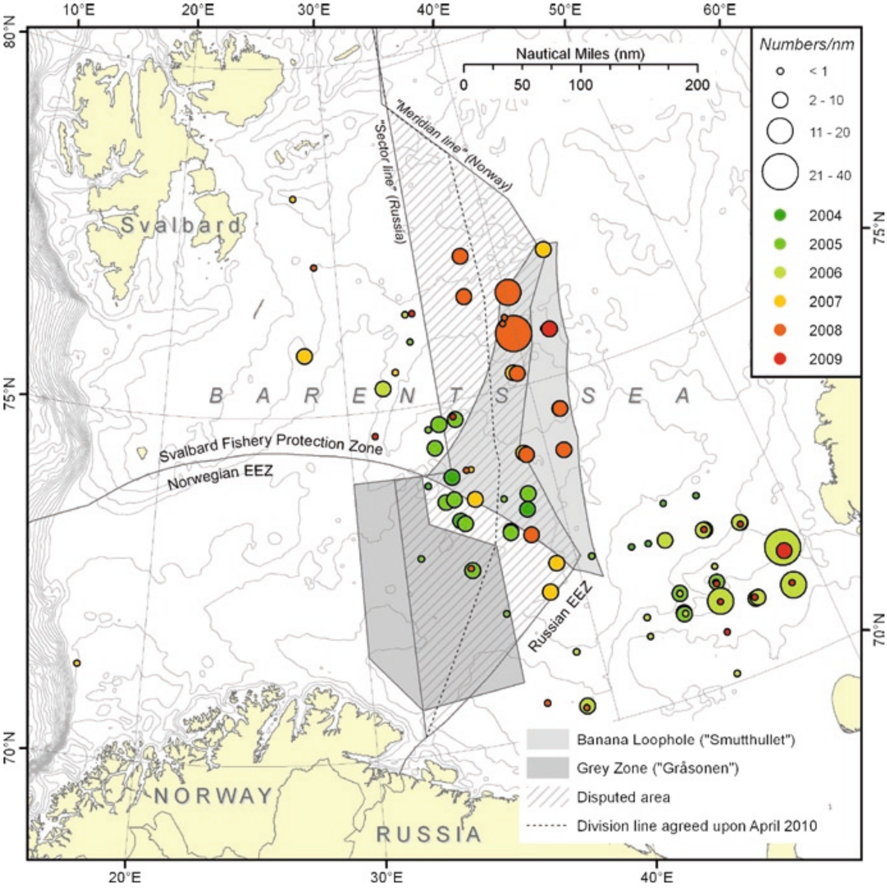

**Fig. 3** Abundance of snow crab (*Chionoecetes opilio*) in the Barents Sea estimated during the Norwegian bottom-trawl surveys 2004–2009 (T. Thangstad, Institutet of Marine Research Norway, unpublished data 2010)

more crabs were found in the eastern part of the Barents Sea. A significant number was also captured in the central Barents Sea. The known range of the introduced snow crab is between 79°N and 69°N, 56°E–27°E. When comparing the known distribution patterns in 2009 and 2006, an increase in the overall abundance of crabs, especially in the eastern part of the Barents Sea is noted. In 2007 the main crab distribution was in northeastern regions, whereas in the following year the crabs were found over a much larger area, including south of Novaya Zemlya. In 2008, three male crabs were captured in southern St. Ann Trough, i.e., north of Novaya Zemlya Island at the entrance to the Kara Sea (V. Pavlov, pers. comm. 2010). Snow crabs have not been reported from the Kara Sea.

The first few specimens in the Barents Sea were captured in 1996 on the Goose Bank. It was not until 6 years later that their numbers increased considerably in the

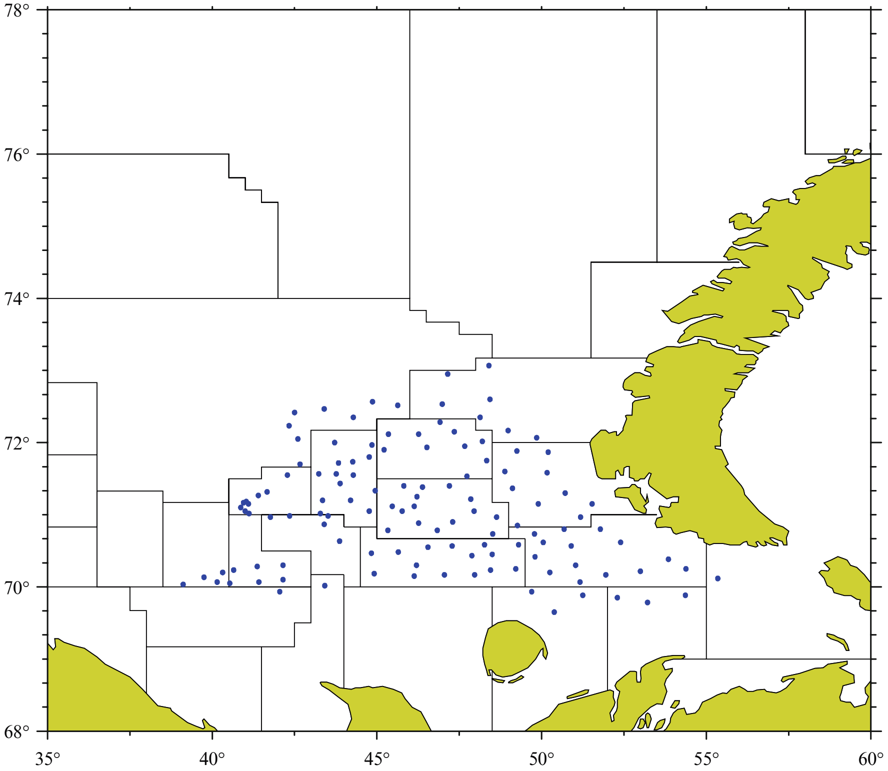

**Fig. 4** Abundance of snow crab (*Chionoecetes opilio*) in the Barents Sea estimated during the Russian snow crab surveys 2007–2009 (Pavlov 2008, 2009)

Russian zone of the Barents Sea and have since increased further (Fig. 5). Both numbers of crabs captured and number of trawl hauls containing crabs has increased since 2002. In the Norwegian zone of the Barents Sea snow crabs were found in significant numbers for the first time in 2004, and their number has remained more or less constant ever since. The Russians conducted targeted surveys in the south-eastern Barents Sea from August to October 2007, and estimated the stock at 6.22 million individuals, with 0.21 million ovigerous females (Pavlov 2008). The results of a similar survey conducted in 2008 put the stock at 7.7 million individuals and 0.8 million ovigerous females (Pavlov 2009). The following year, the estimates were raised yet again to 12.1 million and 2.6 million ovigerous females (Pavlov 2010). Bakanev and Pavlov (2009) estimated the population of snow crabs in the Barents Sea to number 19 million in 2008; 500 times as large as in 2004. This estimate seems high, and more research is required to verify these numbers.

The snow crab distribution on the eastern and western coast of North America seems to be governed by substrate and temperature (Coulombe et al. 1985; Robichaud et al. 1991; Dawe and Colbourne 2002). Orensanz et al. (2004) recorded a range contraction of snow crabs in the Bering Sea due to bottom temperatures

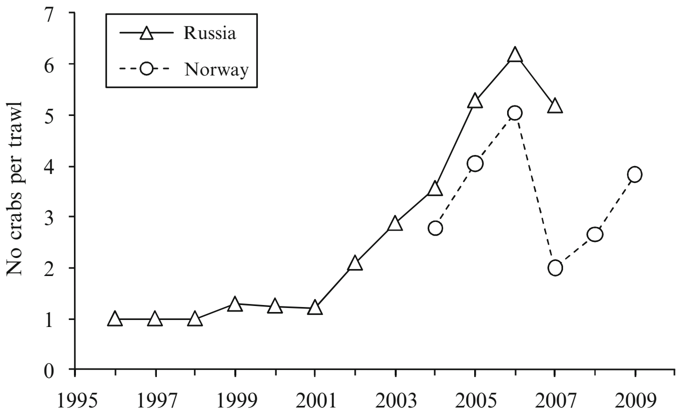

**Fig. 5** Number of crabs captured per trawl hauls with by-catch of snow crab (*Chionoecetes opilio*) in Russian and Norwegian bottom-trawl surveys in the Barents Sea (Russian data; Pavlov 2008. Norwegian data: Thangstad and Agnalt, unpublished)

rising above 2°C and predation by cod. In these areas, young crabs (instars I–III) prefer bottom temperatures between 0°C and 1.5°C, and juveniles in general preferred temperatures lower than 2°C (Dionne et al. 2003; Orensanz et al. 2004). In the early 2000s water temperature in the Barents Sea of the near-bottom layer at sites where snow crab had been collected ranged from –0.6°C in the Hope Island Deep, to +5.9°C in the southwestern part (Pavlov and Sokolov 2003). In succeeding years the temperature at these sites varied from –1.6°C to 5.9°C. The majority of crabs were found in waters colder than 2°C. It seems that high water temperature could to be a limiting factor (see Pavlov 2006; Alvsvåg et al. 2009). Based on average bottom temperatures (1929–2007) in the Barents Sea, the 2°C isotherm change between summer (September) and winter (March) (Anonymous 2009), will likely limit the range of at least juvenile snow crabs to areas north of 73° N and east of 35° E.

## 4 Size Distribution

During the Norwegian surveys, 2004–2008, 239 individuals were collected, 161 males and 78 females. The size distribution differs between the sexes; males were generally larger compared with the females (Fig. 6). The largest male was 136 mm CW compared while the largest female of 93 mm CW. About 40% of the males were larger than 90 mm CW, but only two females. Many of the specimens, regardless of sex, were small, 10–30 mm CW (Fig. 6). These small crabs were found during both the winter and summer surveys in 2006 and 2008. There are indications of several peaks in the overall size distribution, e.g., a peak at 22 mm CW, and 30–34 mm CW for both sexes. These peaks correspond approximately to instar VI and VIII respectively, following Lovrich et al. (1995) and Alunno-Bruscia and Sainte-Marie (1998).

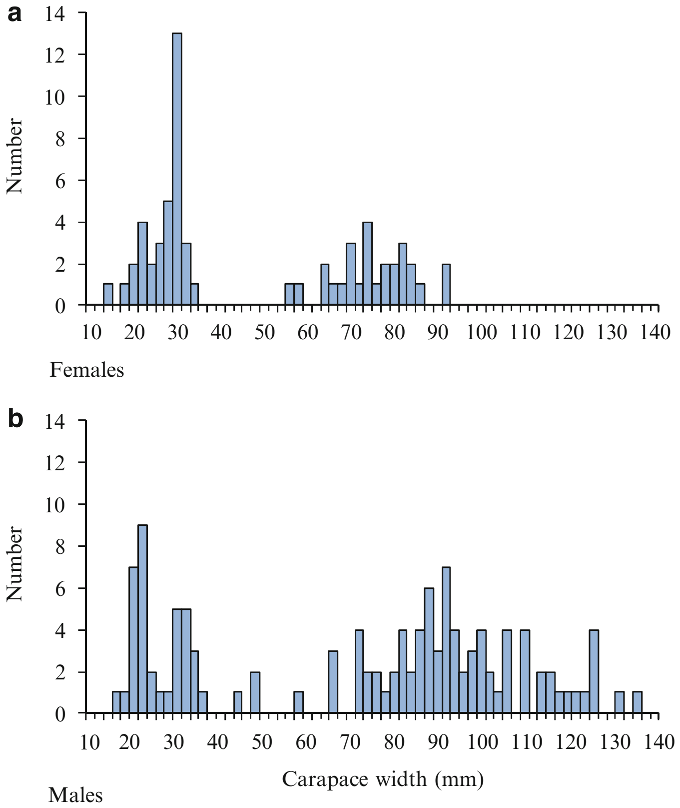

**Fig. 6** Size distribution of (**a**) female and (**b**) male snow crab (*Chionoecetes opilio*) captured in the Norwegian bottom-trawl surveys in the Barents Sea from 2004 to 2008 (Agnalt, unpublished data)

In the Russian zone, the smallest juvenile on record was 7 mm CW, collected in 2004 from the western Barents Sea (73°30′ N, 52°36′ E) at 76 m in depth. The largest male, 166 mm CW, was caught in 2005 in Murmansk Shallows (70°10′N, 39°48′E) at a depth of 200 m (Pavlov 2006). The maximum size of the snow crab recorded in the Russian Far East was 178 mm CW (Perveeva 2005). These records support the hypothesis that juveniles and females are only caught in north and east while large males are found along the coast of Finnmark.

## 5 Reproductive Characteristics

Ovigerous (egg-carrying) females have been recorded since 2004. Brood development varied from recently extruded (bright orange in colour) to eggs close to hatching (dark-brown coloration with the eyes spots of the zoea visible). Females with recently

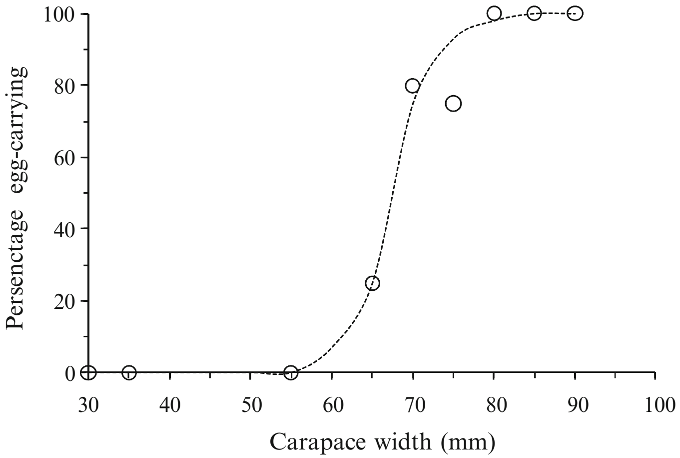

**Fig. 7** Percentage of egg-carrying females of snow crab (*Chionoecetes opilio*) at carapace width (mm), captured in the Barents Sea from 2004 to 2008 (Agnalt, unpublished data)

extruded eggs were found both in winter and summer, whereas females bearing eggs about to hatch were only caught in February. The ovigerous females were larger than 55 mm CW (Fig. 7). The smallest ovigerous female measured 65 mm CW, and the largest 93 mm. All females larger than 80 mm CW were ovigerous. Size at 50% maturity (based on presence of extruded eggs) for female snow crabs in the Barents Sea was about 66 mm CW, slightly larger (50 mm CW) than in the Gulf of St. Lawrence crabs (Watson 1970; Jewett 1981; Elner and Beninger 1995). Most female crabs (> 90%) were captured on the Goose Bank and adjacent areas, at depths from 100–317 m (Pavlov 2006; Alvsvåg et al. 2009). The northernmost ovigerous female was collected in November 2005 at 76°07′N, 32°23′E, at 317 m depth (Pavlov 2006).

The presence of spermatophores indicated that the minimum size of mature male snow crab in the Barents Sea is 43 mm CW (Filina 2009; Filina and Pavlov 2009). All males larger than 45 mm CW were mature. In the northwestern Atlantic males were found to reach maturity at 40–50 mm CW (Watson 1970; Sainte-Marie and Hazel 1992; Otto 1998; Comeau et al. 1999). A female may extrude 10,000–1,60,000 eggs, depending on its size (Jewett 1981; Yosho 2000; Burmeister 2002). The spawning and hatching period in the northwestern Atlantic lasts from April to June, depending on temperature (Robichaud et al. 1989; Webb et al. 2007). In most of the stocks, the fertilized eggs seemed to undergo a 2 year-cycle before hatching (Comeau et al. 1999; Sainte-Marie 1993; Mallet et al. 1993; Burmeister 2002), but a 1-year cycle has been reported in some populations (Burmeister 2002; Webb et al. 2007). Snow crabs in St. Lawrence appear to reproduce twice in their lifetime (Sainte-Marie 1993; Comeau et al. 1999).

Little is known of reproductive biology of the snow crab in the Barents Sea other than size at maturity. There are indications of a 2-year reproductive cycle, but more studies are required to clarify the reproductive potential.

## 6 Predators

The snow crab in Barents Sea is preyed upon by Atlantic cod, haddock, wolffish (*Anarhichas* sp.) and thorny skates (*Raja* spp.) (Pavlov 2006). Cod and *Raja radiata* have been found to predate on snow crab in its natural habitat the Northeastern Atlantic (Waiwood and Elner 1982; Robichaud et al. 1991; Chabot et al. 2008), the former seems to prefer small-sized crabs ca. 6–30 mm CW. Robichaud et al. (1991) found five times more snow crabs consumed by skate than by cod. Orlov (1998) too suggested that deep-water skate preyed heavily on snow crabs off North Kuril Islands and Southeast Kamchatka, with frequencies as much as 30% in the stomachs of some species. Squires and Dawe (2003) found cannibalism to vary from 7% to 17%, and cannibalism was proposed as one of the regulating factors controlling abundance in snow crab populations (Sainte-Marie et al. 1996).

## 7 Diet

The diet of snow crab in the western Atlantic consists of a great variety of prey items – polychaetes, fish (mainly capelin), crustaceans (shrimp, crabs), clams and echinoderms (Wieczorek and Hooper 1995; Lovrich and Sainte-Marie 1997; Squires and Dawe 2003). Squires and Dawe (2003) found that males preyed more on fish compared with the females, which feed more on shrimps.

Investigations of the food composition of snow crabs in the Barents Sea were carried out in the southeastern areas from 2000 to 2005 (Pavlov 2007). The contents of 115 stomachs were analyzed, of which 8.7% were empty. Their prey consisted of benthic organisms and fishery discards (Table 1). Forty-one invertebrate taxa were identified. To estimate feeding intensity, indices of crab stomach fullness have been used (food bolus weight/crab weight × 100) in percent of crab weight. All examined male crabs smaller than 45 mm CW had full stomachs (Table 2). The total stomach filling index for males smaller that 45 mm CW was 0.13 ± 0.053%. Eighty-five percent of larger male crabs (60–99 mm CW) had full stomachs, their feeding intensity ranged from 0.014 to 0.96%. The total stomach filling index for males larger than 100 mm CW averaged 6.02 ± 1.12%. Only 2% of these largest males had empty stomachs. Stomachs of 13% of female crabs were empty, while the stomach filling in those that had eaten was on average 4.01 ± 1.48%. Total stomach filling index of males was 6.45 ± 1.17 and only 4.01 ± 1.48‱ in females, suggesting that males feed slightly more intensively than females.

## 8 Genetics

Few genetic population studies of snow crabs have been published (e.g., Angers et al. 1994; Sévigny and Sainte-Marie 1996; Sainte-Marie et al. 1999). Microsatellite primers had been developed (Urbani et al. 1998a), and used in detailed sperm competition

**Table 1** Stomach contents of snow crab (*Chionoecetes opilio*) captured in the south-eastern Barents Sea from 2000 to 2005 ($n = 115$ including 8.7% empty stomachs; Pavlov 2007). Dominance was calculated as the ratio between numbers of stomachs in which one or other group of food items prevailed and total number of stomachs containing food. The frequency of occurrence (OF) was defined as ratio of quantity of stomachs containing one or other group of food organisms to the total quantity of stomachs and then expressed in percent

| Food items | Weight fraction (%) | Dominance (%) | OF (%) |
|---|---|---|---|
| **Crustacea** | **32.2** | **15.6** | **41.6** |
| Copepoda (*Oithona similes*, *Calanus finmarchicus*) | + | 0.7 | 9.7 |
| Amphipoda | 0.2 | 1.0 | 0.6 |
| Cumacea (*Eudorella*, *Diastylis*) | 4.2 | 0.7 | 5.6 |
| Isopoda (*Saduria sabini*) | 7.5 | 2.0 | 2.4 |
| Euphausiacea | 0.2 | 1.0 | 1.4 |
| Decapoda | 20.1 | 10.2 | 6.6 |
| Shrimps (*Pandalus borealis*) | 6.9 | 8.9 | 2.3 |
| Hermit crab (*Pagurus pubescens*) | 12.4 | 0.3 | 0.7 |
| Crabs (*Chionoecetes opilio, Hyas sp.*) | 0.8 | 1.0 | 4.8 |
| **Polychaeta**[a] | **18.9** | **25.4** | **52.6** |
| **Sipunculoidea** (*Golfingia oculata*, *Phascolion strombus*) | **2.5** | **0.7** | **0.9** |
| **Mollusca** | **8.3** | **15.3** | **44.4** |
| Bivalvia[b] | 6.6 | 10.9 | 34.0 |
| Gastropoda[c] | 1.3 | 2.7 | 17.1 |
| Scaphopoda (*Antalis entalis*) | 0.4 | 1.7 | 3.3 |
| **Echinodermata** | **8.1** | **8.8** | **20.2** |
| Ophiuroidea (*Ophiura sarsi*) | 8.1 | 8.8 | 20.2 |
| **Foraminifera** | **0.2** | **4.4** | **6.1** |
| **Bryozoa** | **+** | **0.3** | **0.3** |
| **Pisces** | **17.9** | **14.9** | **27.5** |
| **Nematoda**[d] | **+** | **0.6** | **1.0** |
| **Detritus** | **9.4** | **9.5** | **20.6** |
| **Inorganic components**[e] | **2.5** | **4.5** | **18.8** |

[a] *Myriochele heeri*, *Myriochele* sp., *Galathowenia oculata*, *Maldane sarsi*, *Melinna* sp., *Spiochaetopterus typicus*, Nephtyidae g. sp., Polynoidae g. sp

[b] *Yoldia hyperborea, Astarte crenata*, *Nuculana pernula*, *Cardium* sp., *Bathyarca* sp., *Mya* sp., *Arctinula greenlandica*, *Macoma* sp., *Yoldiella lenticula*, *Y. nana*, *Leonucula tenuis*, *Hiatella arctica*

[c] *Lunatia pallida*, *Marsenina glabra*, *Frigidoalvania janmayeni*

[d] *Anisakis simplex l.*, *Hysterothylacium aduncum*

[e] Sand and clay inclusions

+ Below the accuracy of data presented

investigations (Urbani et al. 1998b). Another set of microsatellite markers were developed (Puebla et al. 2003), and used in a geographic study of the genetic structure of the crab population off Canada and Greenland (Puebla et al. 2008). The analyses revealed distinct genetic differentiation between the two main areas, but minor differences were also found within each of the two areas. DNA was extracted from the samples collected in 2004 in the Barents Sea at Institute of Marine Research in Bergen

**Table 2** Food composition of snow crab in the southeastern part of the Barents Sea in 2000–2005, expressed in % (Pavlov 2007)

| | Males CW <45 mm | | | Males CW 60–99 mm | | | Males CW ≥ 100 mm | | | Females | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | W | D | OF | W | D | OF | W | D | OF | W | D | OF |
| Mollusca | 40 | 20 | 50 | 6 | 11 | 33 | 4 | 17 | 46 | 17 | 21 | 29 |
| Echinodermata | 15 | 7 | 17 | 3 | 9 | 21 | 14 | 9 | 25 | 3 | 9 | 14 |
| Crustacea | 9 | 27 | 67 | 24 | 18 | 40 | 20 | 12 | 43 | 49 | 15 | 22 |
| Polychatea | 6 | 7 | 17 | 13 | 24 | 67 | 26 | 30 | 78 | 3 | 24 | 46 |
| Inorganic components | 2 | 13 | 67 | 0.5 | 5 | 12 | 3 | 4 | 10 | 3 | 3 | 8 |
| Pisces | 0.3 | 20 | 50 | 30 | 16 | 41 | 7 | 12 | 36 | 7 | 18 | 29 |

*W* weight fraction, *D* dominance, *OF* frequency of occurrence
See Table 1 for calculations of OF and D

and sent to the laboratory in Mont-Joli, Canada, for preliminary testing of microsatellite variation. Surprisingly, these samples did not cluster with any of the samples from the West Atlantic. This result thus raised the question of a possible genetic relationship of Barents Sea populations with those of the north Pacific. Similar relations were observed for other trans-Arctic invasive species as Pacific herring (Jørstad 2004), the gadoid fish *Theragra finmarchicus* (Christiansen et al. 2005) and bivalve molluscs (Väinölä 2003; Nikula et al. 2007). Samples obtained during recent investigations in the Barents Sea (Alvsvåg et al. 2009), were again sent to Mont-Joli for microsatellite analyses. The mtDNA analyses indicated a linkage with Canadian populations (Sévigny and Sainte-Marie 2009). The origin of the snow crab population introduced into the Barents Sea is yet unclear and needs to be investigated further.

## 9 Discussion

The newly introduced population of snow crab in the Barents Sea is found at depths, temperature range and substrate similar to its native habitat in the Northwest Atlantic and North Pacific. The biological characteristics of the Barents Sea population seem similar to those of populations in the native distribution areas. Adaptation of alien species into new environments outside their natural geographic distribution is sometimes associated with genetic bottlenecks, a cause of reduction in genetic variation. Examples are the intended introduction of Atlantic salmon (Reilly et al. 1999), and rainbow trout (Ward et al. 2003), into Australia as aquaculture species. With regards to the intentional introduction of *Paralithodes camtschaticus* into the Barents Sea, no indications of bottlenecking have been detected (Jørstad et al. 2007; Zelenina et al. 2008), possibly due to the massive number of individuals released over many years (Orlov and Ivanov 1978).

Was the snow crab introduced to the Barents Sea in ballast water? Has it been present in the Arctic-Atlantic basins, but not in the Barents Sea? Or is it yet another example of trans-arctic interchange? The Bering Strait was created about 3.5 million years ago during the warm mid-Pliocene epoch allowing interchange between the Atlantic and Pacific Ocean (e.g., Väinölä 2003; Reid et al. 2007; Vermeij and Roopnarine 2008). Vermeij (1991) identified trans-Arctic interchange of 295 molluscan species, mostly of Pacific origin. In this century too the Bering Strait has been ice free (Gerland et al. 2008; Reid et al. 2010), and species such as the snow crab could have entered the Arctic Ocean from the Pacific to inhabit suitable areas such as the Barents Sea. Genetic profiling may help identify and clarify the source of the Barents Sea population. Further, estimates of the genetic relationship with potential donor populations may provide important genetic and biological information about the spread potential of invasive species (Andrew and Ward 1996; Ward and Andrew 1995; Murphy and Schaffelke 2003; Roman 2006). This has been shown for *Carcinus maenas* by Geller et al. (1997), who estimated the region of origin for a number of crab invasions. Even more detailed information can be obtained by using microsatellite DNA (Bagley and Geller 2000; Roman and Palumbi 2004). The preliminary results from microsatellite and mtDNA analyses carried out to date are not conclusive (Sévigny and Sainte-Marie 2009; Jørstad 2009) and there is a need for further investigation. The sample size in the preliminary investigations was relatively small, and larger series should be examined. Further, new microsatellite DNA primers have been developed and should be included in future genetic analysing program. Most importantly, additional samples should include material collected from the Russian regions of the Barents Sea.

Since 1996, when the first few specimens of snow crab were collected in the Barents Sea (Kuzmin et al. 1999), the population expanded its size and distribution, mostly in the early 2000s. Expansion may be linked to climatic conditions, as the snow crab prefers temperatures lower than 5°C. The species diversity in the Barents Sea is typically lower than in e.g. warmer seas (Worm et al. 2006), and implies vulnerability to introductions of new species. The snow crab and the red king crab, the latter intentionally introduced to this region in the 1960s (Jørgensen this volume), are considered "aliens". The red king crab is generally found closer to the coast, whereas the snow crab is confined to deeper and central areas of the Barents Sea. However, there are areas where their populations may overlap. The ecological consequences of the presence of both large-bodied crustaceans in the Barents Sea are unknown at present. Major concerns with invasion include transfer of disease, parasites, and replacement/displacement of native species due to competition for habitat and food, direct predation and hybridization (see Galil 2007 and references therein). There is an urgent need for in-depth studies on the invasive snow crab population, including biological and genetic characterization. Little is known of the reproductive biology of the snow crab in the Barents Sea, and studies are needed to understand its potential, and thus evaluating its dispersal as well as abundance.

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# Alien Malacostracan Crustaceans in the Eastern Baltic Sea: Pathways and Consequences

**Nadezhda A. Berezina, Victor V. Petryashev, Arturas Razinkovas, and Jūratė Lesutienė**

**Abstract** The recent invasion history of malacostracan crustaceans into the eastern Baltic Sea is reviewed with 16 alien species being recorded from the easternmost area. These invasives constitute 3% of the total species richness (50% of the alien biota), and comprise up to 80% of the total benthic biomass in several localities. The Ponto-Azov-Caspian species are the most diverse and abundant component. Their taxonomical and ecological dominance could be explained by a combination of factors including similarities between the Baltic, the donor regions and the waterway network that allows their dispersal. The high vulnerability of the Baltic Sea to invasion may be a consequence of low native biodiversity coupled with anthropogenic and natural factors. The potential impact of alien Malacostraca on the native community was assessed following predatory studies of alien amphipods on native benthic biota. These studies indicated that the alien amphipods may alter the structure of their prey communities. Alien crustaceans have outnumbered or even completely replaced native species and/or earlier established invaders locally in the eastern Baltic Sea.

**Keywords** Alien Malacostraca • Benthic Community • Invasion History • Predatory Impact • Baltic Sea • Curonian Lagoon • Vistula Lagoon • Neva Estuary

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# 1 Introduction

The Baltic Sea is a brackish ecosystem characterized by low species diversity, and as other mesohaline seas, is easily colonized by alien species (Stachowicz et al. 1999). The increasing number of newly recorded aliens in the last decades has been attributed to the escalating anthropogenic stress on the Baltic Sea ecosystem (Gomoiu et al. 2002).

A large catchment area combined with dense human population and intensive exploitation of natural resources of the Baltic Sea have caused the destabilization of a marine ecosystem already disturbed by natural or anthropogenic factors (e.g., extreme storms, bottom dredging), alteration due to previous introductions (habitat engineering), and eutrophication (Schernewski and Schiever 2002; Schiewer 2008). As a result a number of species are no longer recorded from the region and the food web has become weakly articulated giving rise to "vacant niches". These according Zaiko et al. (2007) are then occupied by alien species. Such species as a rule are eurybiotic organisms, *r*-strategists and able to establish themselves in new habitats, including environments that have been disturbed. About 100 alien species have been recorded in the Baltic Sea during the last two centuries, and most of them have been unintentionally introduced by ballast water, hull fouling or by spreading from their primary sites of introduction into adjacent water bodies (Leppäkoski et al. 2002).

The main introductory pathways of crustaceans into the Baltic Sea basin have been analyzed in details (see Jażdżewski 1980; Bij de Vaate et al. 2002; Leppäkoski et al. 2002; Berezina 2007b; Ojaveer et al. 2007). The most important factors facilitating the arrival and successful establishment of alien species are the elimination of natural barriers due to construction of canals, reservoirs, drainage systems, the network of waterways cross Europe, shipping, climatic change and destruction of habitats. The Baltic Sea is susceptible to invasions as it forms a nexus of waterways connecting the North, White, Black, Azov and Caspian Seas, and it is the recipient of ca. 250 rivers. Assessment of impact in newly invaded habitats and preventive control of alien species are important ecological problems for the Baltic Sea ecosystem, especially in coastal and estuarine areas (Schernewski and Schiever 2002).

This chapter reviews the history of invasive malacostracans in the coastal habitats in the eastern Baltic Sea (primarily Gulf of Finland, Curonian and Vistula (Russian part) lagoons), describes the biological traits that make these crustaceans successful invaders and attempts to characterize their effects on native invertebrate communities (mainly through trophic interactions) in recipient ecosystems.

# 2 The Study Area

The tidal less Baltic is a shallow brackish inland sea with a mean depth of 55 m of which 17% is <10 m deep (Voipio 1981). The area of study is focused on the coastal areas in the eastern region to include the Gulf of Finland in the northeast and the Curonian and Vistula lagoons in the southeast (Fig. 1). The salinity in

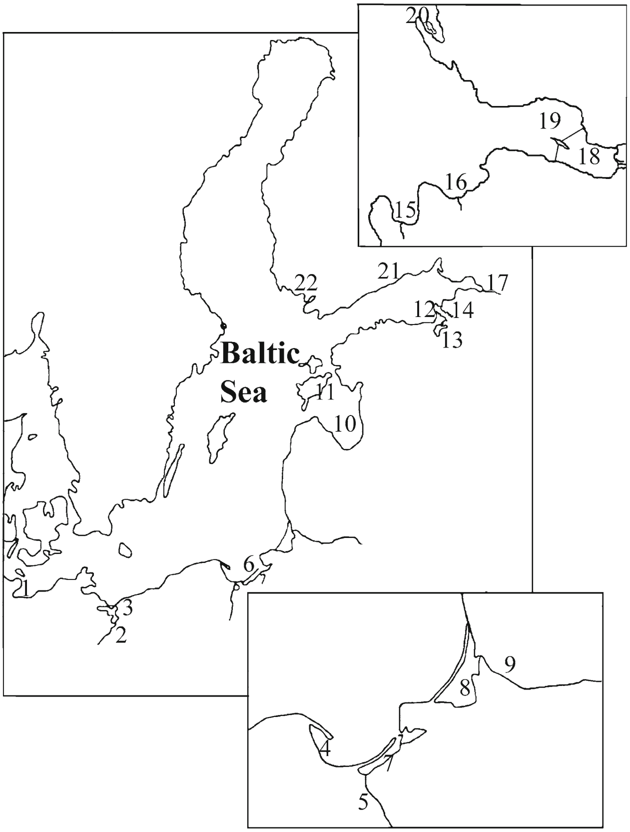

**Fig. 1** Study regions of the Baltic Sea: 1. Mecklenburg Bay, 2. Oder River, 3. Oder Estuary, 4. Puck Bay, 5. Vistula River, 6. Gulf of Gdansk, 7. Vistula Lagoon, 8. Curonian Lagoon, 9. Neman River, 10. Gulf of Riga, 11. Saaremaa Island, 12. Narva Bay, 13. Lake Peipsi, 14. Luga River, 15. Luga Bay, 16. Koporskaya Bay, 17. Neva River, 18. Neva Bay, 19. Neva Estuary, 20. Vyborg Bay, 21. Kotka, 22. Turku

these areas varies from 0 to 3 psu in inner and estuarine waters, through 7 psu in the open areas.

The Baltic Sea is connected to the Atlantic Ocean through the Danish Straits, and to the Ponto-Caspian region via a system of waterways, for which construction began in the 1770s (Bij de Vaate et al. 2002). The estuaries, the Neva Estuary, Curonian and Vistula lagoons, serve as halfway houses for alien species and centres of xenodiversity. These transitional waters are affected by wind-mixing, stochastic water exchange with the Baltic Sea proper, horizontal gradients of salinity, high nutrient load leading to occasional phytoplankton blooms, high productivity, accumulation of humic material, and domination by eurybiotic species (Telesh et al. 2008; Schiewer 2008).

The Neva Estuary (3,600 km$^2$) is one of the largest in the Baltic. The Neva River (74 km long) flows out of Lake Ladoga, the largest lake in Europe, and discharges 76 km$^3$ water annually into the inner and outer parts of the Neva Estuary. The total particulate organic matter (POM) of the river ranges between 4.6 and 12.0 mg $l^{-1}$ (Telesh et al. 2008). The surrounding Neva Bay is shallow with a mean depth of 4 m, (maximum depth 12 m), and oligohaline (ca. 0.1 g $l^{-1}$). A storm-surge barrier has separated the bay from the estuary since the early 1980s. The mean and maximal depths of the inner and outer estuary are 12 and 60 m respectively, and the salinity ranges from 0.21 to 2.5 $gl^{-1}$. The total phosphorus in the estuary ranges between 30 and 340 $mgm^{-3}$.

Curonian Lagoon (1,584 $km^2$) is separated from the sea by a sand spit, with a narrow (0.4–1.1 km) opening (Klaipeda port area). The average depth of the lagoon is 3.8 m, with a dredged waterway to 14 m depth (Gasiūnaitė et al. 2008). This freshwater lagoon is greatly influenced by the Neman River inflow. The eastern side of the lagoon (mainland shore) slopes gently westward to a depth of 1–2 m, whereas the western side is up to 4 m depth (Gasiūnaitė et al. 2008).

The Vistula Lagoon (838 $km^2$) has an average and maximal depth of 2.7 and 5.2 m respectively, excluding the dredged navigable channel, and is separated from the sea by a sandy barrier. The lagoon was formed in 1916 when the Vistula River was diverted to the Baltic Sea and changed from a freshwater estuary to an estuarine lagoon (Chubarenko and Margoński 2008).

## 3 Invasion History of Crustaceans in the Gulf of Finland, Curonian and Vistula Lagoons

The majority of alien crustaceans arrived in the Baltic Sea from the Volga River, Caspian Sea, Black Sea and the Sea of Azov, following the construction of waterway systems that formed inland invasion corridors (Bij de Vaate et al. 2002; Leppäkoski et al. 2002). Large-scale intentional introductions with the aim of improving fisheries by augmenting the food items of fish species of commercial interest are to blame for the amphipod, mysid and isopod invasions of the inland waters of European Russia (Nikolaev 1963; Arbačiauskas 2002; Orlova et al. 2006; Berezina 2007b). Between the 1950s and 1980s scores of amphipod and mysid species from Ponto-Caspian region were transported through the former USSR (Jażdżewski 1980; Arbačiauskas 2002; Berezina 2007b).

Climate change such as warming could trigger the expansion of alien species of Malacostraca from the Ponto-Caspian and the Black Sea to the Baltic Sea (Berezina 2007b). Some Ponto-Caspian gammarids and the mysid *Hemimysis anomala* have reached the northeastern Baltic (including Neva Bay), and other Ponto-Caspian mysids, *Paramysis lacustris* and *Limnomysis benedeni*, are currently restricted to the southern Baltic (Razinkovas and Zemlys 2008). Effects of climate change in the Baltic Sea forecast a significant rise in sea level, decreased salinity and an increase of temperature especially during winter (Razinkovas and Zemlys 2008). These changes would be reasonable to expect that alien species limited by cold winter and tolerant to oligohaline waters (such as crustaceans from Ponto-Caspian and Mediterranean regions) will continue to expand their ranges into the northeastern part of the Baltic Sea

## 4 Amphipods

Nine alien amphipod species have been recorded in the eastern Baltic Sea (Table 1). The species of Ponto-Caspian origin, *Chaetogammarus ischnus* (Stebbing, 1899), *C. warpachowskyi* (Sars, 1894), *Chelicorophium curvispinum* (Sars, 1895), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Obesogammarus crassus* (Sars, 1894) and *Pontogammarus robustoides* (Sars, 1894), form the leading group among amphipod invaders (Berezina and Panov 2003; Ezhova et al. 2005; Orlova et al. 2006; Malyavin et al. 2008). Two amphipod species, *Gmelinoides fasciatus* (Stebbing, 1899) and *Gammarus tigrinus* Sexton, 1939, originate in Lake Baikal, Siberia (Panov and Berezina 2002), and the Atlantic coast of North America respectively (Ezhova et al. 2005; Berezina 2007b; Bacela et al. 2008). Another Ponto-Caspian species, *Dikerogammarus villosus* (Sowinsky, 1894), is widespread in Europe (Grabowski et al. 2007; Bacela et al. 2008) and may further disperse into the eastern Baltic Sea in the near future.

**Table 1** List of alien species and their first records in the eastern Baltic Sea according to Berezina and Panov 2003; Ezhova et al. 2005; Pienimäki et al. 2004; Daunys and Zettler 2006; Orlova et al. 2006; Berezina 2007a, b, c and unpublished data; Herkül and Kotta 2007; Ojaveer et al. 2007; Malyavin et al. 2008; Herkül et al. 2009; Kalinkina and Berezina 2010

| Species | Gulf of Finland | Gulf of Riga | Curonian Lagoon | Vistula Lagoon (Russian part) |
|---|---|---|---|---|
| Amphipoda | | | | |
| *Chaetogammarus warpachowskyi* | 2004 | – | 1960s | – |
| *Chaetogammarus ischnus* | – | – | 1920s | 1920s |
| *Chelicorophium curvispinum* | 2005 | – | 1920s | 1920s |
| *Dikerogammarus haemobaphes* | – | – | – | 1999 |
| *Obesogammarus crassus* | – | – | 2000 | 2000s |
| *Pontogammarus robustoides* | 1999 | 2009 | 1999 | 1999 |
| *Gmelinoides fasciatus* | 1996 | – | – | – |
| *Gammarus tigrinus* | 2003 | 2003 | 2003 | 1999 |
| *Orchestia cavimana* | 2002 | 2002 | – | 1980s |
| Mysidacea | | | | |
| *Hemimysis anomala* | 2003 | – | 1960s | – |
| *Limnomysis benedeni* | | – | 1960s | – |
| *Paramysis lacustris* | – | – | 1960s | – |
| *Paramysis intermedia* | 2008 | 2008 | – | – |
| Isopoda | | | | |
| *Jaera sarsi* | 2004 | – | – | – |
| Decapoda | | | | |
| *Eriocheir sinensis* | 1933 | 1990s | 1980s | 1980s |
| *Palaemon elegans* | 2003 | – | 2004 | 2000 |

In the 1960s three Ponto-Caspian amphipods, *P. robustoides*, *O. crassus* and *C. warpachowskyi*, had been introduced from the Black Sea basin to Kaunas Reservoir (Neman River), from which they spread to Lithuania, Latvia and Russia (Leningrad province). Their native regions include brackish and freshwater bays in the Marmara, Black, Azov and Caspian seas, coastal lakes and lagoons and the lower courses and estuaries of the rivers Volga, Don, Bug, Dnepr, Dniester, Danube, Prut, Terek, Kura, Kuban, etc. (Kalinkina and Berezina 2010). By the end of the twentieth century, *P. robustoides* had spread along the Vistula, Oder, Neman, and Elbe Rivers, also entering some lakes and reservoirs (Rudolph 1997; Zettler 1998; Arbačiauskas 2002; Jażdżewski and Konopacka 2002; Jankauskienė 2002; Ezhova et al. 2005). It is common in the Vistula and Curonian lagoons where it coexists with another common Ponto-Caspian amphipod alien, *O. crassus* (Berezina, unpublished data). In the past decade it was recorded in the Neva Estuary (Berezina and Panov 2003), Narva Bay, Estonia (Herkül et al. 2009), the lower reaches and mouths of Latvian rivers (Grudule et al. 2007), and along the Gulf of Riga (Kalinkina and Berezina 2010). *Chaetogammarus warpachowskyi* was reported from the Curonian Lagoon and inland lakes of Lithuania in the 1990s (Olenin and Leppäkoski 1999; Jankauskienė 2002). In addition, during 2004 it was recorded near St. Petersburg, where likely it had arrived with ballast water from other parts of the Baltic Sea. However, subsequent surveys of this area in 2005–2008 failed to record *C. warpachowskyi*. Consequently it may have been an ephemeral population, or it is only present in small number (Berezina et al. 2008).

*Chelicorophium curvispinum* is native to the Caspian and Azov-Black Seas. The species has been recorded from the Volga, Don, Ural, Dnepr, Dniestr and Danube rivers (Malyavin et al. 2008). This amphipod species arrived in the Baltic Sea probably through the waterway network in 1920–1930s, and established populations in the Curonian and Vistula lagoons (Nikolaev 1963; Jażdżewski 1980; Malyavin et al. 2008). In 2005 it was found along the Estonian coast (Herkül and Kotta 2007), and in 2006 it reached abundances of 29–171 ind. m$^{-2}$ at the mouth of the Luga River and at Luga Bay (Malyavin et al. 2008).

*Chaetogammarus ischnus* has spread like the previous species and has been established in the Baltic basin since the early twentieth century. It has been recorded in the Vistula and in the Curonian Lagoon, but has not been found to date along the Russian coast (Jażdżewski and Konopacka 2002; Jankauskienė 2002; Berezina and Razinkovas, unpubl. data).

*Gammarus tigrinus* is native to estuaries of the Atlantic coast of North America and has an extensive invasion history (Pinkster et al. 1977). The first Baltic record dates to 1975, when it was found in Schlei fjord, Germany (Bulnheim 1976). By 1994 it reached the Mecklenburg (Rudolph 1994), the Odra Estuary (Gruszka 1999; Jażdżewski and Konopacka 2000) and spread along the entire Baltic coast of Germany (Zettler 2001), Puck Bay on the western Gulf of Gdańsk, Poland (Szaniawska et al. 2003), and the Vistula Lagoon (Jażdżewski et al. 2002; Ezhova et al. 2005). In 2003 it was recorded in the northern Gulf of Riga (Herkül et al. 2006), off the Finnish coast (Pienimäki et al. 2004), the Curonian Lagoon (Daunys and Zettler 2006), and, in 2005, from the Neva Estuary (Berezina 2007a). It is likely that these have been secondary introductions due to ballast water. In 2008 and 2009, *G. tigrinus* was frequently recorded from the northern and western regions of the Neva Estuary. It may now spread through the extensive waterway networks to many Eastern European lakes.

*Gmelinoides fasciatus* is native to Lake Baikal and Siberian rivers (Angara, Barguzin, Irtysh, Lena, Pyasina, Tunguska, Selenga, Yenisey). In the 1970s it was intentionally introduced into lakes and reservoirs in the former USSR, including the Baltic Sea basin (lakes of the Karelian Isthmus) to supplement fish feed (Berezina 2007b). As a consequence this species spread through the aquatic systems of Eastern Europe. During the 1990s it reached Neva Bay and the oligohaline Neva Estuary. At present, it is common in habitats of the eastern Gulf of Finland with salinity range of 0.05–2.0 psu (Berezina and Panov 2003). It has established an abundant population in the mouth of the Luga River, where it was first recorded in 2004 (Berezina 2008) This species may have arrived here either from the Neva Estuary or the Narva River, where it has been abundant since the 1990s (Panov et al. 2000).

The first record of the semi-terrestrial talitrid amphipod, *Orchestia cavimana* (Heller, 1865), was from the Northeastern Baltic Sea. It dates to 1999 when it was found in damp wracks cast up on Saaremaa Island, Estonia (Kotta 2000). In the early 2000s the species spread to Northwestern Estonia. *Orchestia cavimana* is widely distributed in the Mediterranean, Black Sea, Red Sea, and the eastern Atlantic, from North Africa to the Southern North Sea. In the Baltic Sea it reported from German and Polish estuaries and lagoons (Żmudziński 1990; Spicer and Janas 2006). The latter are the likely donor populations. In 2009 *O. cavimana* was found for the first time in the main Vistula channel at Świbno, colonizing this locality by a natural spread up the river obviously from the Baltic coast (Konopacka et al. 2009). These records of *O. cavimana* and its high biomass in newly invaded habitats indicate that the species continues to extend its range along the Baltic coastline. Algal biomass has increased in recent decades with the eutrophication of the Baltic Sea. Since wrack biomass appears to be a predictor of *O. cavimana* abundance, this amphipod may have dispersed with drifting algae, although unintentional anthropogenic transport cannot be excluded.

## 5 Mysids

Four Ponto-Caspian species, *Hemimysis anomala* Sars, 1907, *Limnomysis benedeni* (Czerniavsky, 1882), *Paramysis lacustris* (Czerniavsky, 1882), and *Paramysis intermedia* (Czerniavsky, 1882), have been established in the eastern Baltic Sea basin. *Hemimysis anomala* is native to the western and northwestern coast of the Black Sea, the Azov Sea, mouth of the Don River, the eastern Caspian Sea and the Volga River delta. *Limnomysis benedeni* and *P. lacustris* are native to the Black and Azov Seas, and the shallow waters of the Caspian Sea mostly in river mouths (Derjavin 1939; Pauli 1957; Bacescu 1969). The latter species has a native distribution that includes the Marmara Sea and adjacent river basins. Following the description of the southern Russian congener, *P. sowinskii* (Daneliya, 2002), the Baltic basin population of *Paramysis* is in need of clarification.

In the 1950s large-scale introductions from Ponto-Caspian basin into different lakes, rivers and reservoirs of Ukraine, Moldova and southern Russia took place. Between 1962 and 1985, the three mysid species had been repeatedly introduced from the Dnieper basin to lakes and reservoirs in Lithuania, including the Kaunas reservoir on the Nemunas River (Arbačiauskas 2002). Here they have established viable populations and have spread downstream to the Curonian Lagoon.

In the Curonian Lagoon, *L. benedeni* and *P. lacustris* are common species (Arbačiauskas 2002; Lesutienė 2009), whereas *H. anomala* is much less abundant (Razinkovas A. pers. comm. 2008). Only *H. anomala* was recorded in the Gulf of Finland. It was first found in the open marine area of the Baltic Sea near western edge of the Gulf of Finland in 1992 (Salemaa and Hietalahti 1993), and later dispersed eastwards to the inner parts of the gulf. At present *H. anomala* is a common species near the northern coast of the Gulf of Finland from Turku to Kotka, as well as along the eastern coast of Sweden and in the Gulf of Gdansk (Lundberg and Svensson 2004; Janas and Wysocki 2005). The species is known to be transported in ballast tanks (Gollasch et al. 2002). A single record, dating back to 1963, of *P. lacustris* is known from the Estonian coast (Yarvekyulg 1979), but no further occurrences in the Gulf of Finland have been confirmed.

*Paramysis intermedia* was first found in the Baltic Sea in 2008, near Ruhnu Island in the Gulf of Riga and close to the mouth of the Narva River. Like its congener, it was intentionally introduced to serve as food for commercially valuable fish. It was introduced to Lake Peipsi, bordering Estonia and Russia, in the 1970s. Although it had not established a population in the lake, the species may have survived in the Narva River, later dispersing to the Baltic Sea (Herkül et al. 2009).

## 6 Isopods

The isopod *Jaera sarsi* Valkanov, 1936, was first found in 2004, in the brackish waters (2 psu) of Koporskaya Bay, in the Gulf of Finland (Orlova et al. 2006). The Baltic specimens are similar to the subspecies *sarsi* from the Black Sea (Petryashev, unpublished data). The species may have been vessel-transported, or associated with the intentional introduction of mysids and amphipods mentioned above (Nikolaev 1963; Orlova et al. 2006). Its native distribution is limited to the brackish water lagoons of the Black and Azov Seas, the lower reaches of their rivers (Danube, Dnepr, Don, Volga, Ural), some adjacent lakes (Abrau Lake, Lake Varna-Beloslav Lake complex), and in the Caspian Sea (Kussakin 1988; Schotte et al. 1995; van der Land 2001).

# 7 Decapods

The Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards, 1853, is native to the Northwestern Pacific. Its global dispersal with ballast water and trade together with its environmental and economic impacts, make it one of the most cited examples of invasive alien species (see Bentley 2011). The crab is well established in many estuaries and adjacent rivers bordering the North Sea (Peters et al. 1936; Ojaveer et al. 2007). The species may have entered the Baltic Sea by current-swept larvae, active migration of adults or in ballast tanks (Ojaveer et al. 2007).

In the North Sea basin *E. sinensis* was first found in 1912 in the Aller River, Germany. In 1926–1928 it was recorded in the Baltic Sea near German and Polish coasts (Boettger 1933), and in 1933 in Vyborg Bay, Gulf of Finland (Haahtela 1963; Herborg et al. 2003). According to Haahtela (1963), specimens inhabiting the Baltic may have been transferred from the North Sea as larvae or juvenile specimens. In the 1980s this species was recorded in the River Vistula mouth and Gdansk Bay (Normant et al. 2000), and in the Russian part of the Vistula Lagoon (near Kaliningrad). In the eastern Gulf of Finland, near St. Petersburg, *E. sinensis* was first found in 1982 (Panov et al. 2003). Since 2000, it was amply recorded from the inner Neva Estuary (Zelenogorsk-Ushkovo, to the north-west of St. Petersburg), in the city port and in the Neva River itself (Petryashev V.V. 2000). In spite of numerous findings of adult specimens in different parts of the eastern Baltic Sea, there is still no evidence that the species is able to reproduce successfully in waters of eastern part of the Baltic Sea. Obviously it can establish stable self-reproducing populations only in marine waters of the Vistula Lagoon, near German and Danish coasts. Whereas megalops and young crabs drifting eastwards support the ephemeral population in the eastern Baltic Sea.

The euryhaline rockpool prawn *Palaemon elegans* Rathke, 1837, is distributed in the Mediterranean, Black, Caspian seas and in the African and European coast of the Atlantic (from Namibia to Norway) (Udekem d'Acoz 1999). In the 1950s it was unintentionally introduced to the Aral and Caspian Seas (Zenkevich 1963). A massive increase occurred during 2001 in the Vistula Lagoon and along the Russian shoreline (Ezhova 2009). In 2002 it was first found in the Arkona Basin and the Gulf of Gdańsk, in the southern Baltic Sea (Janas et al. 2004; Grabowski et al. 2005) Later in 2003 it was reported from the Gulf of Finland (Kekkonen 2003), and in 2004 from the Curonian Lagoon (Daunys and Zettler 2006).

# 8 Species Richness and Abundance of Alien Species in the Eastern Baltic Sea

Alien crustaceans constitute over 40% of the total number of introduced invertebrate species in the Baltic Sea. In the easternmost Baltic Sea they contribute up to 3% of the total species richness (50% of the aliens), and dominate (up to 80%) the benthic biomass.

Alien amphipods alone (*P. robustoides, G. fasciatus, G. tigrinus*) contribute more than 50% of the total biomass in the littoral zones of the Neva Estuary. The abundance of *P. robustoides* and *G. fasciatus* in Neva Bay has changed significantly since the early post-establishment period in the late 1990s. An early period (2002–2005) of high abundance (up to 2,500–3,500 ind. $m^{-2}$) was followed (2006–2008) by decline and stabilization (1,000–2,000 ind. $m^{-2}$), dynamics that correspond to the classic scenario for the species entering new habitats (Odum 1975).

In the Vistula Lagoon (Russian) littoral zones, *P. robustoides*, *O. crassus* and *D. haemobaphes* constitute over 80% of the zoobenthic biomass. These species dominated in August 2002, near Kaliningrad, over all other amphipods with their combined abundance reaching 25–30% of the total (Berezina, unpublished data). In the (Lithuanian) Curonian Lagoon, *P. robustoides, O. crassus* and *G. tigrinus*, had the highest occurrence (79%) of all benthic malacostracan crustaceans (Daunys and Zettler 2006), during 2004, while the other alien crustaceans (*P. lacustris*, *L. benedeni*, *C. warpachowskyi* and *C. curvispinum*) were much less frequent (1–13%). In July 2005 the freshwater part of the Curonian Lagoon was dominated by *P. robustoides*, while in the oligohaline area *O. crassus* was the most numerous (Arbačiauskas 2008). In 2008 and 2009 *O. crassus* was the most abundant species (up to 4,500 ind. $m^{-2}$) in several coastal areas of the Curonian Lagoon while *P. robustoides* dominated the biomass with values reaching 30 $gm^{-2}$ (Berezina and Razinkovas, unpublished data).

*Chelicorophium curvispinum* was common in macrophyte covered habitats, while *G. tigrinus* was rarely found. The alien mysid *L. benedeni* is abundant in the submersed vegetation zone of the Curonian Lagoon, especially in June-August (Razinkovas 1996; Lesutienė et al. 2005). In August 2008, it is abundance in *Potamogeton* beds reached (0.5–1 m) 500–800 ind. $m^{-2}$, 20 times that of *P. lacustris* (Petryashev and Berezina, unpublished data). The latter species is abundant in summer at 1.5–2.5 m depths, reaching 50–60 ind. $m^{-2}$. In late summer and autumn the population density increases significantly (Razinkov 1990; Lesutienė et al. 2008). There is little quantitative data on *E. sinensis* catches in the eastern Baltic Sea, though scores of specimens were collected near Kotka and Neva Bay (Ojaveer et al. 2007).

## 9 Role of the Alien Crustaceans in the Food Web and Assessment of Possible Predation Impact

Although the number of alien crustaceans in the Baltic Sea has increased considerably in recent years, only a few species can be considered as invasive or hazardous. The alien crustaceans may interact with native species by predation, resource competition or habitat modification, causing the decimation or even local extinction of species (or genetically unique populations), resulting in irreversible losses of genetic diversity. The impact of the alien species is mainly related to species characteristics (primarily with its abundance, food habits and behaviour) and hierarchical complexity and anthropogenic disturbance of the recipient ecosystem (Elton 1958; Lozon and MacIsaac 1997). Several attempts to evaluate or compare possible predation impacts of alien crustaceans have been made (e.g., Telesh et al. 2001; Berezina 2008; Bollache et al. 2008), revealing the ecological significance of the alien species.

The selective predation on planktonic and benthic invertebrates by some amphipods, mysids and decapods is considered the main mechanism explaining the replacement and shifts in density of native species. Examples of impact by predatory crustaceans on native populations/communities have been described in detail (Dick et al. 2002; Kelly et al. 2006; Berezina 2007b, c). As a rule, the predation pressure depends on the predatory nature of invasive crustacean species and the abundance and availability of prey in particular habitats.

## 10 Amphipoda

Microscopic analysis of gut contents of the alien gammaridean amphipods demonstrated that they are omnivorous, possessing mixed feeding strategies and acting as grazers, collector/gatherers and predators (Dick and Platvoet 2000; Devin et al. 2003; Kelly et al. 2006; Berezina 2007c; Bollache et al. 2008). The authors here suggest that their diverse diets allow them to partition resources when available and to successfully compete with native species that tend to be more stenophagous. Although being omnivorous, differences in the food spectra were identified between the alien amphipod species and mean proportions of animal food in the diet increased from smaller to larger species. The large-sized amphipod *P. robustoides* starts to predate at a young age (body length 6–7 mm) attacking the larvae of chironomids and oligochaetes, which are often larger than the species itself (Berezina and Panov 2003). In the littoral zone of Neva Bay, predation by *P. robustoides* on other benthic organisms was the main reason for the densities of prey species to decrease, and the main cause by which the native *G. lacustris* and an earlier established alien amphipod, *G. fasciatus*, were replaced or notably decreased in abundance (Berezina and Panov 2003; Orlova et al. 2006).

The distinct ontogenetic differences in diet and proportion of consumed animal and plant food were recorded for many amphipods (Limen et al. 2005; Berezina 2007c). For example, there were significant differences in the proportion of food categories in the gut contents of *P. robustoides* from the Neva Estuary with size-dependent food preferences (see Fig. 2; Berezina 2007c). The contribution of animal food increased significantly with body size. The juveniles (body length 5–7 mm) were mainly detritivorous (70–80% gut content). Macrophytes (mainly *Potamogeton* sp.) and small invertebrates associated with macrophytes (small oligochaetes, infusorians, rotifers and chironomid larvae) were main food items of middle-sized specimens (8–12 mm). Large *P. robustoides* specimens (larger than 13 mm) are preferentially predaceous, consuming ephemeropteran and chironomid larvae, oligochaetes, isopods, planktonic crustaceans and their own juveniles.

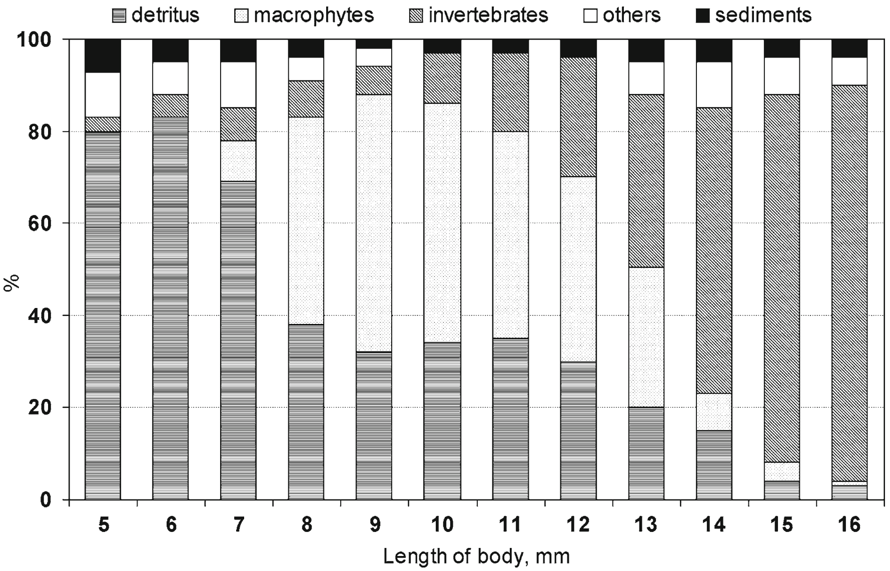

**Fig. 2** Differences in proportion of food categories in gut content of *Pontogammarus robustoides* from Neva Estuary with size-dependent differentiation in food preferences (Developed from Berezina 2007c)

The predation impact index (IP) was proposed for assessment of alien amphipod predation pressure on benthic invertebrates (Berezina 2008). It is calculated as the ratio between consumption rate ($C_{pop}$) of the population and sum production of their preys ($P_{prey}$) for a given period ($IP = C_{pop}/P_{prey}$). The IP of *P robustoides* was ranked as high ($IP > 1$), middle ($0.5 < IP < 1$) and low ($0 < IP < 0.5$). Data on the dynamics of invertebrate communities in the coastal zone of the Neva Estuary in 2002–2008 were used for examination. Food spectra and the proportion of different food items in the diet of both amphipod species depending on their body length were analyzed microscopically and the consumption rates of the invaders measured experimentally (Berezina et al. 2005; Berezina 2008).

The proportion of animal food in the diet of i-sized group of *P. robustoides* ($K_i$, %) was calculated as: $K_i = 0.01 \times L_i^{3.22}$. Consumption rate ($C_i$, %) was calculated as: $C_i = 2.72 \times W_i^{-0.79}$; $W = 0.027 \times L_i^{2.75}$ or $C_i = 47.2 \times L_i^{-2.17}$, where $L_i$ is body length (mm) and $W_i$ is wet weight of i-sized specimens. The consumption rate of the predaceous part of the amphipod population was estimated as $C_{pop} = \sum K_i \times C_i \times B_i$, where $B_i$ is biomass of all i-sized groups in habitats. Oligochaetes, isopods, juvenile amphipods (body length 1.5–6 mm) and chironomid larvae, ephemeropterans, trichopterans and other insects were considered as potential prey following earlier gut content studies (Berezina et al. 2005; Berezina 2008). The production rate of each taxon was calculated using rates of their somatic growth or specific production rate ($p_s$, Golubkov 2000) and biomass ($P_j = p_s \times B_j$).

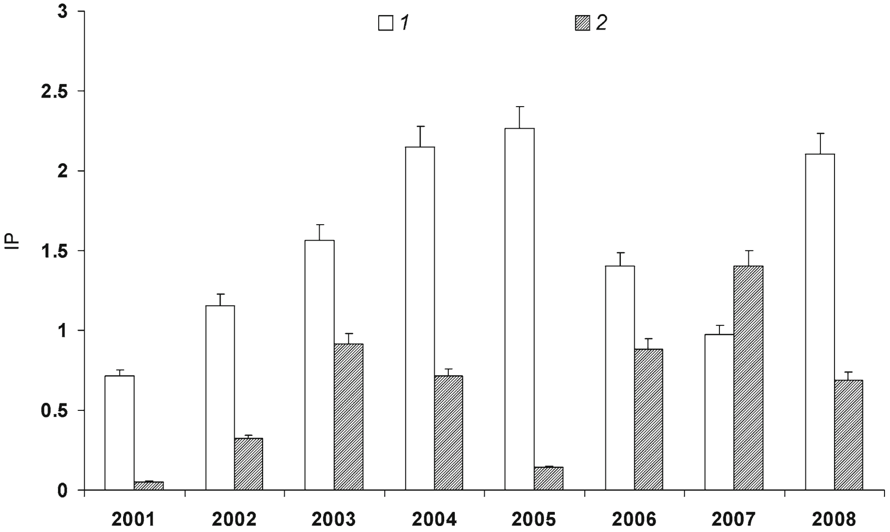

**Fig. 3** Changes in IP indices (mean ± SE) for *Pontogammarus robustoides* in the southern (1) and in the northern (2) locations of the Neva Estuary between 2001 and 2008

The index varied between sampling dates, reaching a maximum in the beginning of summer and autumn, when large specimens were abundant. According to the 2005 data, predation pressure was strongest in June and low (<1) in August, when juveniles constituted a large component in the population. In autumn IP increased to 1.2–1.9 (with a maximum in late September, IP = 4.7), which demonstrates a strong predation impact on the invertebrate community including other crustaceans (native amphipods, isopods and the previously introduced amphipod *G. fasciatus*). Assessment of this impact in 2002–2008 demonstrated that the influence of alien amphipods on the littoral macrofauna reached a maximum in 2005–2006, and later decreased (Fig. 3).

## 11 Mysidacea

Alien mysids are abundant of in the Curonian Lagoon, and play an important part in its trophic structure (Razinkov 1990; Lesutienė 2009). Vertical nocturnal migrations emerged as an important feature of mysid feeding behaviour (Razinkovas 1996; Lesutienė et al. 2005). Stomach content analysis of *P. lacustris* revealed a significant proportion of planktonic crustaceans, suggesting that the mysids feed on mesozooplankton during their nocturnal migrations (Jankauskienė 2003). These results contradict previous works claiming *P. lacustris* fed preferentially on phytoplankton and phytodetritus (Komarova 1991). Stable isotopes were used to reconstruct its diet i.e., identify the primary carbon sources ($\delta^{13}C$) and estimate the

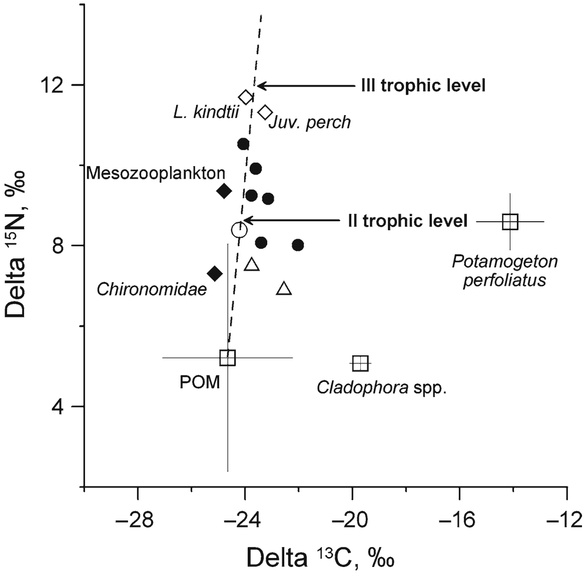

**Fig. 4** Position of the Ponto-Caspian crustaceans in the food web of the Curonian Lagoon revealed by stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$, ‰; mean ± SD). Squares denote primary sources of organic matter (POM- particulate organic matter over past 3 weeks); filled diamonds – primary consumers, open diamonds – carnivores. Circles indicate mysids: filled – *Paramysis lacustris*, open – *Limnomysis benedeni*; triangles – amphipods of the family Pontogammaridae. Dashed line shows the hypothetical food chain for POM as primary source of organic matter, 3.4 and 0.5‰ enrichment per trophic level for $\delta^{15}N$ and $\delta^{13}C$, respectively

position of Ponto-Caspian mysids in the food chain ($\delta^{15}N$) in the Curonian Lagoon (Lesutienė et al. 2007; Lesutienė et al. 2008). All investigated consumers used POM as primary source of organic matter, whereas distinct $\delta^{13}C$ ratios from that in littoral macrophytes indicate minor importance of this source in the secondary production (Fig. 4). A similar $\delta^{13}C$ signal in mesozooplankton and chironomids implies that the isotopic ratios in suspended and sedimented POM are indistinguishable. This however hampers further evaluation of mysid relative use of water column or epibenthic surfaces as feeding environments (Fig. 4). The third trophic level in the POM based food chain is taken by the carnivorous cladoceran *Leptodora kindtii* and planktivorous juvenile perch (Fig. 4). All individuals of *P. lacustris* are less enriched in $^{15}N$ than the cladoceran and the perch, and take intermediate position between the herbivores and true carnivores. *Limnomysis benedeni*, feeding on detritus, phytoplankton and occasionally rotifers, represented the true herbivore on the $\delta^{15}N$ to $\delta^{13}C$ plot (Jankauskienė 2003).

The variability of $\delta^{15}N$ signatures in *P. lacustris* is largely determined by ontogenetical diet changes (Lesutienė et al. 2007). The significant enrichment of mysid $\delta^{15}N$ values with the increasing size about 3 PSU between the smallest (3 mm) and largest (12 mm) individuals, suggests that during the ontogenetic development, mysid diet changes nearly one trophic level (assuming 3.4 psu as one trophic level enrichment factor).

Juvenile mysid diet is composed largely by phytoplankton, whereas immature or subadult individuals have mixed diets. As indicated by the similarity between the $\delta^{15}N$ values in the stomachs and ambient zooplankton, mysid become largely carnivorous and start to feed actively on mesozooplankton at the threshold size of 8.7±0.7 mm (Lesutienė et al. 2007). Individuals of >8.7 mm length prevail in the population only from late autumn to spring.

*Paramysis lacustris* does not have a significant effect on the zooplankton community in the Curonian Lagoon in summer, as the population consists largely of small herbivorous and omnivorous individuals. The largest carnivorous specimens of *P. lacustris* accumulate at greater depths (>2 m) in the summer (Razinkovas 1996), which reduces their competition with the zooplanktivorous juvenile fish that are largely distributed at shallower depths. Indeed, the spring diet and habitat overlap between *P. lacustris* and fish larvae is highly possible and needs further investigations. In addition, after establishment of the Ponto-Caspian mysids, fish larvae were gradually replaced with mysids in the diet of juvenile predatory fish (Razinkov 1990). Nowadays mysid share in the diet of >1–2 years age perch and pikeperch is 62% and 98%, respectively (Ložys 2003). Tus, reduced mortality of fish larvae is likely to compensate for possible negative mysid effect of competition for zooplankton.

During the autumn *P. lacustris* becomes the key species in the littoral food web. The use of littoral particulate organic matter, detritus from the decaying macrophytes, and some meiobenthos as food sources by mysids improves their nutritional conditions when phytoplankton and zooplankton decline. The differences of $\delta^{15}N$ values between the size groups minimizes during this period (Lesutienė et al. 2007, 2008), which corresponds well to decreased zooplanktivory of large sized mysids. Mysids increase organic matter transfer efficiency in the macrophyte detritus food chain during autumn when other important littoral consumers, such as amphipods, are scarce (Lesutienė pers. obs.). Calculated *Paramysis lacustris* cumulative consumption is 9 g DW $m^{-2}$ (estimated using data from the three autumn months). This is a substantial quantity of the organic material, mainly originating from the decaying submersed vegetation that is remineralized by the mysids in the littoral zone and becomes available to the higher trophic levels. In the meantime, inshore-offshore horizontal migrations of mysids can increase the horizontal transport of assimilated organic matter.

## 12 Decapoda

The Chinese mitten crab feeds on a wide variety of benthic invertebrates (Anger 1990). Too little is known of its impact in the eastern Baltic Sea; however, predation pressure on native plants and small macroinvertebrates was recorded from other regions (Ojaveer et al. 2007) and likely competes for food with fish and birds. Some fishermen from eastern Gulf of Finland testified also about the negative influence of the crabs on the local fisheries, i.e., destroying nets (Petryashov, unpublished data). The crab may transport sessile biota attached to its carapace, and smaller member of the Nematoda, Bivalvia, Crustacea, Oligochaeta and Gastropoda in the dense setal patches on its claws (Ojaveer et al. 2007).

*Palaemon elegans* plays a significant role in the trophic web of the coastal areas of the Baltic Sea in that it forages on certain food components and is itself consumed by predators (Berglund 1980; Janas and Barańska 2008). It could potentially affect the assemblages of aquatic plants and benthic animals. In the Puck Bay (Poland), detritus (>80%) and filamentous algae (36–88%) was the dominant food item with respect to frequency of occurrence in *P. elegans* diet (Janas and Barańska 2008). Also, crustaceans (Ostracoda, Amphipoda, Harpacticoida) and insect larvae (Chironomidae) made an important contribution to the stomach content. Occupying the same habitat as native prawn species *P. adspersus* Rathke, 1837 and *Palaemonetes varians* (Leach, 1814), *P. elegans* often dominates in the assemblages and even has replaced the natives (Grabowski 2006; Janas and Barańska 2008).

The recent increase in abundance of alien malacostracan crustaceans poses an additional risk of both structural and functional changes in the Baltic Sea ecosystems. The invasion of malacostracans may results in a high ecological impact, leading to changes in pre-existing biota, losses of species diversity and destabilization of recipient ecosystems through food web alterations. The results indicate that alien amphipods, mysids, decapods and other crustaceans have become important components of the food web of the Baltic littoral. Their role is dependent on their ontogenetic stage and food supply. The dietary plasticity and ability to alternate feeding strategies allows these crustaceans to turn from predatory to non-predatory (scavenging) mode on low-calorie food (detritus or plants) when prey is scarce. *Pontogammarus robustoides* and the Chinese mitten crab are invaders with potentially high ecological impacts. Other alien crustaceans have low impact on the Baltic food webs as they do not have the potential to dominate the ecosystems and coexist with populations of native species without affecting the dynamic structure and stability of the ecosystem.

## 13 Management

The contemporaneous development of regional commercial fishery in newly built reservoirs based on alien crustaceans and invasive species research effort during the last decade resulted in a body of scientific knowledge useful for management purposes.

The first Baltic Sea Alien Species Database provided a reference system on alien species in the Baltic Sea area. It has been available online since 1997 for environmental management, research and education (Baltic Sea Alien Species 2006). Lithuanian, Russian and Polish scientists have attempted to develop environmental and risk assessment indices (Olenin et al. 2007; Arbačiauskas et al. 2008; Panov et al. 2009), with particular reference to range expansion by inland waterways and the most important vectors of introduction for malacostracans (Jażdżewski 1980). These attempts are regarded as useful suggestions in establishing a framework for the incorporation of alien species into the European Water Framework Directive (Cardoso and Free 2008). In spite of the continued attention being paid by the scientific community, the local governments of the Eastern Baltic Sea still have little concern with regard to preventing new aliens from entering the Baltic Sea. Introduced higher crustaceans are included in the 'black' lists of species that are under control of environmental agencies. However, enforcement of the local regulations is partial.

The prevention of species crossing borders, including international commitments such as the regulations concerning trade in wildlife (European Community 1997) and use of alien and locally absent species in aquaculture (European Community 2007), could be more powerful than local laws. The HELCOM countries have agreed to ratify by 2010, or at the latest by 2013, the 2004 International Convention on the Control and Management of Ships' Ballast Water and Sediments initiated by International Maritime Organization. This will help to reduce the ballast-transported aliens and may prevent the further spread of mysids, decapods and amphipods (Ovčarenko et al. 2006).

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# Alien Crustaceans Along the Southern and Western Baltic Sea

**Krzysztof Jażdżewski and Michał Grabowski**

**Abstract** A detailed account is given as to when and how alien crustaceans have entered the Baltic Sea, with special emphasis on the regions to south and west. The biogeographic origin of the species, their vectors and arrival pathways, as well as ecological and economic impacts are discussed. Altogether 19 alien crustacean species were hitherto recorded in the south-western Baltic Sea; of which 8 are of Ponto-Caspian and 4 of North American origins. The impact of these newcomers upon the Baltic ecosystem has not been perceived as significant. However, in some lagoons and estuaries, the rapid increase of population abundance in some species did cause disturbances.

## 1 Introduction

The Baltic Sea, a semi-enclosed brackish basin, at most 12,000 years old, it is a relatively new body of water. Its history encompassed freshwater and polyhaline brackish periods leading to the present day phase of mesohaline/oligohaline basin. This latter phase has started no earlier than 3,000 years ago (Segerstråle 1957; Olenin and Leppäkoski 1999). With a surface area including Kattegat of about 412,000 km$^2$, the Baltic Sea is among the world's largest brackish water bodies. Its catchment area is over 1,700,000 km$^2$ and more than 200 rivers discharge their waters into the sea. The Vistula and Oder in the south and the Nemunas and Dvina (Daugava) in the southeast are the largest rivers in the Baltic drainage system.

The combination of a tide-less shallow basin with an average depth of ca. 60 m and a limited exchange of seawater with the NE Atlantic, results in a surface salinity decreasing from ca. 20 psu at the south-western end to some 2 psu in eastern and northern regions of the Gulf of Finland and the Gulf of Bothnia (Fig. 1). Below locally,

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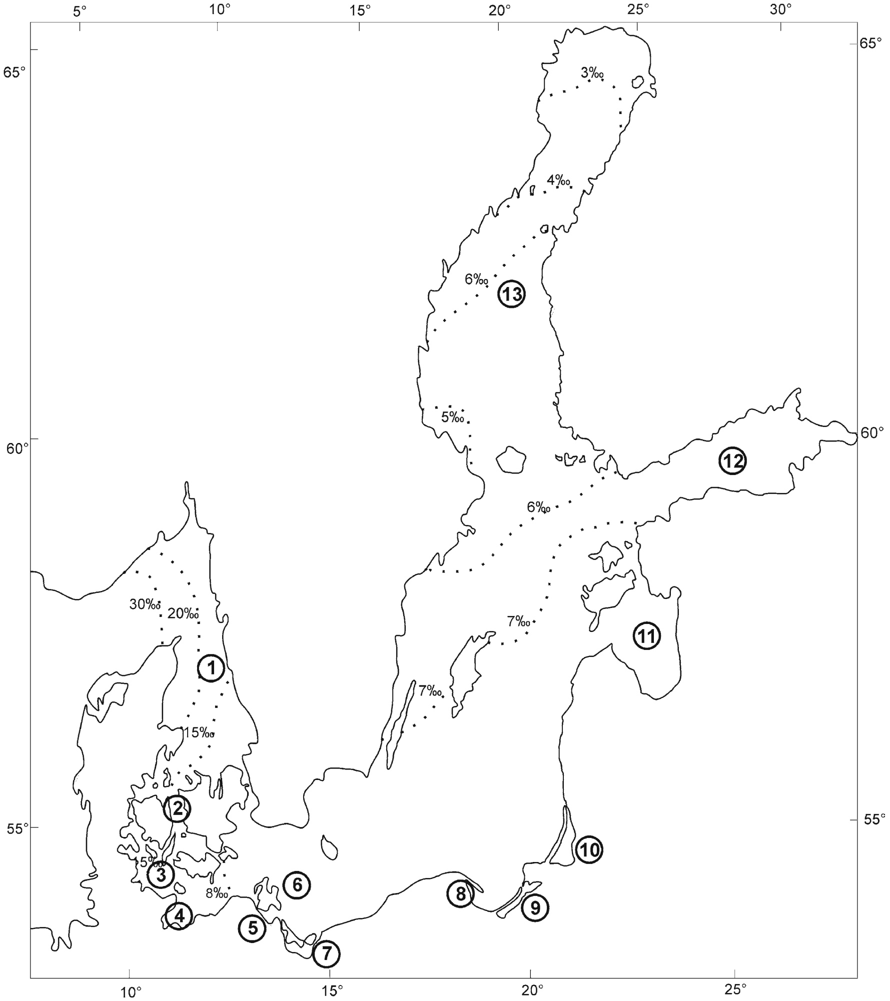

**Fig. 1** Geography of the Baltic Sea: 1 - Kattegat, 2 - Belt Sea, 3 - Kiel Bight, 4 -Bay of Mecklenburg, 5 - Greifswald Lagoon, 6 - Arkona Basin, 7 - Szczecin Lagoon, 8 - Gulf of Gdańsk, 9 - Vistula Lagoon, 10 - Curonian Lagoon, 11 - Gulf of Riga, 12 - Gulf of Finland, 13 - Gulf of Bothnia. Isohalines for surface water inserted

the halocline salinity is higher than the surface (by 3–4 psu), due to the submergence of heavier, more saline Atlantic waters (Segerstråle 1957; Voipio 1981; Olenin and Leppäkoski 1999; Stigebrandt 2001; HELCOM 2009a). Water temperature varies among the sub-basins, with mild Atlantic-boreal temperatures in the southwest, though surface ice occurs occasionally in some bays of the central Baltic.

The principal abiotic gradients (salinity and temperature) are the main cause of the sharp decrease of marine biodiversity from the Atlantic end (Skagerrak/Kattegat) to the central Baltic (ca. 10–15 times) (Voipio 1981; Leppäkoski and Bonsdorff 1989; Bonsdorff 2006). However, the fauna in the inner bays, lagoons and estuaries is enriched by euryhaline freshwater and oligohaline brackish water species (such as chironomids, oligochaetes, and copepods) (Segerstråle 1957; Haahtela 1996; Nohren et al. 2009).

The present paper discusses the occurrence of alien (non-indigenous) crustaceans along the western and southern shores of the Baltic Sea, between 10° and 20° E. These waters, besides Kattegat, are the so-called central or Baltic proper. The average surface salinity in the main part of this area ranges from some 15 psu in the Gulf of Kiel to about 7 psu at the Sambian Peninsula. Anoxic areas occur east of Bornholm and in the Gdańsk deep, at the depths below 80–90 m; their extent may be reduced following strong inflows of Atlantic waters.

The southern and western parts of the Baltic Sea are divided into several larger and smaller basins (Fig. 1), more or less isolated from the open sea, namely the Kiel Bight (surface salinity 10–20 psu), Mecklenburg Gulf (8–18 psu) with its innermost part, Lübeck Bay (2–10 psu), then Darss-Zingst Bay (2–8 psu), several half-enclosed bays surrounding Rügen Island (5–10 psu), Greifswalder Bodden (5–10 psu), Pomeranian Bay (7–9 psu) and the Gulf of Gdańsk (7–8 psu), with its innermost part, Bay of Puck (6–7 psu). The Szczecin and Vistula Lagoons are large, shallow basins isolated from the open sea and having a special hydrological regime. These two basins are greatly influenced by the largest Baltic rivers, the Oder and the Vistula. The Szczecin Lagoon is the nearly enclosed Oder estuary. The inflow of this river keeps the salinity at a low level (0.5–1.5 psu). Prior to 1915 the Vistula Lagoon too was a low salinity basin, but following natural events and canal constructions, the lagoon now only receives ca. 15% of the outflow of the Vistula and its salinity ranges between 2 and 5 psu. These two lagoons and many southern Baltic estuaries have become important invasion gateways where many oligohaline brackish water alien species have become established. From these "hotspots" of xenodiversity the aliens have dispersed further in the Baltic (Gruszka 1999; Leppäkoski and Olenin 2001; Jażdżewski et al. 2002, 2004; Leppäkoski et al. 2002; Nehring 2002; Gruszka et al. 2003; Gollasch and Nehring 2006; Grabowski et al. 2006, 2007; Panov et al. 2009).

## 2 Human Impact on the Baltic Sea

Over 80 million people inhabit the Baltic drainage area. The input of phosphorus and nitrogen increased throughout the last century, especially during the second half. A two-fold increase of organic matter sedimentation was recorded by Jonsson and Carman (1994). The transparency (Secchi depth) of Baltic waters decreased by 2–5 m (Messner and von Oertzen 1991; Trzosińska 1992), inducing the decline of depth extension of several macrophytes. Due to eutrophication large phytoplankton blooms occur more often and include toxic cyanobacterial ones, especially of *Microcystis aeruginosa* (Pliński 1990). Baltic primary production increased by 30–70% (Elmgren 1989). These changes have resulted in a cascading trophic effect observed as a deterioration of zooplankton abundance and Baltic planktivorous fish populations (HELCOM 2009a). Recently, some amelioration has been observed (Larsson et al. 1985; HELCOM 2009b).

In the shallow waters above the halocline the share of crustaceans in bottom communities, and especially Arctic relict species, like *Saduria entomon* or *Monoporeia affinis*, sharply decreased, whereas the biomass of bivalves has increased (Leppäkoski 1975; Pliński 1990; Warzocha 1994; Kube et al. 1997). In the first half of twentieth century the crustacean fauna of the Baltic Sea was dominated, in principle, by species of Atlantic origin with an important admixture of the above mentioned Arctic relicts (also *Limnocalanus grimaldii*). Locally, especially in the northeast, these species contributed prominently to the composition of benthic or planktonic assemblages (Segerstråle 1957; Warzocha 1994). These faunal changes may stem from the increasing pollution combined with climatic phenomena such as North Atlantic Oscillations (HELCOM 2009a).

During the last century a general zoogeographical trend, the replacement of Arctic and Arctic-boreal elements by Atlantic-boreal and cosmopolitan species, was observed in the Baltic (Leppäkoski 1975; Leppäkoski and Mihnea 1996; Leppäkoski and Olenin 2001). During the same period no changes were observed in the composition of the Arkona Basin bottom fauna, where the abundance of benthic species increased (Zettler et al. 2008).

The brief existence of the Baltic Sea and its special abiotic features are the primary cause for the low number of its native species. High anthropogenic pressure tends to reduce even these numbers.

## 3 Species Inventory, Biogeographic Patterns, Pathways and Vectors

The alien crustacean species recorded in the SW Baltic Sea, along with dates of their first findings or publication, ecological characteristics and biogeographic origin, are listed in Table 1. The first record of alien species in Baltic waters is often preceding their initial appearance in the southwestern part of this basin.

Among the 19 species of alien crustaceans known from the SW Baltic Sea, two main groups may be distinguished in terms of their biogeographic origins (Table 1, Fig. 2).

The largest group comprises six amphipods, one mysid and one water-flea of Ponto-Caspian origin. The other is composed of four North American (mostly Western Atlantic) species: three decapods and an amphipod. The remaining aliens are of Eastern Atlantic (two species), Northwestern Pacific (one species) origin or remain cryptogenic (four species).

Shipping traffic has increased exponentially in the twentieth century, resulting in the transport of many alien species to Baltic harbours in ballast water or as hull fouling. Shipping has been the major vector of the introduction into the western and southern Baltic Sea for *Amphibalanus improvisus*, *Acartia tonsa*, *Rhithropanopeus harrisii* and *Callinectes sapidus* (Table 1, Fig. 3).

The earliest noted alien crustacean species in the Baltic Sea was the cryptogenic barnacle, *Amphibalanus improvisus*, recorded in eastern Baltic (near Kaliningrad, earlier Königsberg) already in 1844 (Leppäkoski et al. 2002), i.e., 10 years before

**Table 1** Checklist and basic characteristics of alien Crustacea colonizing SW Baltic Sea

| Species | Origin | Salinity preferences | Ecological characteristics | First Baltic record | First record in SW Baltic |
|---|---|---|---|---|---|
| **Copepoda** | | | | | |
| *Acartia tonsa* Dana, 1848 | Cg | o-p | Planktonic | 1925 | 1925 |
| **Branchiopoda** | | | | | |
| *Cercopagis pengoi* (Ostroumov, 1891) | P-C | l-m | Planktonic | 1992 | 1999 |
| **Cirripedia** | | | | | |
| *Amphibalanus improvisus* (Darwin, 1854) | Cg | o-p | Benthic-sessile | 1844 | 1844 |
| **Amphipoda** | | | | | |
| *Chelicorophium curvispinum* (G. O. Sars, 1895) | P-C | l-o | Benthic-tube building | 1926 | 1926 |
| *Chaetogammarus ischnus* (Stebbing, 1899) | P-C | l-o | Benthic | 1964 | 1969 |
| *Gammarus tigrinus* Sexton, 1939 | N Am | l-p | Benthic | 1975 | 1975 |
| *Dikerogammarus haemobaphes* (Eichwald, 1841) | P-C | l-o | Benthic | 2000 | 2000 |
| *Dikerogammarus villosus* (Sovinsky, 1894) | P-C | l-o | Benthic | 2004 | 2004 |
| *Obesogammarus crassus* (G.O. Sars, 1894) | P-C | o-m | Benthic | 1962 | 2002 |
| *Pontogammarus robustoides* (G.O. Sars, 1894) | P-C | l-m | Benthic | 1962 | 1999 |
| *Orchestia cavimana* Heller, 1865 | Cg | l-e | Semi-terrestrial | 1899 | 1899 |
| *Platorchestia platensis* Krøyer, 1845 | Cg | e | Semi-terrestrial | ca. 1940 | ca. 1940 |
| **Mysidacea** | | | | | |
| *Hemimysis anomala* G.O. Sars, 1907 | P-C | l-m | Nekto-benthic | 1962 | 2003 |
| **Decapoda** | | | | | |
| *Callinectes sapidus* Rathbun, 1896 | N Am | p-e | Benthic | 1951 | 1951 |
| *Eriocheir sinensis* H. Milne Edwards, 1853 | N Pac | l-p | Benthic | 1926 | 1926 |
| *Rhithropanopeus harrisii* (Gould, 1841) | N Am | o-m | Benthic | 1948 | 1948 |
| *Orconectes limosus* (Rafinesque, 1817) | N Am | l-o | Benthic | 1938 | 1938 |
| *Palaemon elegans* Rathke, 1837 | Atl | o-m | Benthic | 1920 | 1920 |
| *Palaemon longirostris* H. Milne Edwards, 1837 | Atl | m-p | Benthic | 1999 | 1999 |

Legend: *Atl* Atlantic, *Cg* cryptogenic, *N Am* North American, *N Pac* North Pacific, *P-C* Ponto-Caspian; *e* euryhaline, *l* limnic, *o* oligohaline, *m* mesohaline, *p* polyhaline

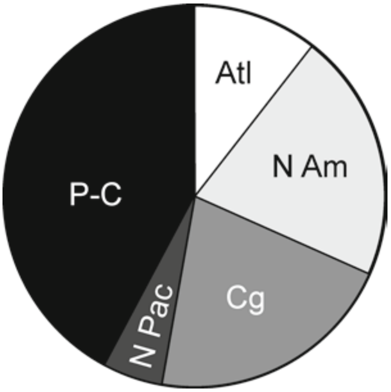

**Fig. 2** Biogeographic composition of the alien crustacean fauna colonising the SW Baltic Sea: Cg – Cryptogenic, E Atl – East Atlantic, N Am – North American, NW Pac – North-West Pacific, P-C – Ponto-Caspian

its formal description by Darwin. This euryhaline species occurs now in the entire Baltic Sea, including estuaries and lagoons, where it is abundant on rocky shores, coastal constructions and even *Phragmites* stems in oligohaline lagoons and in the north-easternmost shallow parts of the Baltic (Leppäkoski and Olenin 2001).

*Orchestia cavimana* was first recorded in the Baltic by Seligo (1899), who mentioned this species from the shores of the Gulf of Gdańsk in the list of "westpreussische Krebstiere". The distribution of this semiterrestrial amphipod extends from the shores of the Black and Red Seas, the Mediterranean, the Eastern Atlantic from North Africa to the North Sea, and into the Baltic Sea, where it has reached the entrance of the Gulf of Finland (Baltic Sea Alien Species Database 2004; Herkül et al. 2006). Judging by its wide distribution, it should be characterized as a cryptogenic species.

In the early 1920s further alien crustaceans were recorded in the Baltic Sea and/or its lagoons: the cryptogenic calanoid copepod *Acartia tonsa* (see Rzóska 1938), the Ponto-Caspian corophiid amphipod *Chelicorophium curvispinum* (see Riech 1926) and the Chinese mitten crab, *Eriocheir sinensis* (Peters 1933).

*Acartia tonsa* is now a common and occasionally abundant element of the entire Baltic zooplankton. Due to its preference for warmer water it occurs especially abundantly in mid summer in shallower parts of the Baltic, in the uppermost 15 m layer (Segerstråle 1957; Siudziński 1977; Leppäkoski 1984; Postel et al. 1995).

*Eriocheir sinensis* was first recorded in the Baltic Sea in 1926 (Peters 1933). The population of *E. sinensis*, which grew rapidly before World War II, decreased precipitously thereafter. Only single specimens have been recorded in the southern Baltic in the late twentieth century (Grabda 1973; Jażdżewski and Konopacka 1995). Recently the crab has become common again in the SW Baltic Sea (Zettler 1998; Gruszka 1999; Normant et al. 2000).

The American crab *Rhithropanopeus harrisii* has been first noted in the Gulf of Kiel in 1936 (Köhn and Gosselck 1989) and in the Vistula Lagoon in 1948 (Nikolaev 1951). It became invasive, dominating as adults the local zoobenthos and as larvae the zooplankton, in the oligo-mesohaline parts of the Vistula delta (Dead and Bold Vistula) in the 1950s and 1960s (Ławiński and Szudarski 1960; Pautsch et al. 1969; Turoboyski 1973). This population collapsed in the 1970s and 1980s and proliferated again in the 1990s (Jażdżewski and Konopacka 2000). In the Vistula Lagoon *R. harrisi* is at present common in the shallow, near-shore habitats overgrown with reeds (Grabowski et al. 2005). It is commonly found in smaller and

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**Fig. 3** Main colonisation routes of alien aquatic crustaceans invading the Baltic Sea basin: A – *Acartia tonsa, Amphibalanus improvisus, Callinectes sapidus, Eriocheir sinensis, Orchestia cavimana, Palaemon elegans, Palaemon longirostris, Platorchestia platensis, Rhithropanopaeus harrisi*; B – *Chaetogammarus ischnus, Chelicorophium curvispinum, Dikerogammarus haemobaphes, Dikerogammarus villosus*; C – *Dikerogammarus villosus, Gammarus tigrinus*; D – *place of introduction and migration route of Hemimysis anomala, Obesogammarus crassus, Pontogammarus robustoides; white dot – place of introduction of the three species*; E – *Cercopagis pengoi*; grey dot – place of introduction of *Orconectes limosus* larger harbours located in estuaries throughout the SW Baltic (Köhn and Gosselck 1989; Jażdżewski and Konopacka 1995).

The American spiny-cheek crayfish, *Orconectes limosus*, intentionally introduced in 1890 into the Oder river system, was reported from the Szczecin Lagoon during the 1930s (Pieplow 1938), and was recorded in the Vistula Lagoon in the early 1950s (Żmudziński and Szarejko 1955). It is a euryhaline freshwater species, which has recently been sporadically noted in other estuarine and harbour habitats along the SW Baltic shores (Gruszka 1999).

The talitrid amphipod *Platorchestia platensis* was recorded in the western Baltic Sea in the early 1940s (Schellenberg 1942; Dahl 1946). In the southern Baltic its occurrence was confirmed by Köhn and Gosselck (1989) and Spicer and Janas (2006). Its cosmopolitan distribution suggests it may now be considered as a cryptogenic species.

*Gammarus tigrinus*, a North American species, intentionally introduced in 1957 to the German rivers of the North Sea basin, appeared in the Schlei estuary in Lübeck Bay in 1975 (Bulnheim 1976). Its eastward advance was swift; it was found in the Szczecin Lagoon in the late 1980s (Gruszka 1995), the Vistula Lagoon in 1998 (Jażdżewski and Konopacka 2000), and the Gulf of Finland in 2003 (Pienimäki et al. 2004). The detailed survey of the entire Polish Baltic Sea coast in 2004 revealed that *G. tigrinus* was a dominant species. In some places it replaced the native species in shallow water gammarid assemblages in Szczecin Lagoon, Bay of Puck, Vistula Lagoon, and in most of the small river estuaries along the Baltic coast. Below 2 m depth, in waters distant from the shore, the share of *G. tigrinus* in gammarid assemblages diminishes (Jażdżewski et al. 2005).

The American blue crab *Callinectes sapidus* was recorded in the early 1950s in the Kattegat (Wolff 1954). However, it has not been found in the inner parts of the Baltic Sea.

The late twentieth century witnessed a rapid expansion of Ponto-Caspian crustaceans into European waters (Jażdżewski 1980; Bij de Vaate et al. 2002; Jażdżewski and Konopacka 2002; Grabowski et al. 2007). Due to the long and complex geological history of the region, Ponto-Caspian crustaceans are mostly euryoecious, (in particular euryhaline) species, tolerant of environmental changes (Dumont 1998).

Some of the species immigrate to Central and Western Europe through the rivers draining to the Black, Azov and Caspian seas, partially aided by shipping or intentional introductions and eventually crossing basin boundaries through the canals (Mordukhai-Boltovskoi 1964; Jażdżewski 1980).

Bij de Vaate et al. (2002) discussed three main invasion corridors created by the construction of canals, through which the Ponto-Caspian aquatic fauna colonizes the western regions of Europe. The 'Northern Corridor' is routed through the Volga, Lake Beloye, Lake Onega, Lake Ladoga and the Neva River to the Baltic Sea. The 'Central Corridor' leads through the Dnieper, Vistula, Noteć, Oder, Elbe, Rhine rivers to the North Sea. The 'Southern Corridor' connects the Danube, the Rhine, and the North Sea. The "Central Corridor" plays the most important role in the colonization of the Baltic Sea by the Ponto-Caspian crustaceans.

In 1784 the Królewski and the Ogiński canals were built, connecting the Dnieper largest tributary (the Pripjat) with the Vistula and the Nemunas rivers, respectively. This new waterway connected the Black Sea basin with the Baltic Sea drainage system, and allowed some species to extend their range to the north by natural dispersal and also by shipping.

The first Ponto-Caspian species entering the Baltic watershed via this new canal system were *Chelicorophium curvispinum* and *Chaetogammarus ischnus* (Jażdżewski 1980). *Chelicorophium curvispinum* was first recorded near Berlin, in the Oder and Elbe drainage system (Wundsch 1912), in the lower Vistula (Seligo 1920) in the Vistula Lagoon (Riech 1926) and in Szczecin Lagoon (Neuhaus 1933). It is a euryhaline freshwater species. It occurs in many estuaries of SW Baltic rivers and sometimes abundantly in Baltic lagoons. It is particularly common and abundant in Szczecin Lagoon and in the western part of the Vistula Lagoon. Often this tube-building amphipod inhabits the clumps of another Ponto-Caspian alien, the bivalve *Dreissena polymorpha*, attached to reeds. The gammarid amphipod *Chaetogammarus ischnus* was found in the Vistula River as early as 1928 (Jarocki and Demianowicz 1931), but was noted from its estuary only in the late 1960s (Jażdżewski 1975).

Different pathways and vector combinations were proposed for other Ponto-Caspian crustacean immigrants into the Baltic area. Several amphipod and mysid species originating from the Black Sea drainage basin were intentionally introduced in 1960s to the Kaunas Reservoir on the Nemunas River to enrich fish food sources. Some of these species were found downstream in the Curonian Lagoon during the 1960s (Gasiunas 1964; Arbačiauskas 2002; Arbačiauskas and Gumuliauskaite 2007). Some of these species, namely *Pontogammarus robustoides*, *Obesogammarus crassus* and *Hemimysis anomala*, moved westwards along Baltic coasts during the late 1990s, and were recorded in the SW Baltic (Rudolph 1997; Jażdżewski et al. 2002, 2005; Konopacka and Jażdżewski 2002; Janas and Wysocki 2005). As mentioned above, the gammarid assemblages in the Vistula and Szczecin Lagoons are composed now of three to four Ponto-Caspian species that have reached these basins either through the Baltic southern tributaries, Vistula and Oder, or along the Baltic coast from the Curonian Lagoon (Konopacka 1998; Jażdżewski et al. 2004; Grabowski et al. 2006). The first records of *Hemimysis anomala* in the SW Baltic was from Szczecin Lagoon (Gruszka et al. 2003), and the Bay of Gdańsk (Janas and Wysocki 2005). Two additional Ponto-Caspian gammarid species, *Dikerogammarus haemobaphes* and *D. villosus* appeared in the mouths of largest Baltic tributaries; Oder and Vistula. All four above mentioned amphipods are limnetic, euryhaline species, entering oligohaline waters (estuaries, lagoons) in new regions. They all prefer hard bottoms (stones, pebbles) and/or phytal zone. *Dikerogammarus haemobaphes* arrived in the Baltic lagoons via the Dnieper, Prypjat, Bug, Vistula and Oder. This pathway was confirmed by DNA-analysis of the populations of *D. haemobaphes* in the Vistula and Oder basins (Jażdżewska and Grabowski, unpublished data). It was recorded in the Vistula and Szczecin Lagoons in early 2000 (Jażdżewski et al. 2002; Grabowski et al. 2007). The arrival of *D. villosus* in the Baltic Sea lagoons is an interesting and complicated saga. This species moved westwards via the ‘Southern

Corridor' (Bij de Vaate et al. 2002). It was recorded as far upstream as Slovakian part of the Danube in the 1950s (Straskraba 1962), reaching the Austria and Germany in 1992 (Nesemann et al. 1995). *Dikerogammarus villosus* entered the Rhine basin via the Ludwig's Canal and the Rhine's main tributary, the Main River. From the lower Rhine (Van Riel et al. 2006; Platvoet 2007) it dispersed east to the Elbe and Oder drainage systems (Grabow et al. 1998; Zettler 1999; Rudolph 2002) through the Mittelland-Kanal, and in the late 1990s it was recorded in the lower Oder (Müller et al. 2001). It was subsequently found in the Szczecin Lagoon (Gruszka and Woźniczka 2008), where its population size increased rapidly. Another population of *D. villosus* immigrated through the 'Central Corridor' in the 1990s, entering the Bug from Pripjat in 2003 (Grabowski et al. 2007), the lower middle sector of the Vistula in 2008 (Bącela et al. 2008), and the mouth of the Vistula in 2009 (Konopacka, unpublished data). This is one of the most interesting examples of an invasion through the complex waterway network of Europe.

The predatory Ponto-Caspian cladoceran, *Cercopagis pengoi*, was first noted in the Gulf of Riga in 1992 (Ojaveer and Lumberg 1995). The species spread quickly eastward (Gorokhova et al. 2000) and westward, where it is abundant in the Vistula Lagoon and in the Gulf of Gdańsk (see Hornatkiewicz-Żbik 1999; Żmudziński 1999; Bielecka et al. 2000, Duriš et al. 2000).

It is difficult to distinguish between natural immigrants from the eastern Atlantic and those helped by human activity (e.g., through ballast water transport, biofouling etc.). Some species, like *Carcinus maenas*, known for wandering large distances, or *Palaemonetes varians*, which acclimatised in Baltic estuaries a long time ago, are not recognised as aliens. Others, like *Palaemon elegans*, which spread rapidly in recent years and replaced the previously thriving *Palaemon adspersus*, is suspected to be shipping-transported and regarded as alien.

*Palaemon elegans* is widely distributed in European coastal waters, from the Black Sea and the Mediterranean, to the Atlantic coast of Norway (Smaldon et al. 1993). The species was sporadically noted in Wismar Bay and the western Baltic (Köhn and Gosselck 1989). During the first decade of the twenty-first century the species spread quickly eastwards: it was recorded in Arkona basin in 2002 (Zettler 2002), the Vistula estuary around 2000 (Grabowski et al. 2005), in the Gulf of Gdańsk in 2004 (Janas et al. 2004), reaching as far as the Gulf of Finland in 2003 (Lavikainen and Laine 2004). The species quickly dominated the native *P. adspersus*, formerly the only *Palaemon* species in the Baltic proper. In some areas of the Polish coast *P. elegans* has replaced *P. adspersus* (Grabowski 2006) and is recognized as an invasive. *Palaemon longirostris* too is an East-Atlantic brackish water species, inhabiting mostly estuaries and entering adjacent freshwater catchments. In the Baltic Sea it was reported for the first time in 1999 from Darss-Zingster Boddenkette (Zettler 2002). This species is recorded only sporadically from the German Baltic coast, and it is unknown whether a self-reproducing population exists (Zettler pers. comm.). The connection from the Atlantic through the Danish straits (and Kiel Canal) to the Baltic, serving as another important route for aquatic organisms colonizing this brackish water basin, has recently been defined as the 'Northern Meridian' Corridor (Galil et al. 2007; Panov et al. 2009). These pathways are illustrated in Fig. 3.

The harpacticoid copepod *Ameira divagans* is mentioned in the list of Baltic aliens (Gollasch and Mecke 1996), as well as on the Baltic Alien Species Database (2004). In the latter publication, it was erroneously referred to as a "zooplankton suspension feeder" when in fact it is part of the benthos. The species was described from two female specimens (Nicholls 1939), the description was later augmented by Kunz (1963), who described a subspecies, *A. divagans africana*, from south-western African waters based on a single male. Scheibel (1974) redescribed the species from a larger series of specimens collected in the Gulf of Kiel. He discovered morphological differences between the three populations. Further study, perhaps utilizing molecular methods, is needed in order to determine the status and the origin of *A. divagans*. So far the species cannot be treated as alien.

*Orconectes virilis* too is mentioned in the above lists of aliens in the Baltic Sea. However, recent articles (Souty-Grosset et al. 2006; Holdich and Pöckl 2007) do not mention the species as an alien, even in the drainage area of the Baltic Sea. These cases support the warning voiced by Paavola et al. (2005) that the lists of alien species "often include mistakes and species with uncertain establishment status".

In summary, the Baltic Sea and its watershed face a continuous inflow of alien crustacean species. Two invasion waves can be identified (Fig. 4), one in the 1920s and the second around 2000. It is difficult to elucidate the reasons for the acceleration of alien crustacean colonization. One possible explanation may be a lag effect after an increase of shipping activity at the beginning of the twentieth century. The latter invasions may have resulted from the increase of maritime trade after the break-up of the Soviet block in 1989, coupled with anthropogenic changes in water quality in the waterways joining the Ponto-Caspian region with the Baltic basin; or it may be related to global climate warming (Leppäkoski and Olenin 2001; Grabowski et al. 2009).

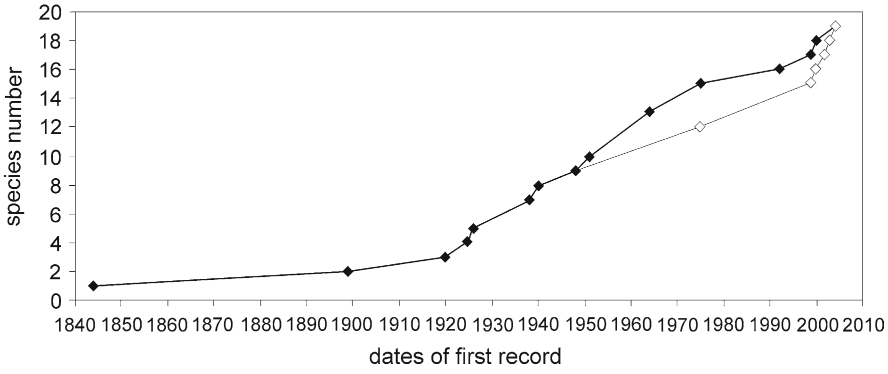

**Fig. 4** Cumulative curve illustrating the rate of colonization of the Baltic Sea by alien Crustacea, based on the dates of first records in the entire Baltic (filled rhombs, thick line) and in its SW part (empty rhombs, thin line)

## 4 Ecological Impact

The ecological effects of invasive alien species in the Baltic Sea and other enclosed brackish basins (i.e., Black Sea, Caspian Sea) have been discussed recently, and authors deplore the lack of quantitative studies (Olenin and Leppäkoski 1999; Leppäkoski and Olenin 2000; Leppäkoski 2002; Leppäkoski et al. 2002; Paavola et al. 2005). The inter-specific relations between alien and native species, and the impact of the former upon the Baltic pelagic and benthic systems, are unknown. Most alien crustaceans colonize only the shallowest regions of the Baltic Sea i.e., the littoral zone down to a depth of only few meters. In general the impact of aliens on the benthic crustacean fauna appears insignificant (Jażdżewski et al. 2005; Zettler et al. 2006).

The alien crustaceans entered an ecosystem poor in species where, presumably, competition with, and predation by native biota was reduced, and where there may have been certain resources (such as space or food) not fully utilized by resident populations (Leppäkoski et al. 2002). This may be the case for the barnacle *Amphibalanus improvisus*, a suspension filter-feeder, which occupies all possible hard bottom habitats in the shallowest zone throughout the Baltic. It densely encrusts hard substrates, and shares this habitat only with native mussel *Mytilus* and, to a lesser extent, in lagoons with low salinities, with the alien mussel *Dreissena polymorpha*. The omnivorous and predatory decapods such as *E. sinensis*, *R. harrisii*, and *O. limosus*, occupied oligohaline bays, estuaries and lagoons and do not fully utilize the resources as did the native palaemonid shrimps, which are now absent or scarce. However, some interesting and unexpected food chains formed following the introduction of invaders from various geographic origins i.e., *O. limosus* preys mainly upon the older Ponto-Caspian invader, the coelenterate *Cordylophora caspia*, which in turn feeds upon planktonic larvae of *D. polymorpha* and *R. harrisii* consumes *Dreissena* as a food resource while its young prey on *Amphibalanus* larvae and *Cordylophora* (Leppäkoski and Olenin 2001). The Chinese mitten crab had been reported to prey on native bivalves (*Sphaerium*, *Pisidium*, *Anodonta*, *Unio*) in German estuaries and inland waters (Peters 1933). Moreover, *Eriocheir sinensis* may act as an "habitat": its carapace serves as a substratum for sessile flora and fauna such as barnacles, and the densely setose claws harbour several species of nematodes, bivalves, harpacticoid copepods, amphipods, oligochaetes, gastropods, chironomids and halacarid water mites (Normant et al. 2007; Ojaveer et al. 2007).

However, ecological studies on the impact of alien crustaceans upon Baltic habitats are scarce. For example, the role of *A. tonsa* within the Baltic zooplankton is unknown. Its arrival to the Baltic area dates to the early 1920s when thorough studies of plankton composition were lacking and consequently do not allow any sound ecological conclusions.

The recent invasion of *C. pengoi* has been well studied especially in the eastern Baltic where it has been evaluated and monitored since 1996 (Hornatkiewicz-Żbik 1999; Ojaveer and Lumberg 1995; Gorokhova et al. 2000; Ojaveer et al. 2004;

Litvinchuk and Telesh 2006). This predatory planktonic water flea quickly attained over 20% of total zooplankton biomass in some regions (Gorokhova et al. 2000), constituting an important element of the diet of several Baltic fish (Ojaveer et al. 1998; Antsulevich and Välipakka 2000). Ojaveer et al. (2000) argue that its invasion may complicate energy flow to higher trophic levels and, as a result, increase the stability of the Baltic ecosystem.

Native gammaroid crustaceans, which are a major faunal element of the littoral and upper-sublittoral near-shore habitats, were comparatively well studied in the southern Baltic Sea before the massive invasions during the late 1970s of *G. tigrinus* and in the late 1980s by Ponto-Caspian pontogammarids (Kinne 1954; Micherdzinski 1959; Żmudziński 1967; Arndt 1965; Jażdżewski 1973, 1975; Bulnheim 1976; Wiktor et al. 1980; Kolding 1981; Jażdżewski and Konopacka 1995). The native gammaroid fauna was supplemented by six alien species (Table 1). Along the open Baltic shores, native gammarids appeared to withstand this invasion, constituting, as in late 1960s, the majority of gammaroid assemblages. However, in some samples from this region it was noted that alien *G. tigrinus* was present in large numbers (Jażdżewski et al. 2005).

The gammaroid assemblages in the Vistula Lagoon have been studied over the past 50 years, so the succession of events can be tracked (Żmudziński and Szarejko 1955; Jażdżewski et al. 2004; Grabowski et al. 2006). Two native gammarids, *Gammarus duebeni* and *G. zaddachi*, were present in the eutrophic lagoon during the late 1970s, with the more resilient *G. duebeni* outnumbering *G. zaddachi*. At the end of the 1990s, the aliens *G. tigrinus*, *D. haemobaphes*, *O. crassus* and *P. robustoides* appeared (Jażdżewski and Konopacka 2002; Jażdżewski et al. 2004). At first, the four alien gammaroids occurred in similar proportions, but each species dominated a different habitat, i.e., *D. haemobaphes* was abundant in low-salinity (below 2 psu) parts of the lagoon. By 2004, *G. tigrinus* dominated the gammaroid fauna, and specimens of the native *G. duebeni* were rare (Jażdżewski et al. 2004; Grabowski et al. 2006). A recent survey (Surowiec and Dobrzycka-Krahel 2008) showed the overwhelming success of *G. tigrinus* in the Vistula Lagoon; the only other gammaroid species occurring in low numbers was *P. robustoides*. It was postulated that the success of alien gammaroids was due to their reproductive strategy and tolerance to a wider range of salinity (Grabowski et al. 2007).

A similar scenario occurred in the Szczecin Lagoon, where *G. tigrinus*, *P. robustoides*, *D. haemobaphes*, *O. crassus* and *D. villosus* appeared within few years (Gruszka 1999; Müller et al. 2001; Konopacka 2003; Jażdżewski et al. 2005). *Gammarus tigrinus* dominated the other Ponto-Caspian gammaroids in some early samples (Jażdżewski et al. 2005), and between 2002 to 2004 the two native gammarids, *G. duebeni* and *G. zaddachi* became absent, whereas *D. villosus* became the most common species (Gruszka and Woźniczka 2008), supposedly due to its omnivorous habits (Dick and Platvoet 2000).

The gammaroid assemblages in the shallow sandy bottoms of Puck Bay (part of the Gulf of Gdańsk) were studied in the early 1960s (Jażdżewski 1973) and again between 1996 to 98 (Jęczmień and Szaniawska 2000). The neighbouring waters of the Gulf of Gdańsk were studied in the late 1970s (Wiktor et al. 1980). Up until the end of the twentieth century the local gammarid fauna consisted of six native species: *G. salinus*, *G. zaddachi*, *G. oceanicus*, *G. inaequicauda*, *G. locusta* and *G. duebeni.* Of these natives, the first three were more dominant than the latter. In 2001, *G. tigrinus* was found in the Bay of Puck (Gruszka 2002), and soon dominated the gammarid assemblages (Szaniawska et al. 2003). In the most recent samples *G. tigrinus* still dominates the gammarid fauna in the shallow sites, whereas in deeper sites native species still occur, though *G. inaequicauda* is no longer to be found present (Jażdżewski et al. 2005).

Zaiko and Olenin (2004) studied the impact of alien gammaroids in Curonian Lagoon. They found high densities of the aliens *P. robustoides*, *O. crassus*, and to a lesser extent, *C. ischnus*. Native gammarids were absent from fine sand or sand and pebbles habitats. This was ascribed to the restricted burrowing behaviour of the native gammarid amphipods compared to the wider burrowing preferences of aliens. The authors demonstrated that the burrowing behaviour of the alien amphipods increased the amount of resuspended sediment in the near-bottom layer, thereby changing the habitat.

*Palaemon elegans* was recorded only from the Bay of Wismar until 2002 (Köhn and Gosselck 1989), when it spread widely in the Baltic (see above). The species is an efficient predator feeding upon a variety of prey, but with no negative effect observed (Janas and Baranska 2008). However, at the same time it replaced the native *Palaemon adspersus* in many places along the Polish Baltic Sea coast (Grabowski et al. 2005; Jażdżewski et al. 2005).

According to Persson (2001) and Spicer and Janas (2006) *Platorchestia platensis* outcompetes other talitrid species in the Baltic supralittoral.

## 5 Economic Impact

Among the alien crustaceans in the Baltic Sea, *A. improvisus*, *C. pengoi* and *E. sinensis* have caused economic losses, though in the case of the latter species, the damage is in the Baltic catchment area rather than in the sea. In the 1920s and 1930s, large numbers of Chinese mitten crabs in the Elbe and Oder rivers were reported to enter traps intended for eels, consume the bait, and substantially reduce the catch of eels (Panning, 1939). They were also reported to feed on commercially important smelt and bream and to have damaged hydrotechnical facilities (Peters 1933). At present, there are complaints that the crab impacts local coastal fisheries by destroying nets, competing with fish for food and damaging fish caught in nets (Czerniejewski and Filipiak 2001). In Poland, mitten crabs are occasionally sold by local fishermen (Czerniejewski and Filipiak 2002).

*Amphibalanus improvisus* densely covers hard substrates, fouling boats, industrial underwater constructions and water pipes, particularly in eutrophic harbour areas (Leppäkoski and Olenin 2001). The large established populations of *Cercopagis pengoi* produced a significant shift in the diet of commercially harvested planktivorous fish, becoming an important food resource for herring and sprat (Ojaveer et al. 2000; Gorokhova et al. 2004). Ojaveer et al. (2000) argue that the introduction of *C. pengoi* may overall prove beneficial to commercial fisheries if it enhances transfer of previously less-utilized mesozooplankton to planktivorous fishes (e.g., *Bosmina* → *Cercopagis* → planktivorous fish), though the fishhook waterflea is known to clog and foul fishing gear, mainly in the eastern Baltic, causing financial losses (Panov et al. 1999; Birnbaum 2006).

## 6 Future Trends

It is difficult to predict the fate of the alien species that already colonized the Baltic Sea. Recent studies have shown that some of the gammarid species have become an important part of local trophic webs, often with negative effects upon the native fauna (Orav-Kotta et al. 2009). Some alien species (e.g., *G. tigrinus*) undoubtedly will become established elements of the local benthic communities, predominating only in the shallowest nearshore regions. However, some alien populations may undergo dynamic changes as noted for *E. sinensis*, *R. harrisii* and several species of alien gammarids (Jażdżewski et al. 2004; Grabowski et al. 2006). It is possible that after the initial bloom most alien populations will survive a decline and remain stable.

New crustacean aliens will certainly enter the SW Baltic. Known candidates include the Ponto-Caspian species *Paramysis lacustris* and *Chaetogammarus warpachowskyi* already recorded in the Curonian Lagoon. The East-Asian estuarine shrimp *Palaemon macrodactylus* has already colonized some parts of the North Sea coast in Germany and is likely to enter the westernmost parts of the Baltic (Gonzalez-Ortegon and Cuesta 2006). There is no doubt that due to its unique environmental features, the Baltic Sea will continue to be a melting pot for alien species and deserves the moniker “Sea of Aliens”.

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# Checklist of Cryptogenic and Alien Crustacea of the European Atlantic Coast

**Pierre Y. Noël**

**Abstract** An overview is presented of 49 species of alien and cryptogenic marine and estuarine crustaceans established along the Atlantic coast of Europe. The alien species include Diplostraca (1 species), Ostracoda (1), Copepoda (10), Cirripedia (10), Mysidacea (1), Amphipoda (12), Tanaidacea (1), Isopoda (4), and Decapoda (9). The established introductions are primarily from Indo-Pacific, Atlantic America and Mediterranean-Ponto-Caspian regions, and the primary vectors that have brought these species to Europe are ballast water, ship fouling and mariculture activity.

**Keywords** Alien • Cryptogenic species • Europe • Invasive species • Management • Non-indigenous species • North Sea • Vectors

## 1 Introduction

Presented here is the first synthesis of 49 species of non-indigenous marine and estuarine crustaceans of the Atlantic and North Sea coasts of Europe. Since the earliest overseas explorations in the fifteenth century, vessels returning from Africa, and later, North America, South America, and the Indian and Pacific Oceans, have introduced non-native species to Europe. However, our historical resolution of these earliest invaders is poor, leaving many cryptogenic species in the European fauna. Reviewed here are the established introduced and cryptogenic crustaceans (Table 1, Appendix A), with an additional list of species that are not established or are represented by one-time records (Appendix B). The cryptogenic species treated here are examples only: a great many more species with "cosmopolitan" distributions could be considered as unresolved relative to whether they are native or introduced.

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**Table 1** Introduced and cryptogenic crustaceans of Atlantic Europe

| Species | Status | Origin | First record in | Vectors | Established in: |
|---|---|---|---|---|---|
| **Diplostraca** | | | | | |
| *Penilia avirostris* | C | Eurasia? | 1947 | BW | North Sea, Netherlands |
| **Ostracoda** | | | | | |
| *Eusarsiella zostericola* | I | USA Atlantic | 1870s | M | England |
| **Copepoda** | | | | | |
| *Acartia omorii* | I | Japan-China | 2005 | BW | North Sea, France |
| *Acartia tonsa* | C | Indo-Pacific? | 1912–1916 | BW | UK, Denmark, Belgium, France, |
| *Eurytemora americana* | I | NE Pacific | 1933 | BW | Iceland, England, Netherlands, France |
| *Eurytemora pacifica* | I | North Pacific | 1985 | BW | France |
| *Midicola spinosus* | I | Pacific | 1963 | M | France |
| *Myicola ostreae* | I | NW Pacific | 1972 | M | Ireland, Netherlands, France |
| *Mytilicola intestinalis* | I | Mediterranean | 1949 | M | Ireland, UK, and Denmark to France |
| *Mytilicola orientalis* | I | NW Pacific | 1977 | M | Ireland, UK, Netherlands, France |
| *Porcellidium ovatum* | C | Unknown | 1990s | BW | Ireland, UK |
| *Spiophanicola spinosus* | C | California | 1990s | BW | Scotland |
| **Cirripedia** | | | | | |
| *Austrominius modestus* | I | SW Pacific | 1943 | SF, BW | Shetland Islands to Gibraltar, Madeira |
| *Amphibalanus amphitrite* | I | Indo-Pacific | 1914 | SF, BW | Ireland, UK, Netherlands to Portugal |
| *Amphibalanus eburneus* | I | Atlantic Americas | 1940 | SF, BW, M | Netherlands, France, Spain |
| *Amphibalanus improvisus* | C | Indo-Pacific | 1850s | SF, BW | Norway to Spain |
| *Amphibalanus reticulatus* | I | Indo-Pacific | 2002 | SF, BW | Belgium |
| *Amphibalanus variegatus* | I | Indo-Pacific | 1997 | SF | Belgium |
| *Balanus trigonus* | I | East-Pacific | 1887 | SF | Azores, UK, Netherlands, Belgium |
| *Megabalanus coccopoma* | I | Tropical seas | 1851 | SF | Netherlands to France |
| *Megabalanus tintinnabulum* | C | West Africa | 2000s | SF | Belgium |
| *Solidobalanus fallax* | I | | 1995 | SF | UK, France, Spain, Portugal |

| | | | | | |
|---|---|---|---|---|---|
| **Mysidacea** | | | | | |
| *Hemimysis anomala* | I | Ponto-Caspian | 1998 | BW | Ireland, Netherlands, Belgium, France |
| **Amphipoda** | | | | | |
| *Caprella mutica* | I | NW Pacific | 1994 | SF | Norway to France |
| *Chelicorophium curvispinum* | I | Ponto-Caspian | 1935 | SF,canals | Ireland, UK, Netherlands to Portugal |
| *Corophium multisetosum* | C | Unknown | 1940s? | SF | Netherlands to France |
| *Echinogammarus berilloni* | I | SW Europe | 1930s? | BW | Germany, Netherlands, Belgium, France |
| *Gammarus tigrinus* | I | Atlantic America | 1931 | BW, DI | Ireland, England, North Sea |
| *Grandidierella japonica* | I | NW Pacific | 1999 | BW | England, Netherlands, Belgium |
| *Incisocalliope aestuarius* | I | Atlantic America | 2003 | SF, BW | Netherlands, Belgium |
| *Melita nitida* | I | Atlantic America | 2003 | SF, BW | England, Belgium, France |
| *Monocorophium acherusicum* | C | Unknown | 1965 | SF, BW | UK to Portugal |
| *Monocorophium sextonae* | I | New Zealand | 1930s | SF, BW | Ireland, UK, Germany to Spain |
| *Orchestia cavimana* | I | Ponto-Caspian | 1900–1930 | Canals | Germany to Spain |
| *Platorchestia platensis* | C | Unknown | 2001 | SB, drift | Norway to Netherlands. |
| **Tanaidacea** | | | | | |
| *Sinelobus stanfordi* | C | Unknown | 2009 | SF, BW | Netherlands, Belgium |
| **Isopoda** | | | | | |
| *Limnoria lignorum* | C | Boreal | 1790s | SF | Scandinavia, UK, Netherlands, France |
| *Limnoria quadripunctata* | I | S IndoPacific | 1940s | SF | Ireland, England, Netherlands to Spain |
| *Limnoria tripunctata* | I | S IndoPacific | 1950s | SF | British Isles |
| *Synidotea laticauda* | I | Japan | 1975 | SF, M | France |

(continued)

**Table 1** (continued)

| Species | Status | Origin | First record in | Vectors | Established in: |
|---|---|---|---|---|---|
| **Decapoda** | | | | | |
| *Callinectes sapidus* | I | Atlantic America | 1900 | BW | Denmark to Portugal |
| *Chionoecetes opilio* | I | N Pacific, NW Atlantic | 1996 | BW | Barents Sea, Norway and Russia |
| *Dyspanopeus sayi* | I | NW Atlantic | 1950s | BW, M | UK-Wales |
| *Eriocheir sinensis* | I | NW Pacific | 1912 | BW | Finland to Portugal |
| *Hemigrapsus sanguineus* | I | NW Pacific | 1999 | BW, SF | Netherlands to France |
| *Hemigrapsus takanoi* | I | NW Pacific | 1994 | BW, SF | Netherlands to Spain |
| *Palaemon macrodactylus* | I | NW Pacific | 1999 | BW | UK, Germany to Spain |
| *Paralithodes camtschaticus* | I | N Pacific | 1960s | DI | Barents Sea, Norway |
| *Rhithropanopeus harrisii* | I | W Atlantic | 1870 | BW, SF | Norway to Spain |
| *Rhithropanopeus harrisii* | I | W Atlantic | 1870 | BW, SF | Norway to Spain |

Vectors: *SF* Ship fouling, *BW* Ship ballast water and sediments, *SB* Ship solid ballast (rocks, sand), *M* Mariculture, *DI* Deliberate introduction by humans (e.g., fisheries, fish food)
Status: *I* Introduced, *C* Cryptogenic

# 2 Methods

For the purposes of this review, marine species are defined as those reproducing in salt or brackish water. Freshwater species that enter brackish water but do not reproduce there are excluded here. Data were derived from the author's own records and from ERMS (2009), WoRMS (2009) SeaLifeBase (2009), DAISIE (2009) and primary literature. Key additional publications include Eno et al. 1997 (United Kingdom), d'Udekem d'Acoz 1999 (Europe), Reise et al. 1999 (North Sea), Jażdżewski and Grabowski (2010) (Baltic Sea), Galil et al. 2002 (Mediterranean), Noël 2002 (France), and Wolff 2005 (The Netherlands). Brachyuran systematics follows Ng et al. (2008).

Excluded here are (1) neustonic species, such as the crab *Planes* spp., the isopod *Idotea metallica* and the barnacle *Lepas* spp., that are naturally dispersed on floating objects (Leppäkoski et al. 2003), (2) native species that have been treated by some authors as introduced (Appendix B), and (3) species that are dispersing northward along the European coast due to climate change, although it is recognized that such species may have an ecological impact once they extend their range.

## 2.1 *Vectors*

Ten species (20%) arrived via ship fouling, 18 species (36%) arrived via ballast water, and 13 species (26%) arrived by either ballast or fouling. Eight species (16%) were introduced through mariculture activity. Only two species appear to be introduced, or spread, via canals, an artifact of restricting this review to brackish and marine species, and thus only a few such species are sufficiently euryhaline to permit dispersal by this means. Only one species, *Platorchestia platensis*, seems to have been transported by solid (rock and sand) ballast (although solid ballast historically also no doubt dispersed a large number of supralittoral, maritime isopods; see Carlton and Eldredge 2009).

Thus shipping is the most important source of introduction of species to the Atlantic coast of Europe. Cargo-vessel ballast (water and sediment) is a factor for many organisms, especially larvae and small crustaceans (Jażdżewski 1980); examples are copepods (*Acartia omorii*, *A. tonsa*, *Eurytemora pacifica*), mysids (*Hemimysis anomala*), many amphipods (*Corophium* spp., *Echinogammarus berilloni*, *Gammarus tigrinus, Grandidierella japonica*, *Incisocalliope aestuarius*, *Melita nitida*), tanaids (*Sinelobus stanfordi*), and most decapod larvae. Fouling on ships' hulls is also a common source of introductions (De Man 1913; Bertelsen and Ussing 1936; Guinot and Macpherson 1987), this holds true especially for barnacles and may also apply to caprellids (*Caprella mutica*) and some crabs (*Hemigrapsus* spp., pilumnids). Wooden vessels were vectors for *Limnoria* spp.

Transplantation along with commercial oysters and other shellfish is one of the common means of introducing species (Carlton 1985, 1987). Shellfish culture is responsible for the introduction of parasites and fauna associated with oysters and oyster shells (*Eusarsiella zostericola*, *Myicola ostreae*, *Mytilicola intestinalis*, *Mytilicola orientalis*, *Midicola spinosus*, and possibly *Synidotea laticauda* and *Hemigrapsus takanoi*). Natural expansion through canals and rivers, facilitated by fouling on ships' hulls, is also a possibility for some corophiids and gammarids. Floating structures such as buoys, ropes, nets, and aquaculture equipment are also recognized as a possible factor of dispersal for some species (*Menippe mercenaria*, Appendix B and barnacles). Imports of live crustaceans for human consumption (lobsters, penaeids shrimps) occur as well.

Finally, deliberate introductions include *Gammarus tigrinus* (Schmitz 1960; Bulnheim 1985), *Palinurus elephas* (Heerebout 2001) and *Paralithodes camtschaticus* (Anisimova et al. 2004). Fortunately such movements are far fewer in the marine environment than in freshwater.

## 2.2 Biogeographic Origins and Affinities

The introduced crustacean fauna of Atlantic Europe derives from a number of biogeographic regions (Table 1): 8 species (16%) derive from Atlantic America, 26 species (52%) derive from Indo-Pacific, 2 species (4%) derive from Africa, 3 species (6%) derive from Ponto-Caspian region, 2 species (4%) derive from Mediterranean, 3 species (6%) derive from boreal regions, and 6 species (12%) from unknown regions. Interesting is that no species are derived from South America, although it is likely that the failed invasion of *Pilumnoides inglei* (Apppendix B) was derived from this continent.

Some aliens, such as the copepod *Acartia tonsa*, the barnacle *Megabalanus tintinnabulum*, and the crab *Callinectes sapidus*, are thermophilic and originate from tropical or sub-tropical areas of Asia or the Americas. Others, including the amphipods *Orchestia cavimana* and *Chelicorophium curvispinum* have a Ponto-Caspian origin; these tolerate wide variations in salinity and extend their distribution with the help of shipping through man-made canals in Central Europe (connection via the Donau-Rhein canal).

## 2.3 Spatial Patterns

The number of introductions depends to some extent on the length of coasts and the quality of habitats. The countries with the most alien crustaceans (Table 1) are also those that have a long coastline, and include France (with 31 species) and the UK (with 28 species), followed by Germany, the Netherlands and Belgium, with 20, 33, and 36 species, respectively. The presence of large ports and mariculture activities in these countries further accounts for this pattern. The most invaded ecosystems and habitats are often those already impacted by human activities and transport, such as estuaries (brackish waters), ports (manmade structures such as pontoons and buoys), and coastal areas next to shellfish farms. At present, there are no records of alien species from the open sea off Europe.

There are several "hotspots" for introduced crustaceans, such as the Oosterschelde Estuary in The Netherlands, Le Havre Harbour and Arcachon Bay in France, Thames and Tage Estuaries in England and Portugal respectively.

## 3 Management and Future Trends

Prevention, eradication and control are widely accepted as the basic management tools of invasive alien species. As far as marine crustaceans are concerned, little has been done to limit their numbers, spread and impacts. The issue of alien aquatic organisms transported in ballast water was first raised at IMO in 1988. Sixteen years later, a diplomatic conference adopted the International Convention for the Control and Management of Ships' Ballast Water and Sediments. Though aquaculture is an important pathway for the introduction of alien crustaceans, EU aquaculture regulations show little concern for that issue, concentrating on disease control (http://eur-lex.europa.eu/LexUriServ), yet quarantine regulations against shellfish parasites and pests are obviously insufficient.

The 100 worst alien species in Europe include these crustaceans present on European Atlantic coasts: *Amphibalanus improvisus*, *Dikerogammarus villosus*, *Eriocheir sinensis*, *Marsupenaeus japonicus*, and *Paralithodes camtschaticus*. The aim of the European Union's ambitious Marine Strategy Framework Directive, adopted in June 2008, is to protect more effectively the marine environment across Europe. The Member States are required to develop strategies for their marine waters, and "non indigenous species" are considered "qualitative descriptors for determining good environmental status" (http://eur-lex.europa.eu/LexUriServ).

The rising trend of crustacean invasions can hardly be expected to be reversed. Global changes such as climate warming may facilitate the acclimatization of some thermophilic species. Warm water from power stations is known to benefit species such as *Amphibalanus amphitrite* (Bamber 1987b) and *Brachynotus sexdentatus* (Naylor 1957, 1965). Eradication and mitigation are difficult to apply in the marine environment, and thus prevention must be central to the management of marine alien invasions.

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# Appendix A Inventory of Alien and Cryptogenic Species on the European Atlantic Coast

Unless otherwise stated, ecological, environmental, economic or other impacts are unknown; the absence of such reports should not be taken as the absence of impacts.

## Branchiopoda Diplostraca ("Cladocera")

Sidiidae

*Penilia avirostris* Dana, 1849

A marine cladoceran. Native to Eurasia? Sub-cosmopolitan: Mediterranean Sea and Black Sea (Russia, Bulgaria, Romania, Turkey, Ukraine, Georgia), Red Sea, China. Introduced to Canada, and possibly elsewhere in the cited range. North-East Atlantic: introduced to The Netherlands and North Sea (Carlton 1985; Johns et al. 2005) but said to be native to Germany (Greve et al. 2004). Biology/ecology: marine, brackish, fresh. Vector(s): possibly ballast water. Status: Cryptogenic.

## Ostracoda

Sarsiellidae

*Eusarsiella zostericola* (Cushman, 1906) [*Sarsiella zostericola*]

A marine ostracod. Native to the USA Atlantic coast. North-East Atlantic: Introduced to South-East English estuaries by the end of nineteenth or first half of twentieth century (Bamber 1987a, b; Eno et al. 1997). Biology/ecology: see Bamber 1987a, b. Vector(s): Importations of the American oyster *Crassostrea virginica* (Eno et al. 1997). Comments: Information on the occurrence of this very small species in other European localities is limited. Status: Introduced.

## Copepoda

Acartiidae

*Acartia omorii* Bradford, 1976 [*Acartia* (*Acartiura*) *omorii*]

A calanoid copepod. Native to Japan-China. Introduced to California and Chile. North-East Atlantic: Dunkerque, France (Brylinski 2009; Razouls et al. 2009), North Sea (Seuront 2005). Biology/ecology: epipelagic. Vector(s): ballast water (Razouls et al. 2009). Status: Introduced.

*Acartia tonsa* Dana, 1849 [*Acartia tonsa cryophylla*]

An estuarine copepod. Cosmopolitan, native distribution unknown, possibly Indo-Pacific. North-East Atlantic range: First reported from France (Rémy 1927), but first European records are from Dutch waters about 1912–1916 (Redeke 1935); also occurring in UK, Belgium and Denmark (Polk 1963; Brylinski 1981; Eno et al. 1997; Reise et al. 1999; Wolff 2005). Biology/ecology: Tolerant to low salinities. Diapause eggs present (Zilhoux and Gonzalez 1972). Vector(s): ballast water. Status: Cryptogenic.

Temoridae

*Eurytemora americana* Williams, 1906

An estuarine copepod. Native to North-East Pacific (Canada, Alaska, Oregon, USA). Introduced to Argentina (Hoffmeyer et al. 2000). North-East Atlantic: Iceland: (Jespersen 1940), Oosterschelde, The Netherlands (Bakker 1994; Wolff 2005), English Channel, Port of Dunkerque, Straight of Dover (Razouls et al. 2009). Biology/ecology: Brackish ponds; coastal waters. Vector(s): Ballast water. Status: Introduced.

*Eurytemora pacifica* Sato, 1913

A calanoid copepod. Native to North Pacific (China, Korea, Japan, Alaska). North-East Atlantic range: France only Charente estuary (Goulletquer et al. 2002, 2004). Biology/ ecology: marine and brackish waters. Vector(s): Ballast water. Status: Introduced.

Myicolidae

*Midicola spinosus* (Raffaele and Monticelli, 1885) [*Pseudomyicola spinosus*]

A parasitic copepod. Native to Pacific, widely distributed, Japan to Mexico. Introduced (possibly) to Indian Ocean: Madagascar and the Atlantic: North Carolina, Bermuda, West Indies, Brazil, Mediterranean Sea, Black Sea (Humes 1968). North-East Atlantic: Arcachon Bay, France (Goulletquer et al. 2002). Biology/ecology: optional parasitic. Vector(s): Mariculture. Status: Introduced.

*Myicola ostreae* Hoshina and Sugiura, 1953

A parasitic copepod. Native to North-West Pacific (Japan, Korea). North-East Atlantic: The Netherlands, Ireland, France (Comps 1972; Reise et al. 1999; Goulletquer et al. 2002, 2004; Wolff 2005). Biology/ecology: parasitic in oysters. Vector(s): Mariculture: Accidentally introduced into France with imports of *Crassostrea gigas* from Japan in the 1970s (His 1979), since then has been found in several European countries (Streftaris et al. 2005). Status: Introduced.

Myticolidae

*Mytilicola intestinalis* Steuer, 1902

A parasitic copepod. Native to Mediterranean. North-East Atlantic: Established in Denmark, The Netherlands, Germany, Belgium (Leloup and Lefevere 1952; Polk 1963), Ireland, UK, France (Davey 1989; Goulletquer et al. 2002, 2004; Wolff 2005; Kerckhof et al. 2007). Biology/ecology: Parasitic in mussels. Impacts: Relatively harmless (Dare 1985). Vector(s): Mariculture. Status: Introduced.

*Mytilicola orientalis* Mori, 1935

A parasitic copepod. Native to North-West Pacific. Introduced to the Pacific coast of Canada and the United States. North-East Atlantic: France (His 1977, 1979), The Netherlands, Ireland, UK (Wolff 2005). Biology/ecology: Parasitic in *Crassostrea gigas*, *Mytilus edulis*, *Ostrea edulis* (Stock 1993a, b). Vector(s): Mariculture. Accidentally introduced into Europe with Pacific oysters (Stock 1993a). Status: Introduced.

Porcellidiidae

*Porcellidium ovatum* Haller, 1879

A harpacticoid copepod. Native region unclear: first described from Italy, and since recorded from Kenya, Indonesia, and the Caribbean Sea. North-East Atlantic:

Ireland, UK and surrounding seas (Holmes et al. 1997; Minchin and Eno 2002; Stokes et al. 2004). Biology/ecology: estuaries. Vector(s): possibly ballast water or ballast sediments or fouling on ships' hulls. Status: Cryptogenic.

Spiophanicolidae
*Spiophanicola spinosus* Ho, 1984 [*Spiophanicola spinulosus* Ho, 1984]
A poecilostomatid copepod. Possibly native to California, but perhaps circumboreal. North-East Atlantic: introduced to Cullercoats, Scotland (O'Reilly 1999). Biology/ecology: associated with the polychaete *Spiophanes kroyeri*. Vector(s): possibly ballast water or ballast sediments. Status: Cryptogenic.

## Cirripedia

Archeobalanidae
*Austrominius modestus* (Darwin, 1854) [*Elminius modestus*]
An Australasian barnacle. Native to Australia, New Zealand. North-East Atlantic: First specimens found in Portsmouth, England in 1943 (Stubbings 1950), then extended range progressively. This species is now found in Ireland, Shetland Islands, Denmark, The Netherlands, Germany to Gibraltar and Madeira (Crisp 1958; Eno et al. 1997; Wolff 2005; Minchin 2007). Biology/ecology: Rapid growth and tolerant to turbid waters with low salinity. Reaches maturity by first year, several broods per year. Impacts: Competes with other barnacles such as *Balanus* spp. and *Chthamalus* spp. (Eno et al. 1997; Kerckhof 2002; Kerckhof et al. 2007). Vector(s): pelagic larvae in ballast waters, fouling on ships' hulls. Comments: Established along most European Atlantic coastlines where it is fairly common on several intertidal hard substrates. Status: Introduced.

Balanidae
*Amphibalanus amphitrite* Darwin, 1854
The striped or purple acorn barnacle. Native to Tropical Seas: South-western Pacific and Indian Oceans (according to fossil records), and introduced to North Pacific and Atlantic Ocean (cosmopolitan). North-East Atlantic: first found in 1914 in La Rochelle (France) and 1937 in Sussex (UK). Scattered established populations present in some places around UK, Ireland and in some European countries, from The Netherlands to Portugal (Breton et al. 1995; Eno et al. 1997; Wolff 2005; Minchin 2007). Recorded from Mediterranean and Black Sea (de Kluijver and Ingalsuo 2009). Biology/ecology: Lives in warm waters (settlement may be aided by thermal effluents from power stations). Impacts: Competition with *Semibalanus balanoides* and *Austrominius modestus* (Kerckhof 2002). Vector(s): shipping, larvae in ballast waters, or fouling on ships' hulls. Status: Introduced.

*Amphibalanus eburneus* Gould, 1841 (Fig. 1)
The ivory barnacle. Native to Atlantic coast of Americas, from Boston to Rio de Janeiro. Introduced to many regions around the world including the Mediterranean and Black Sea and Pacific Ocean. North-East Atlantic: The Netherlands, France, Spain (Reise et al. 1999, Goulletquer et al. 2002, Wolff 2005). Biology/ecology: Often associated with mussels or other bivalves. Vector(s): fouling on ships' hulls, ballast water, possibly mariculture. Status: Introduced.

**Fig. 1** *Amphibalanus eburneus* (Berre (France) © F. André)

*Amphibalanus improvisus* Darwin, 1854

The bay barnacle or acorn barnacle. Native to the North Atlantic Ocean. Introduced to Indo-Pacific, Australasia, Japan, Pacific North America, and elsewhere. North-East Atlantic: Established from Norway and The Netherlands to Spain, Ireland and UK (Reise et al. 1999; Wolff 2005; Minchin 2007). Biology/ecology: marine and brackish environments with low salinity (Polk 1963), ports, pontoons (Breton et al. 1995; Kerckhof 2002), sometimes as epibionts on crabs. Feeds on detritus and phytoplankton. Impacts: This species is regarded as a pest and is given as one of the 100 worst alien species in Europe (DAISIE 2009). Competes with other alien species such as *Amphibalanus amphitrite* and *Austrominius modestus*. Vector(s): Often dispersed by shipping: ballast water, fouling on hulls. Status: Cryptogenic; considered as introduced by some authors and native by others (see discussions in Kerckhof 2002; Wolff 2005; Kerckhof et al. 2007).

*Amphibalanus reticulatus* (Utinomi, 1978) [*Balanus reticulatus*].

Native to Indian Ocean, Indo-West Pacific, and invasive to Southwest Atlantic. North-East Atlantic: Belgium (Kerckhof 2002). Biology/ecology: fouling species, on buoys. Vector(s): ship fouling, ballast water. Status: Introduced.

*Amphibalanus variegatus* (Darwin, 1854)

Native to Indo-Malayan and Australia. North-East Atlantic: Reported from Belgium on buoys in 1997 and 1999 (Kerckhof 2002). Biology/ecology: on man-made structures, sheltered bays. Vector(s): ship fouling, ballast water. Status: Introduced.

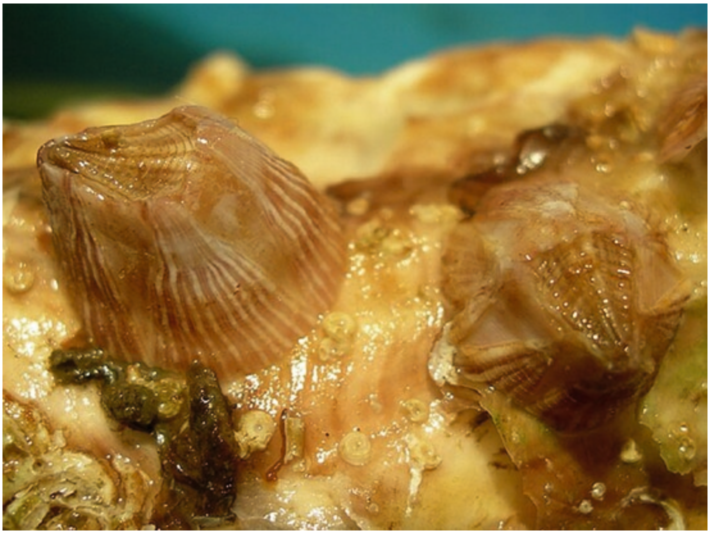

**Fig. 2** *Balanus trigonus* (Thau (France) 15/12/2006 © F. André)

*Balanus trigonus* Darwin, 1854 (Fig. 2)
Native to Pacific and Indian Oceans. North-East Atlantic: First reported from Azores in 1887 (Cardigos et al. 2006), now reported from The Netherlands and Belgium (Adema 1990; Kerckhof and Cattrijsse 2002). Biology/ecology: sublittoral, on floating objects, on invertebrates (Kerckhof 2002). Vector(s): ship fouling (Zullo 1992). Status: Introduced.

*Megabalanus coccopoma* (Darwin, 1854)
The titan acorn barnacle. Native to Pacific coasts of central and South America. North-East Atlantic: The Netherlands to France; established in Belgium in 1976 (Wolff 2005). Biology/ecology: Shallow waters, often found on buoys in ports. Vector(s): fouling on ships' hulls and other man-made structures (Newman and McConnaughey 1987). Comments: First recorded in 1851, probably on a ship's hull from Le Havre, France (Kerckhof and Cattrijsse 2002). Status: Introduced.

*Megabalanus tintinnabulum* (Linnaeus, 1758)
The giant barnacle. Native to tropical seas. North-East Atlantic: France, The Netherlands and Ireland, and established in Belgium (Wolff 2005; Minchin 2007). Biology/ecology: hard substrates in ports (hulls, buoys). Impacts: Unknown. Vector(s): fouling on ships' hulls. Status: Cryptogenic.

Archeobalanidae
*Solidobalanus fallax* (Broch, 1927)
Native to African west coast. North-East Atlantic: Spain, Portugal, France and Great Britain (Eno et al. 1997; Kerckhof 2002). Biology/ecology: On lobster or crab pots, floating objects, shells such as the bivalve *Aequipecten opercularis* (Kerckhof, 2002). Vector(s): shipping, fouling. Status: Introduced.

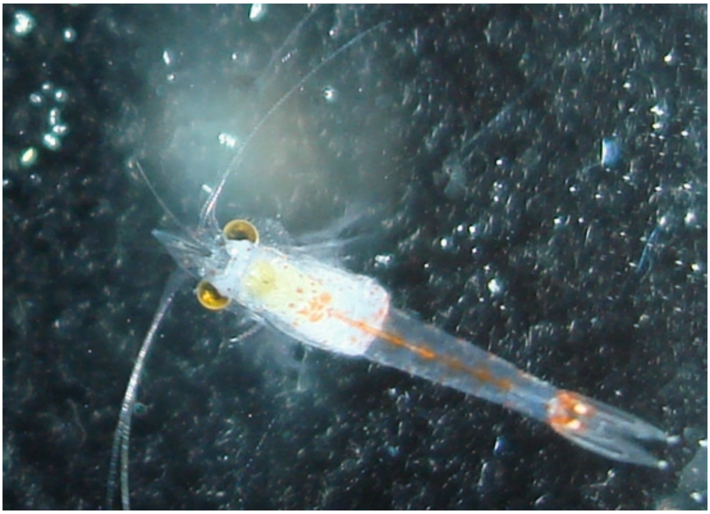

**Fig. 3** *Hemimysis anomala* (Torcy (France) 16/05/2009 © J. Dumas)

## Mysidacea

Mysidae

*Hemimysis anomala* G. O. Sars, 1907 (Fig. 3)

The bloody-red mysid or Ponto-Caspian Mysid). Native to Ponto-Caspian area. North-East Atlantic: The Netherlands, Belgium, France, Ireland (Faasse 1998; Devin et al. 2005; Wolff 2005; Holdich and Pöckl 2007; Minchin and Holmes 2008). Biology/ecology: Fresh waters (rivers) and brackish waters (estuaries). Impacts: Dramatic effects on zooplankton composition and abundance (Ketelaars et al. 1999). Vector(s): shipping, ballast water (Ketelaars et al. 1999). Intentionally introduced for enrichment of fish feed in tributaries of the Baltic Sea (Salemaa and Hietalahti 1993). Status: Introduced.

## Amphipoda

Caprellidae

*Caprella mutica* Schurin, 1935 [*Caprella macho* Platvoet, De Bruyne and Gmelich Meyling, 1995] (Fig. 4)

The Japanese skeleton shrimp. Native to North-East Asia. Introduced to many regions in the world. North-East Atlantic: Celtic Sea, Ireland, England, Scotland, North Sea, Norway, Germany, The Netherlands (first record in Europe in 1994: Platvoet et al. 1995), Belgium, English Channel, and France (Breton 2005; Wolff 2005; Minchin 2007). Biology/ecology: Occurs in high numbers on artificial structures (boats hulls, buoys, pontoons, ropes and nets, aquaculture equipments) and biogenic reefs constructed by mussels (*Modiolus modiolus*, *Mytilus edulis*) and tubeworms (*Sabellaria alveolata* and *Serpula vermicularis*) (Cook et al. 2007a, b).

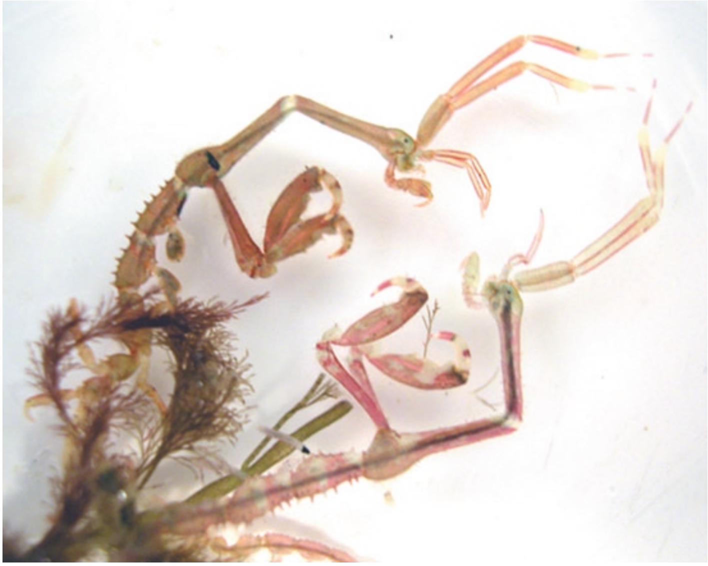

**Fig. 4** *Caprella mutica* ((UK) © E. Cook)

Impacts: Largely unknown, but see Boos et al., this volume. Vector(s): ship hull fouling. For details on this species, see Boos et al. 2010. Status: Introduced.

Corophiidae
*Chelicorophium curvispinum* (Sars, 1895)
The Caspian mud shrimp. Native to Ponto-Caspian area. Also introduced to Canada and USA. North-East Atlantic: Ireland, England, The Netherlands, Germany, Belgium, France (Wundsch 1912; Devin et al. 2005; Wolff 2005; Holdich and Pöckl 2007; Minchin 2007). Biology/ecology: Salt, brackish and fresh waters. Rivers and estuaries (Buckley et al. 2004; de Kluijver and Ingalsuo 2009). Impacts: altering invaded habitats by predation, competition and causing changes to the substrate (Wittenberg 2006). Vector(s): Natural expansion through canals and rivers, facilitated by fouling on ships' hulls. Status: Introduced.

*Corophium multisetosum* Stock, 1952
Native distribution undefined. Distributed along Atlantic coasts of Europe and Baltic; North-East Atlantic: Ireland, Wales, England, Germany, The Netherlands, France, Spain, Portugal (Stock 1952; Hayward and Ryland 1990; Bachelet et al. 2003). Biology/ecology: In brackish fish ponds (Bachelet et al. 2003); estuaries, near the limit of saline penetration (Buckley et al. 2004); burrows and constructs mud tubes, sometimes with seagrass *Zostera noltii* (de Kluijver and Ingalsuo 2009). Vector(s): Hull fouling. Comments: Usually considered as alien in different countries, but whether this species is introduced or not is questionable. The recent occurrence of *C. multisetosum* in German Baltic waters (Zettler et al. 2000) is possibly due to a natural range extension (Leppäkoski et al. 2003). Status: Cryptogenic.

*Monocorophium acherusicum* (da Costa, 1851 [nom. nud.] 1857) [*Corophium acherusicum* Costa, 1851 *Corophium ascherusicum*]
Native range uncertain; first described from Italy. North-East Atlantic: France, Belgium, England (Naylor 1965; Bachelet et al. 2003). Biology/ecology: constructs tubes on algae, hydroids and other organisms, in shallow sublittoral habitats of reduced salinity, often in sheltered harbours and estuaries. Vector(s): ballast water, ballast sediments or fouling on ships' hulls. Status: Cryptogenic.

*Monocorophium sextonae* Crawford, 1937
The New Zealand mud shrimp. Native to New Zealand. North-East Atlantic: First introduced to Plymouth (UK) in 1930s (Crawford 1937), and later to Ireland. At present recorded from Ireland, Scotland, England and Germany to The Netherlands, Belgium, France, Portugal (Eno et al. 1997; Wolff 2005). Also present in Mediterranean (de Kluijver and Ingalsuo 2009). Biology/ecology: estuaries, open sea on *Laminaria, Himanthalia*, *Buccinum* eggs, hard substrates (Wolff 2005). Vector(s): ballast water or ballast sediments, fouling on ships' hulls. Status: Introduced (Kerckhof et al. 2007).

*Grandidierella japonica* Stephensen, 1938
The Japanese amphipod. Native to China, Japan, Korea; introduced to Australia, Hawaii, Pacific coast of USA (Chapman and Dorman 1975). North-East Atlantic range: Suffolk (UK), North Sea (Smith et al. 1999; Ashelby 2006). Biology/ecology: tube dwelling species on sediments; brackish waters. Vector(s): ballast water, ballast sediments or fouling on ships' hulls. Status: Introduced.

Gammaridae

*Echinogammarus berilloni* (Catta, 1871) [*Gammarus berilloni*]
An Iberian amphipod. Native to Atlantic part of Southwestern Europe: Spain, France (Pinkster 1973; Bachelet et al. 2003). North-East Atlantic: The Netherlands, Belgium, Luxembourg, Germany, Northern and eastern France (Peeters et al. 2003; Devin et al. 2005; Holdich and Pöckl 2007). Biology/ecology: Estuaries, brackish waters, canals, also inland waters. Vector(s): Floating structures, shipping (ballast water and/or sediments). Status: Introduced.

*Gammarus tigrinus* Sexton, 1939
The tiger sideswimmer or tiger gammarid. Native to Atlantic coast of North America, from St Lawrence Estuary, Canada, to Florida. North-East Atlantic: Ireland, Germany, The Netherlands, Belgium and France (Schmitz 1960; Devin et al. 2005; Wolff 2005; Minchin 2007). Common in the Baltic Sea. Biology/ecology: Estuaries, brackish waters, canals, also inland waters (de Kluijver and Ingalsuo 2009). Impacts: predatory impacts on macroinverebrates, can outcompete other amphipods (Pinkster et al. 1977). Vector(s): ballast water (Carlton 1985); deliberate introductions (Schmitz 1960; Bulnheim 1985). Status: Introduced.

Pleustidae

*Incisocalliope aestuarius* (Watling and Maurer, 1973) [*Parapleustes assimilis* (G. O. Sars, 1882); *Pleusymtes glaber* (Boeck, 1861)]
Native to Atlantic coast of North America (USA). North-East Atlantic: The Netherlands and Belgium (Faasse and Moorsel 2003, Wolff 2005). Biology/ecology: Estuaries (Kerckhof et al. 2007). Vector(s): ballast water, hull fouling. Status: Introduced.

Melitidae

*Melita nitida* Smith, 1837

Native to Atlantic coast of North America. North-East Atlantic: The Netherlands (Faasse and van Moorsel 2003, Wolff 2005). Biology/ecology: Estuaries, under stones, among sediments. Vector(s): ballast water or sediment, ships' hull fouling. Status: Introduced.

Talitridae

*Orchestia cavimana* Heller, 1865

A freshwater riparian amphipod or semi-terrestrial amphipod. Native to Ponto-Caspian and Eastern-Mediterranean; Red Sea. North-East Atlantic: Germany, The Netherlands, Belgium, France, Spain (Tétry 1939; Kinzelbach 1972; Bachelet et al. 2003; Devin et al. 2005; Wolff 2005; Gollasch and Nehring 2006). Also along the Atlantic coast of Africa (de Kluijver and Ingalsuo 2009). Biology/ecology: demersal, semiterrestrial, under stones close to brackish waters, fresh waters. Vector(s): expansion along shipping canals (Kinzelbach 1972, 1995). Status: Introduced.

*Platorchestia platensis* (Krøyer, 1845) [*Orchestia platensis*]

The beach flea or sandhopper. Native distribution unknown, considered to be world-wide, but a likely species complex (Lowry 2000; Spicer and Janas 2006). North-East Atlantic: Specimens present or populations established in Norway, Sweden, The Netherlands, Germany (Persson 2001; Wolff 2005) [Baltic: Sweden, Denmark, Poland]. Biology/ecology: in wrack beds on hard substrates such as rocks, stones, gravels and shore meadows. Vector(s): Possibly dry ballast or natural dispersal with drifting algae. Status: Cryptogenic.

## Tanaidacea

Tanaidae

*Sinelobus stanfordi* (Richardson, 1901) [*Tanais stanfordi*]

A brackish water tanaid. Native distribution unknown, reported as cosmopolitan (WoRMS 2010), and possibly a species complex; Pacific: Japan, New Zealand, and USA; Central West Atlantic: Mexico and USA (Vittor 2001). Central East Atlantic: Cameroon-Nigeria, South Africa. North-East Atlantic: Belgium, The Netherlands (van Haaren and Soors 2009). Biology/ecology: brackish waters of estuaries, ports. Vector(s): hull fouling, ballast water. Status: Cryptogenic.

## Isopoda

Limnoriidae

*Limnoria lignorum* (Rathke, 1799) [*Cymothoa lignora*]

The common gribble. Native distribution still uncertain; a boreal species, recorded from the East and West coasts of North America (Schotte et al. 1995; de Kluijver and Ingalsuo 2009). North-East Atlantic: Reported from Scandinavia, UK, The Netherlands, France (Jones 1963; Wolff 2005). Biology/ecology: Lives in brackish waters of estuaries, ports. Impacts: reported as an important wood borer in many regions. Vector(s): Widely dispersed in the days of wooden sailing ships. Comments: Cryptogenic; see discussion in Wolff (2005).

*Limnoria quadripunctata* Holthuis, 1949
The quadripunctate gribble. Probably native to the South Pacific or Indian Oceans (Carlton, pers. comm. 2009), and introduced widely around the world (Schotte et al. 1995). North-East Atlantic: Described from The Netherlands, and reported from there, England, Ireland, France, and Spain (Jones 1963; Wolff 2005). Biology/ecology: Lives in brackish waters of estuaries, ports. Impacts: unknown in Europe, but reported as an important wood borer in many regions. Vector(s): Widely dispersed in the days of wooden sailing ships. Status: Introduced.

*Limnoria tripunctata* Menzies, 1951
The tripunctate gribble. Probably native to the South Pacific or Indian Oceans (Carlton and Eldredge 2009), and introduced widely around the world (Schotte et al. 1995). North-East Atlantic: British Isles (Jones 1963); also present in Mediterranean (Bourdillon 1958). Biology/ecology: wood boring isopod. Impacts: unknown in Europe, but reported as an important wood borer in many regions. Vector(s): Widely dispersed in the days of wooden sailing ships. Status: Introduced.

Idoteidae
*Synidotea laticauda* Benedict, 1897 [*Synidotea laevidorsalis* pro-parte]
Native to Japan, but species-level taxonomy remains in dispute (Chapman and Carlton 1991; 1994; Poore 1996). Also introduced to the Atlantic coast of the USA. North-East Atlantic: Reported from Gironde estuary, France since 1975 (Mees and Fockedey 1993 as *S. laevidorsalis*) and later from South-West Spain in 1996 (Cuesta et al. 1996 as *S. laevidorsalis;* Poore 1996; Drake et al. 2002 as *S. laticauda*). Biology/ecology: Littoral zone. Lives in brackish waters of estuaries and reported from docks, buoys and floating lines. Vector(s): Ship fouling or mariculture (oysters). Status: Introduced.

## Decapoda

Portunidae
*Callinectes sapidus* Rathbun, 1896 (Fig. 5)
The American blue crab. Native to Western Atlantic, from Canada to Argentina. Introduced to Japan, Pacific, as well as to Mediterranean (Galil et al. 2002). North-East Atlantic: Records are first from France (Bouvier 1901) then from Denmark, Germany, The Netherlands, Belgium, France, Spain and Portugal (d'Udekem d'Acoz 1999; Wolff 2005; Nehring 2010). Biology/ecology: brackish waters, estuaries, ports (Vincent 1986); reproduction is not really documented on North-East Atlantic. Impacts: Low in region under consideration, since records are scarce on North-East Atlantic. Vector(s): ballast water (larvae). Status: Introduced.

Majidae
*Chionoecetes opilio* (O. Fabricius, 1788) [*Cancer opilio*]
The snow crab. Naturally distributed in North Pacific and North-West Atlantic: Canada, Saint Pierre and Miquelon, USA, and Greenland (Tremblay 1997). North-East Atlantic: Barents Sea, Norway and Russia (d'Udekem d'Acoz 1999; Alvsvåg et al. 2009; Fey 2009). Biology/ecology: Lives in cold and deep waters.

**Fig. 5** *Callinectes sapidus* (Dunkerque (France) © P. Lesur)

Impacts: Competition with other crabs. Vector(s): ballast water (larvae). For details on this species, see Agnalt et al. 2010. Status: Introduced.

Panopeidae
*Dyspanopeus sayi* (Smith, 1869) [*Neopanope sayi*]
The Say mud crab. Native to North-West Atlantic Ocean (USA). North-East Atlantic: introduced into Swansea Docks, Wales (Naylor 1960; d'Udekem d'Acoz 1999) and Mediterranean (Galil et al. 2002). Biology/ecology: estuaries and coastal lagoons. Impacts: Unknown for North-East Atlantic; elsehere may affect local clam farming (Galil et al. 2002). Vector(s): ballast water or mariculture. Status: Introduced.

*Rhithropanopeus harrisii* (Gould, 1841) [*Pilumnus tridentatus* Maitland, 1874; *Heteropanope tridentate; Pilumnus harrisii*] (Fig. 6)
The estuarine or Harris or white-tipped mud crab, Zuiderzee crab. Native to West-Atlantic from New Brunswick to North-East Brazil. North-East Atlantic: This crab is the first known decapod to be introduced to Europe, having first been collected in the 1870s in the Zuiderzee, where it was mistakenly described as a new species. It is established at present in most European countries (Eno et al. 1997). Population size has fluctuated recently; in some places, the crab has almost disappeared (Christiansen 1969; Ingle 1980; d'Udekem d'Acoz 1999; Wolff 2005). Also introduced into the Mediterranean (Galil et al. 2002). Biology/ecology: Lives in muddy waters of low salinity. Sometimes associated with the tube worm *Ficopomatus enigmaticus*. Impacts: Competes with native crabs (Marchand and Saudray 1971). Vector(s): Shipping. Status: Introduced.

**Fig. 6** *Rhithropanopeus harrisii* (Veerse Meer (The Netherlands) © V. Maran)

**Fig. 7** *Eriocheir sinensis* (Dunkerque (France) 27/04/2008 © F. Cordier)

Varunidae

*Eriocheir sinensis* H. Milne-Edwards, 1853 (Fig. 7)

The Chinese mitten crab. Native to North-West Pacific (Asia) between 40° N (Japan and Korean Peninsula) and 26° N (China). North-East Atlantic: First found in Germany in 1912, subsequently spread to other European countries, from Finland to Portugal. Populations of this crab increased in southern England, especially in Thames River, by the end of twentieth century. By contrast, the mitten crab is quite rare in France, for

**Fig. 8** *Hemigrapsus sanguineus* (Le Havre (France) 07/03/2009 © D. Ingratta)

instance in Seine River (Vincent 1996). Biology/ecology: Catadromous; this crab is able to migrate long distances along rivers, and reproduces in brackish water. Impacts: It is regarded as a pest and is considered one of the 100 worst alien species in Europe (DAISIE 2009). It may impact soft sediment banks through burrowing. Vector(s): larvae in ballast water. Comments: Multiple invasions seemed to have occurred (Hänfling et al. 2002). For more details see Bentley (2010). Status: Introduced.

*Hemigrapsus sanguineus* (De Haan, 1835) (Fig. 8)
The Asian or Japanese shore crab. Native to North-West Pacific (Asia), from Sakhalin Island to Taiwan. Also introduced to North-West Atlantic/USA, and to the Mediterranean (Galil et al. 2002). North-East Atlantic: France, The Netherlands (Breton et al. 2002; Campbell and Nijland 2004; Wolff 2005). Whether the European populations originate directly from Asia or indirectly from USA is unknown. Biology/ecology: Rocky places with algae, under stones. Impacts: Competition with other crabs such as *Carcinus*. Vector(s): ballast water, fouling. Status: Introduced.

*Hemigrapsus takanoi* Asakura and Watanabe, 2005 [*Hemigrapsus penicillatus* (De Haan, 1835) *pro-parte*: European specimens] (Fig. 9)
The brush-clawed penicilate shore crab. Systematic note: Soon after the description of *H. takanoi* (Asakura and Watanabe 2005; Asakura 2006), Sakai (2007) synonymised it with *Hemigrapsus penicillatus*. After carefully examinating a large series of specimens, Ng et al. (2008) considered both species as valid. All European specimens so far examined are referrable to *H. takanoi*. Native to North-West Pacific (Asia), from Sakhalin Island to Taiwan. North-East Atlantic: Established first in France and Spain (Noël et al. 1997) then in The Netherlands, Belgium (Vincent and Breton 1999; Wolff 2005). Since 1995, populations developed swiftly in Charente-maritime, France then expanded north and south, reported from most coastal areas of Bay of Biscay (Noël et al. 1997; Noël and Gruet 2008). Biology/ecology: Omnivorous. Lives beneath stones and among empty oyster shells on mud flats; estuaries, lagoons,

**Fig. 9** *Hemigrapsus tanakoi* (Zeeland (The Netherlands) 05/04/2009 ©J.-P. Corolla)

sheltered places. Impacts: Competition with other crabs such as *Carcinus maenas* and *Pachygrapsus marmoratus*. Southern expansion in Spain likely limited by competition with *Eriphia spinifrons*. Vector(s): Hull fouling, in empty barnacles (Gollasch 1999), ballast water or sediment, oyster mariculture. Six juveniles (of *H. takanoi* or *H. penicillatus*) were collected on the hull of a Japanese vessel in Bremerhaven, Germany, on 14 August 1993 (Gollasch 1999). Status: Introduced.

Palaemonidae
*Palaemon macrodactylus* Rathbun, 1902
The East Asian or oriental shrimp. Native to North-West Pacific (Asia). North-East Atlantic: in most large estuaries in UK, Germany, The Netherlands, Belgium, France and Spain (Cuesta et al. 2004; Ashelby et al. 2004; Béguer et al. 2007; Kerckhof et al. 2007; González-Ortegón et al. 2009). Biology/ecology: Large estuaries, marine and brackish waters. Impacts: Competition with other estuarine palaemonids. Vector(s): ballast water. Status: Introduced.

Lithodidae
*Paralithodes camtschaticus* (Tilesius, 1815) [*Paralithodes camtschatica*]
The Alaskan red king crab. Taxon: Lithodidae. Native to the North Pacific, Bering Sea, Japan Sea. North-East Atlantic range: Larvae, juveniles and adults introduced to the southern Russian Barents Sea (1961–1969), established and spread towards the north Norwegian coast (Finmark and South of the Lofoten Archipelago) by natural dispersion (Jørgensen and Primicerio 2007). Biology/ecology: Predator feeding on a large spectrum of benthic organisms. Impacts: The species is regarded as a pest and considered one of the 100 worst alien species in Europe (DAISIE 2009). Extensive interactions with marine macrofauna (*Chlamys islandica*) and algae (Gudimov et al. 2003). Vector(s): Deliberate introductions of larvae and adults. Comments: For details, see Anisimova et al. 2004; Jørgensen 2010. Status: Introduced.

# Appendix B
# Species Here Considered to be Native or Non-established Aliens in Atlantic Europe

## Cirripedia

Balanidae
*Fistulobalanus albicostatus* (Pilsbry, 1916)
A mangrove barnacle. Native to East Asia, Korea, Japan, Hong Kong, South China Sea, Taiwan. North-East Atlantic: France, some records from Bourgneuf Bay and Le Croisic (1974) but not established (Gruet and Baudet 1997; Goulletquer et al. 2002, 2004). Biology/ecology: Lives in warm waters, mangroves, estuaries, on ships, buoys, piers, docks. Vector(s): Mariculture.

*Megabalanus tulipiformis* (Ellis, 1758)
An acorn barnacle. Native to West coast of Africa; introduced to Mediterranean. North-East Atlantic: France, Spain and Madeira (Wirtz et al. (2006). Probably not established. Biology/ecology: hard substrates in ports (piers, buoys). Vector(s): fouling on ship's hulls. Comments: Known as fossils from Miocene in France (Carriol 2004).

Archeobalanidae
*Chirona hameri* (Ascanius, 1767) [*Balanus hameri*]
An acorn barnacle. Native to North Atlantic deep water species. North-East Atlantic range: Reported from Belgium (Kerckhof 2002). Biology/ecology: Deep waters. Vector(s): fouling.

Lepadidae
*Conchoderma auritum* (Linnaeus, 1767)
The rabbit-ear barnacle. Cosmopolitan species: South Africa, Madagascar (Jones et al. 2000; WoRMS 2009). North-East Atlantic range: Faeroe Islands, Iceland, Norway, Sweden, Irish Sea, Scotland, North Sea, The Netherlands, Belgium, France [Wimereux], Madeira (Wolff 2005; WoRMS 2009; SeaLifeBase 2009). Biology/ecology: boat hulls, drift wood and attached to whale barnacles (de Kluijver and Ingalsuo 2009). Vector(s): Shipping, on ship's hulls. Comments: Whether this species can be considered as introduced to Europe is not clear; According to DAISIE (2009) it is introduced; native according to SeaLifeBase.

## Stomatopoda

Gonodactylidae
*Odontodactylus scyllarus* (Linnaeus, 1758)
A mantis shrimp. Indo-West Pacific. North-East Atlantic range: Saint Malo, Brittany (France) (Noël, unpublished data 2009). Biology/ecology: Impacts: weak if any. Vector(s): Possibly aquarium trade. Comments: A single specimen photographed in situ by a diver.

## Decapoda

Varunidae

*Brachynotus sexdentatus* (Risso, 1827)

A grapsoid crab. Native to Mediterranean (references in d' Udekem d'Acoz C 1999). North-East Atlantic: Introduced into Queens Dock, Swansea, Wales (Naylor 1957), then became extinct (Clark 1986). Further records are scarce, for instance in France at Roscoff [larvae] (Bourdon 1965) and La Rochelle [two specimens] (Noël et al. 1997). Biology/ecology: Lives in shallow waters, on sandy or rocky coasts in sheltered places. Vector(s): Ballast water, fouling, mariculture. There is also a possibility that this species is extending its natural geographical range further north due to climate warming.

Nephropidae

*Homarus americanus* H. Milne Edwards, 1837

The American lobster. Native to Atlantic coasts of North America, from Newfoundland to North-Carolina. North-East Atlantic range: Scattered records of specimens that are most likely escaped from captivity are available for Norway (Oslofjord), Sweeden, Danemark (Øresund), Ireland, UK, and France (d'Udekem d'Acoz 1999; Minchin 2007); it is not known if reproducing populations are established. Biology/ecology: Rocky shores, infralittoral. Vector(s): Mariculture, imports of live crustaceans for human consumption. For details, see Jørstad et al. 2010.

Palinuridae

*Jasus lalandii* (H. Milne Edwards, 1837)

The Cape rock lobster. Native to South Africa, Namibia. North-East Atlantic: Portugal (Guerra and Gaudêncio 1982), no further records; Biology/ecology: Marine, rocky bottoms. Vector(s): Intentional release.

Penaeidae

*Marsupenaeus japonicus* (Bate, 1888) [*Penaeus japonicus*]

The Kuruma shrimp. Native throughout Indo-Pacific including Red Sea. Introduced into Mediterranean (Galil et al. 2002). North-East Atlantic: Some records are available for specimens escaped from aquaculture facilities (Clark 1990a, b; d'Udekem d'Acoz 1999; Minchin 2007). Biology/ecology: Lives in coastal waters; reproduction is not documented on North-East Atlantic coast. Impacts: This shrimp is regarded as a pest and is listed as one of the 100 worst alien species in Europe (DAISIE 2009). Vector(s): Mariculture.

Menippidae

*Menippe mercenaria* (Say, 1818)

The Florida stone crab. Native to Atlantic coasts of USA, Mexico, Cuba. North-East Atlantic range: One living adult female present among fouling in Brittany, France on a buoy originating from Florida and drifting for 18 month across North Atlantic (Noël 2007). Biology/ecology: Tolerant to various salinities and preys on oysters and other molluscs. Burrows in mud and also present on hard bottoms (Tavares 2002). Vector(s): Intercontinental drift on floating objects.

Pilumnoididae
*Pilumnoides inglei* Guinot and Macpherson, 1987
Native distribution: Probably South America; *Pilumnoides* has tropical representatives only. North-East Atlantic range: Early 1900s records from Ireland and England; not recorded since 1913 and considered not established (Vallentin 1900; Ingle 1980; Clark 1986; Guinot and Macpherson 1987; d'Udekem d'Acoz 1999). Biology/ecology: From the hulls of ships docking in ports. Vector(s): Fouling. Comments: Carlton (2009) reviewed the history of this species, which was described as new from the British Isles: however, Guinot and MacPherson (1987) could find no significant differences between it and the South American *P. perlatus* (Poeppig, 1836). Ng et al. (2008) retain it as a distinct species.

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# The Alien Crustaceans in the Mediterranean Sea: An Historical Review

**Bella S. Galil**

**Abstract** One hundred and six alien marine crustacean species have been recorded in the Mediterranean Sea, and many have now established viable populations. Examination of the profound ecological impacts of some of the most conspicuous invasive crustaceans underscores their role, among multiple anthropogenic stressors, in altering the infralittoral communities. The native decapod and stomatopod biota of the soft sediments of the upper shelf in the southeastern Levantine Sea has been substituted by species that have entered the Mediterranean through the Suez Canal (Erythrean aliens). The latter form the majority of aliens in the eastern Mediterranean, whereas shipping and mariculture are powerful means of introduction in the Northwestern Mediterranean. Thermophilic species have been introduced for much of the twentieth century, yet few spread outside the Levantine Basin until the 1990s. It is proposed that the rising seawater-surface temperature (SST) will favour the thermophilic aliens reproduction, growth, and survival, and provides them with a distinct advantage over native temperate Mediterranean taxa. It is likely that both processes i.e., rising SST and the influx of thermophilic aliens, have impacted the local fisheries through displacement of commercially important native species by aliens.

**Keywords** Alien • Crustacea • Global warming • Inventory • Management • Mediterranean Sea • Trends

## 1 Introduction

The recognition that crustaceans had been introduced into the Mediterranean from other parts of the world came gradually. Naturalists noted the many fouling species on vessels reporting from distant regions of the world: “it should not be overlooked,

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that those species, as *Balanus tintinnabulum*, *amphitrite*, *improvisus*, and, in a lesser degree, *B. trigonus* and *Tetraclita radiata*, which seem to range over nearly the whole world (excepting the colder seas), are species which are habitually attached to ships, and which could hardly fail to be widely transported" (Darwin 1854). In 1873 the tri-masted *Karikal* arrived at the port of Marseille from India carrying on its hull a "... petite forêt d'êtres vivants était peuplée de Crustacés" (Catta 1876) including *Planes minutus*, *Pachygrapsus transversus* (reported as *P. advena*) and *Plagusia squamosa*, the latter numbering in the hundreds of specimens. But it was the opening of the Suez Canal that focused scientific attention on the movement of marine species. Even before the Suez Canal was fully excavated it was argued that "Le percement de l'isthme de Suez … offrira … une occasion précieuse de constater les phénomènes que doivent amener l'émigration des espèces et le mélange des faunes" (Vaillant 1865). Indeed, Keller, who traveled to Egypt in 1882 and 1886 to seek evidence for the presence of Red Sea and Mediterranean species in the Canal, considered it "... auch als Karawanenstrasse für die thierischen Bewohner beider Meere benutzt" (Keller 1883). Incidentally, the first crustacean recognized straightway as an alien species in the Mediterranean was the swimming crab *Portunus segnis* (as *Neptunus pelagicus*, Fox 1924), offered for sale in the fishmarkets of Port Said, Alexandria and Haifa, which had entered the sea through the Suez Canal; an augury of the Erythrean invasion to come. Yet, 50 years after the opening of the Canal, no comprehensive study had been undertaken as to answer whether "… an exchange of fauna take place between the two oceans by means of this canal? Do the immigrants from the other side flourish on this or die? Has such an immigration caused important changes in the fauna of the eastern basin of the Mediterranean?" (W. Steinitz 1919). Steinitz studied the marine biota of Palestine in 1924 and 1925 and noted 3 decapod crustaceans of Indo-Pacific origin (W. Steinitz 1929). In 1924 'The Cambridge Expedition to the Suez Canal' embarked on an investigation of the "intermingling of the Mediterranean and Red Sea organisms in the Suez Canal" (Gardiner 1924). The expedition was charged with ascertaining "what forms have passed through the Canal zone from the Mediterranean to the Red Sea and vice versa, when they passed through, whether in the prehistoric period, in the times of the earlier or of the present canal, how they passed through, whether by swimming, by drifting, by attachment to ships, or by other means. All these facts lead up to the question why some forms of life can get through the Canal and others cannot, and it is hoped that the expedition will throw light on marine migrations in general, the area being one which can be periodically investigated at small cost" (Gardiner 1924). The material collected during the 3 months long expedition included 12 crustaceans that had traversed the Canal and were collected at its northern terminus, Port Said (Balss 1927; Calman 1927; Omer-Cooper 1927; Schellenberg 1928). The progression of Erythrean crustaceans in the Levant in the early twentieth century was noted in the inventories of the Levantine biota (Gruvel 1928, 1929, 1930a, b, 1931; Monod 1930, 1931, 1932). Additional records resulted from the survey of the fishery grounds near Alexandria (Broch 1935; Balss 1936; Steuer 1938) and were considered "a welcome contribution to our knowledge of the fauna of that basin in which we find particularly interesting biological conditions on account of … the communication with the Red Sea by the Suez Canal" (Balss 1936). The investigations of the continental shelf biota off Israel by the Sea Fisheries Research Station (SFRS) in 1946–1956 resulted in publications that highlighted the number of the Erythrean taxa that have been established along the coast (Gottlieb 1953; Gottlieb 1960; Ruffo 1959). Based on material collected by the SFRS, Holthuis and Gottlieb (1958) noted 16 species of decapod crustaceans "recent immigrants which arrived in the Mediterranean by way of the Suez Canal". A few years later, eight additional decapod species had been identified as "being of Indo-West Pacific origin" (Lewinsohn and Holthuis 1964). In 1967, a joint program by the Smithsonian Institution, the Hebrew University of Jerusalem, and the SFRS was established to investigate the spread of the Erythrean biota in the Levant (Israel, Cyprus, Rhodes) and its impact on the native biota. At the end of the third year, with some 5,300 samples collected and partially sorted and identified, H. Steinitz (1970) published "A comprehensive list of immigrant animals": of the 140 Erythrean and Indo-Pacific species known to have crossed the Suez Canal into the Mediterranean, 30 were decapod crustaceans. In his pioneering work Holthuis (1961) listed 8 alien decapods off the Mediterranean coast of Turkey. By 1981, when Kocataşpublished his "Liste préliminaire et répartition des crustacés décapodes des eaux turques", 18 had been recorded. By then, it was widely perceived that the littoral and sublittoral biota of the Levantine basin has been undergoing a rapid and profound change (Por 1978). Galil and Lewinsohn (1981) noted that the shallow benthic communities along the Mediterranean coast of Israel had no known parallel outside the Levant because of the great number of Erythrean aliens. Over the past 3 decades records have accumulated on the spread, biology and impact of Erythrean crustaceans along Levantine coast, yet no concerted, targeted effort had been undertaken to survey the entire basin for the presence and abundance of the Erythrean species, and most of the records stem from serendipitous finds.

While Erythrean aliens were pouring into the Levantine basin, alien shellfish and their "associates" were introduced into bays and lagoons along the European coast of the Mediterranean. Though records of shipping and mariculture introduced alien crustaceans kept appearing in the scientific literature, their number and impact were considered negligible and thus they "…have not been the subject of inventories as representative as those of lessepsian migrants" (Zibrowius 1994). The rapid spread and conspicuous impacts of a pair of invasive chlorophytes (Meinesz et al. 2002; Verlaque et al. 2004), have helped raise awareness of the raging problem of alien species in the Mediterranean. The European Commission Environmental Programme and the Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée (CIESM) organized a workshop on "Introduced species in European coastal waters" (Boudouresque et al. 1994), that was followed by CIESM research workshops on "Ship-transported alien species in the Mediterranean and Black Sea" and on the "Impact of mariculture on Mediterranean coastal ecosystems" in 2002 and 2007 respectively (www.ciesm.org). The first comprehensive inventory of alien decapod and stomatopod crustaceans in the Mediterranean was electronically published in 2002 (www.ciesm.org/atlas).

## 2 Materials and Methods

An alien species is here defined as one that will have been intentionally or unintentionally spread by human activities outside its natural range, as documented in scientific publications (Occhipinti-Ambrogi and Galil 2004), i.e., a species lacking geographic contiguity with its native range, associated with invasion vectors or pathways (e.g., associated with shellfish culture, occurring in ship fouling or ballast water, present in the Suez Canal), or a species new to science belonging to a taxonomic group restricted to a different biogeographic province. Records of "Lusitanian" and "Mauritanian" species collected in the Mediterranean are not considered aliens but vagrants, or previously unrecorded rare species. In the Mediterranean Sea extensive biological surveys were conducted in the twentieth century, allowing a reasonable measure of confidence in separating the alien from the native biota.

Since the likelihood of encountering a stray specimen of an alien species is diminishingly small, most recorded aliens are considered as 'established' species that have self-maintaining populations of some duration in the Mediterranean Sea. It is recognized that some alien species may fail to maintain populations over time and thus a single record dating back several decades may be considered an ephemeral occurrence.

The date of the introduction of the *inoculum* is significant for the study of the patterns and processes of invasion, but is extremely difficult to ascertain for unintentional or undocumented intentional introductions. As research efforts vary greatly along the coasts of the Mediterranean, and even the better studied locales suffer temporal and taxonomical lacunae, the author of the present study accepts that the date of collection may be years behind the actual date of introduction, and that identification and publication may lag behind collection.

With the exception of documented intentional introductions (i.e., aquaculture), only rarely are the means and route of introduction of an alien species known from direct evidence. Mostly they are deduced from the biology and ecology (if known) of the species, the habitats and locales it occupies in both the native and introduced range, and its pattern of dispersal (if known), i.e., for a fouling species frequently recorded from ports, shipping is assumed to be the most probable vector. Inference from one case of introduction of a species to another may be fraught with uncertainty as pathways may differ between regions and between primary and secondary introductions. The mode of introduction is listed for the cases it is known from direct evidence (e.g., scraped off a fouled vessel), or associated with a vector e.g., found in or adjacent to ports (vessels), shellfish-farms (aquaculture), or "stepping stones" records from along the coasts of the Levant (canal).

## 3 Results

One hundred and six crustacean species are listed in the present work as alien in the Mediterranean Sea (Table 1). All are littoral and sublittoral and most are benthic or demersal species (or their parasites). Since the shallow coastal zone, and especially the benthos, has been extensively studied, and is more accessible, the chances that

**Table 1** List of alien crustaceans in the Mediterranean Sea, their native range, presumed means of introduction, and the date of collection (or publication) of the first record in each country

| Species | Author | Order | Native Range | Introduction | Eg | IL | Lb,Sy | Cy | Tr | Gr | EAdr | It | Fr | Sp | Al,Mr | LTM[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acartia centrura* | Giesbrecht, 1889 | Calanoida | Indian Ocean | Canals | | 1968 | | | | | | | | | | |
| *Acartia tonsa* | Dana, 1848 | Calanoida | Pantropical | Vessels | | | | | 2001 | | | 1986 | 1966 | | | |
| *Actumnus globulus* | Heller, 1861 | Decapoda | Indian Ocean | Vessels | | | | | | | | 1978 | | | | |
| *Alpheus audouini* | Coutiere, 1905 | Decapoda | Indo Pacific | Canals | 1924 | 1951 | | | 2002 | | | | | | | |
| *Alpheus inopinatus* | Holthuis & Gottlieb, 1958 | Decapoda | Indian Ocean | Canals | 1933 | 1951 | 2006 | | <1969 | | | | | | | <1956 |
| *Alpheus migrans* | Lewinsohn & Holthuis, 1978 | Decapoda | Red Sea | Canals | 1975 | 1977 | | | 1994 | | | | | | | |
| *Alpheus rapacida* | de Man, 1908 | Decapoda | Indo Pacific | Canals | | 1960 | | | <1981 | <2005 | | | | | | |
| *Anilocra pilchardi* | Bariche & Trilles, 2006 | Isopoda | Indo Pacific | Canals | | | 2004 | | | | | | | | | 2009 |
| *Ashtoret lunaris* | (Forsskål, 1775) | Decapoda | Indo Pacific | Canals | | 1987 | | | | | | | | | | |
| *Atergatis roseus* | (Rüppell, 1830) | Decapoda | Indo Pacific | Canals | | 1961 | 1975 | | 1987 | | | | | | | |
| *Balanus improvisus* | (Darwin 1854) | Sessilia | Atlantic NW | Vessels | | | | | | | | 1977 | | | | |
| *Balanus reticulatus* | Utinomi, 1967 | Sessilia | Pantropical | Vessels | | 2003 | | | | | | | 1977 | | | |
| *Balanus trigonus* | (Darwin, 1854) | Sessilia | Pantropical | Vessels | | | | | | | 1968 | | | | | |
| *Bemlos leptocheirus* | Walker, 1909 | Amphipoda | Indian Ocean | Vessels | <1998 | | | | | | | | | | | |
| *Calanopia media* | Gurney, 1927 | Calanoida | Indian Ocean | Canals | | 1965 | 1969 | | | | | | | | | |
| *Calanopia minor* | Scott, 1902 | Calanoida | Indo Pacific | Canals | | | | | 1998 | | | | | | | |
| *Calappa hepatica* | Linnaeus, 1758 | Decapoda | Indo Pacific | Canals | | | | | <2003 | | | | | | | |
| *Calappa pelii* | Herklots, 1851 | Decapoda | Atlantic E | Vessels | | | | | | | | <1996 | | 1991 | | |
| *Callinectes danae* | Smith, 1869 | Decapoda | Atlantic W | Vessels | | | | | | | | 1981 | | | | |
| *Callinectes sapidus* | Rathbun, 1896 | Decapoda | Atlantic W | Vessels | <1963 | <1955 | <1965 | <1986 | 1959 | <1959 | 2004 | 1949 | <1962 | <2005 | | 1972 |
| *Caprella scaura* | Templeton, 1836 | Amphipoda | Indo Pacific | Vessels | | | | | | <2006 | | 1994 | | 2005 | | 2009 |
| *Carupa tenuipes* | Dana, 1851 | Decapoda | Indo Pacific | Canals | | 2002 | | | 1996 | 2009 | | | | | | |
| *Charybdis feriata* | (Linnaeus, 1758) | Decapoda | Indo Pacific | Vessels | | | | | | | | | | 2004 | | |
| *Charybdis helleri* | (A. Milne Edwards, 1867) | Decapoda | Indo Pacific | Canals | 1933 | 1924 | 1964 | <1999 | <1981 | 2004 | | | | | | |
| *Charybdis japonica* | (A. Milne-Edwards, 1861) | Decapoda | Indo Pacific | Vessels | | | | | | | | 2006 | | | | |

(continued)

**Table 1** (continued)

| Species | Author | Order | Native Range | Introduction | Eg | IL | Lb,Sy | Cy | Tr | Gr | EAdr | It | Fr | Sp | Al,Mr | LTM[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Charybdis longicollis* | Leene, 1938 | Decapoda | Indian Ocean | Canals | 1969 | 1961 | 1965 | <1986 | 1954 | 1996 | | | | | | |
| *Charybdis lucifera* | (Fabricius, 1798) | Decapoda | Indo Pacific | Vessels | | | | | | | | 2006 | | | | |
| *Clavellisa ilishae* | Pillai, 1962 | Siphonostomatoida | Indo Pacific | Canals | 2008 | | | | | | | | | | | |
| *Clorida albolitura* | Ahyong & naiyanetr, 2009 | Stomatopoda | Indo Pacific | Canals | | 2006 | | | 2009 | | | | | | | |
| *Coleusia signata* | Paulson, 1875 | Decapoda | Indo Pacific | Canals | 1969 | 1953 | 1977 | | <1981 | 2005 | | | | | | |
| *Cristapseudes omercooperi* | (Larwood, 1954) | Tanaidacea | Indian Ocean N | Canals | 2008 | 2005 | | | | | | | | | | |
| *Ctenocalanus citer* | Bowman & Heron, 1971 | Calanoida | Subcosmopolitan | Vessels | | | | | 1998 | | | | | | | |
| *Cymothoa indica* | Schioedte et Meinert, 1884 | Isopoda | Indo Pacific | Canals | | | 2004 | | | | | | | | | |
| *Daira perlata* | (Herbst, 1790) | Decapoda | Indo Pacific | Canals | | | | | 1988 | | | | | | | |
| *Dorippe quadridens* | Fabricius, 1793 | Decapoda | Indo Pacific | Canals | | 2004 | | | | | | | | | | |
| *Dromia spinirostris* | Miers, 1881 | Decapoda | Atlantic E | Vessels | | | | | | | | 1969 | | | | |
| *Dyspanopeus sayi* | (Smith, 1869) | Decapoda | Atlantic NW | Aquaculture; Vessels | | | | | | | | 1992 | | | | |
| *Elasmopus pectenicrus* | (Bate, 1862) | Amphipoda | Pantropical | Canals;Vessels | 1924 | <1959 | | | 2005 | | | 1980 | | <2006 | | |
| *Elminius modestus* | Darwin, 1854 | Sessilia | Pacific | Aquaculture | | | | | | | | | 1990 | | | |
| *Eocuma rosae* | Corbera & Galil, 2007 | Cumacea | Red Sea | Canals | | 2005 | | | | | | | | | | |
| *Eriocheir sinensis* | H. Milne Edwards, 1854 | Decapoda | Pacific NW | Canals | | | | | | | | 2005 | 1959 | 2006 | | |
| *Erugosquilla massavensis* | (Kossmann, 1880) | Stomatopoda | Indian Ocean | Canals | 1933 | <1938 | <1961 | 1956 | 1959 | 1991 | | | | | | <2006 |
| *Eucrate crenata* | de Haan, 1835 | Decapoda | Indo Pacific | Canals | 1924 | 1994 | | | 1987 | | | | | | | 1985 |
| *Eurycarcinus integrifrons* | De Man, 1879 | Decapoda | Indian Ocean | Vessels | | | | | 2009 | | | | | | | |
| *Fenneropenaeus merguiensis* | (De Man, 1888) | Decapoda | Indo Pacific | Aquaculture | | | | | 2006 | | | | | | | |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gammaropsis togoensis* | Schellenberg, 1925 | Amphipoda | Cosmopolitan | Canals | | <1979 | | | 2005 | | | | | | |
| *Grapsus granulosus* | H. Milne Edwards, 1853 | Decapoda | Red Sea | Canals; Vessels | | | | | | | | | | | 2006 |
| *Halimede tyche* | (Herbst, 1801) | Decapoda | Indo Pacific | Canals | | 1998 | | | | | | | | | |
| *Hemigrapsus sanguineus* | (de Haan, 1835) | Decapoda | Pacific W | Vessels | | | | | | | 2001 | | | | 2003 |
| *Herbstia nitida* | Manning & Holthuis, 1981 | Decapoda | Atlantic E | Vessels | | | | | | | | <2002 | | | |
| *Heteropanope laevis* | (Dana, 1852) | Decapoda | Indian Ocean | Canals | 1924 | | | | | | | <1957 | | | |
| *Heterosaccus dollfusi* | Boschma, 1960 | Kentrogonida | Red Sea | Canals | | 1992 | | | 1994 | | | | | | |
| *Hyastenus hilgendorfi* | de Man, 1887 | Decapoda | Indo Pacific | Canals | | 1960 | | | | | | | | | |
| *Ixa monodi* | Holthuis & Gottlieb, 1956 | Decapoda | Red Sea | Canals | 1977 | 1977 | 1995 | | 1955 | 1999 | | | | | |
| *Labidocera pavo* | Giesbrecht, 1889 | Calanoida | Indo Pacific | Canals | | | 1969 | | 1999 | | | | | | |
| *Leptochela aculeocaudata* | Paulson, 1875 | Decapoda | Indo Pacific | Canals | 1933 | | | | | | | | | | |
| *Leptochela pugnax* | de Man, 1916 | Decapoda | Indo Pacific | Canals | | 1947 | <1994 | | <1981 | | | | | | |
| *Libinia dubia* | H. Milne Edwards, 1834 | Decapoda | Atlantic W | Vessels | | | | | | | | | | | 1996 |
| *Lucifer hanseni* | Nobili, 1905 | Decapoda | Indo Pacific | Canals | 1924 | | | | | | | | | | |
| *Macrophthalmus graeffei* | A. Milne Edwards, 1873 | Decapoda | Indo Pacific | Canals | | 2002 | | | 1994 | | | | | | |
| *Marsupenaeus japonicus* | (Bate, 1888) | Decapoda | Indo Pacific | Canals; Aquaculture | 1924 | 1946 | <1928 | 1961 | <1930 | 1995 | | 1979 | <1972 | 1970 | |
| *Melicertus hathor* | (Burkenroad, 1959) | Decapoda | Indian Ocean | Canals | | 1997 | | | 2002 | | | | | | |
| *Menaethius monoceros* | (Latreille, 1825) | Decapoda | Indo Pacific | Vessels | | | | | | | | <1978 | | | |
| *Metacalanus acutioperculum* | (Ohtsuka, 1984) | Calanoida | Pacific NW | Vessels | | | | | | | | 1995 | | | |
| *Metapenaeopsis aegyptia* | Galil & Golani, 1990 | Decapoda | Indo Pacific | Canals | | 1987 | | 2004 | 2003 | 1996 | | | | | |

(continued)

**Table 1** (continued)

| Species | Author | Order | Native Range | Introduction | Eg | IL | Lb,Sy | Cy | Tr | Gr | EAdr | It | Fr | Sp | Al,Mr | LTM[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Metapenaeopsis mogiensis consobrina* | (Nobili, 1904) | Decapoda | Indo Pacific | Canals |  | 1996 | 2006 |  | 2003 | 1995 |  |  |  |  |  |  |
| *Metapenaeus affinis* | (H. Milne Edwards, 1837) | Decapoda | Indo W Pacific | Vessels |  |  |  |  | 2008 |  |  |  |  |  |  |  |
| *Metapenaeus monoceros* | (Fabricius, 1798) | Decapoda | Indo Pacific | Canals | 1924 | 1946 | 1975 | 1961 | 1959 |  |  |  |  |  |  | 1994 |
| *Metapenaeus stebbingi* | (Nobili, 1904) | Decapoda | Indian Ocean | Canals | 1924 | 1958 | 1975 |  | <1981 |  |  |  |  |  |  | 2006 |
| *Micippa thalia* | (Herbst, 1803) | Decapoda | Indo Pacific | Canals |  |  | 1993 |  | 1994 |  |  |  |  |  |  |  |
| *Mitrapus oblongus* | (Pillai, 1964) | Siphonostomatoida | Indo Pacific | Canals | 2008 |  |  |  |  |  |  |  |  |  |  |  |
| *Myicola ostreae* | Hoshina & Sugiura, 1953 | Poecilostomatoida | Pacific NW | Aquaculture |  |  |  |  |  |  |  |  | 1979 |  |  |  |
| *Myra subgranulata* | Kossmann, 1877 | Decapoda | Indian Ocean | Canals | 1933 | 1929 | 1976 |  | <1930 | 2004 |  |  |  |  |  |  |
| *Mytilicola orientalis* | Mori, 1935 | Poecilostomatoida | Pacific NW | Aquaculture |  |  |  |  |  |  |  |  | 1979 |  |  |  |
| *Notopus dorsipes* | (Linnaeus, 1758) | Decapoda | Indo Pacific | Canals |  | 1962 |  |  |  |  |  |  |  |  |  |  |
| *Ogyrides mjoebergi* | (Balss, 1921) | Decapoda | Indo Pacific | Canals |  | 1947 |  |  | 2005 |  |  |  |  |  |  |  |
| *Palaemonella rotumana* | (Borradaile, 1898) | Decapoda | Indo Pacific | Canals |  | 1948 |  |  | <1999 |  |  |  |  |  |  |  |
| *Panulirus ornatus* | (Fabricius, 1798) | Decapoda | Indo Pacific | Canals |  | 1988 |  |  |  |  |  |  |  |  |  |  |
| *Paracerceis sculpta* | (Holmes, 1904) | Isopoda | Pantropical | Vessels | <1998 |  |  |  |  |  |  | 1981 |  | 1981 |  | 1978 |
| *Paradella dianae* | Menzies, 1962 | Isopoda | Pacific NE | Vessels | <1991 |  |  |  | 2004 |  |  | 1980 |  |  |  | 2001 |
| *Paralithodes camtschaticus* | (Tilesius, 1815) | Decapoda | Pacific N | Vessels |  |  |  |  |  |  |  | 2008 |  |  |  |  |
| *Parvocalanus elegans* | Andronov, 1972 | Calanoida | Indo Pacific | Canals |  |  |  |  | 1998 |  |  |  |  |  |  |  |
| *Parvocalanus latus* | Andronov, 1972 | Calanoida | Indian Ocean | Canals |  |  |  |  | 1998 |  |  |  |  |  |  |  |
| *Penaeus semisulcatus* | de Haan, 1844 | Decapoda | Indo Pacific | Canals | <1930 | 1951 | <1928 |  | <1930 |  |  |  |  |  |  |  |
| *Percnon gibbesi* | (H. Milne Edwards, 1853) | Decapoda | Pacific E;Atlantic | Vessels |  |  |  |  | 2005 | 2004 |  | 1999 |  | <2000 | 2000 | <2001 |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Periclimenes calmani* | Tattersall, 1921 | Decapoda | Indo Pacific | Canals | 1924 |  |  |  |  |  |  |  |  |  |  |  |
| *Photis lamellifera* | Schellenberg, 1928 | Amphipoda | Indian Ocean | Canals |  | 1951 |  |  |  |  |  |  |  |  |  |  |
| *Pilumnopeus vauquelini* | (Audouin, 1826) | Decapoda | Indian Ocean | Canals | 1924 | 1951 |  | <1963 | <1981 |  |  |  |  |  |  | 2002 |
| *Pilumnus hirsutus* | Stimpson, 1858 | Decapoda | Indo Pacific | Canals | <1936 |  |  |  |  |  |  |  |  |  |  |  |
| *Plagusia squamosa* | (Herbst, 1790) | Decapoda | Indo Pacific | Canals; Vessels |  |  | 1968 |  |  |  |  |  | 1873 |  |  | 2006 |
| *Portunus segnis* | (Forsskål, 1775) | Decapoda | Red Sea | Canals | 1898 | <1924 | <1929 | 1961 | <1928 | 1991 |  | <1966 |  |  |  |  |
| *Pseudocyclops xiphophorus* | Wells, 1967 | Calanoida | Indian Ocean | Vessels |  |  |  |  |  |  |  | <2004 |  |  |  |  |
| *Rhithropanopeus harrisii* | (Gould, 1841) | Decapoda | Atlantic NW | Aquaculture; Vessels |  |  |  |  |  |  |  | 1994 | <2001 |  |  | 2003 |
| *Rimapenaeus similis* | (Smith, 1885) | Decapoda | Atlantic W | Vessels |  |  |  |  |  |  |  |  |  |  |  | 2006 |
| *Scherocumella gurneyi* | (Calman, 1927) | Cumacea | Red Sea | Canals |  | 2005 |  |  |  |  |  |  |  |  |  |  |
| *Scyllarus caparti* | Holthuis, 1952 | Decapoda | Atlantic E | Aquaculture; Vessels |  |  |  |  |  |  |  | 1977 |  |  |  |  |
| *Solenocera crassicornis* | (H. Milne Edwards, 1837) | Decapoda | Indo Pacific | Canals | 1971 |  |  |  |  |  |  |  |  |  |  |  |
| *Sphaeroma walkeri* | Stebbing, 1905 | Isopoda | Indian Ocean | Vessels | 1924 | 1971 |  |  | 1976 |  |  |  | 1977 | 1981 |  | 2003 |
| *Sphaerozius nitidus* | Stimpson, 1858 | Decapoda | Indo Pacific | Canals | 1969 |  |  |  |  |  |  |  |  |  |  |  |
| *Tetraclita rufotincta* | (Pilsbry, 1916) | Sessilia | Indo Pacific | Vessels |  |  |  |  |  |  |  |  |  |  |  | <2007 |
| *Thalamita gloriensis* | Crosnier, 1962 | Decapoda | Indo Pacific | Vessels |  |  |  |  |  |  |  | 1977 |  |  |  |  |
| *Thalamita indistincta* | Apel & Spiridonov, 1998 | Decapoda | Indo Pacific | Canals |  |  | 2002 |  |  |  |  |  |  |  |  |  |
| *Thalamita poissonii* | (Audouin, 1826) | Decapoda | Indo Pacific | Canals |  | 1952 | 1975 | <1978 | 1959 | 1983 |  |  |  |  |  |  |
| *Trachysalambria palaestinensis* | (Steinitz, 1932) | Decapoda | Red Sea | Canals | 1971 | 1924 | <1994 |  | 1968 | 1995 |  |  |  |  |  | 1993 |
| *Urocaridella pulchella* | Yokeş and Galil, 2006a | Decapoda | Indo Pacific | Canals |  |  |  |  | 2003 |  |  |  |  |  |  |  |
| *Zeuxo coralensis* | Sieg, 1980 | Tanaidacea | Indo Pacific | Canals |  |  | 2002 |  |  |  |  |  |  |  |  |  |

Eg. Egypt, IL. Israel, Lb, Sy. Lebanon and Syria, Cy. Cyprus, Tr. Turkey, Gr. Greece, EAdr. Eastern Adriatic countries, It. Italy, Fr. France, Sp. Spain, Al, Mr. Morocco and Algeria, LMT. Tunisia, Malta and Libya

[a] Species described from material collected in the Eastern Mediterranean, but assumed to be of Indo-Pacific origin

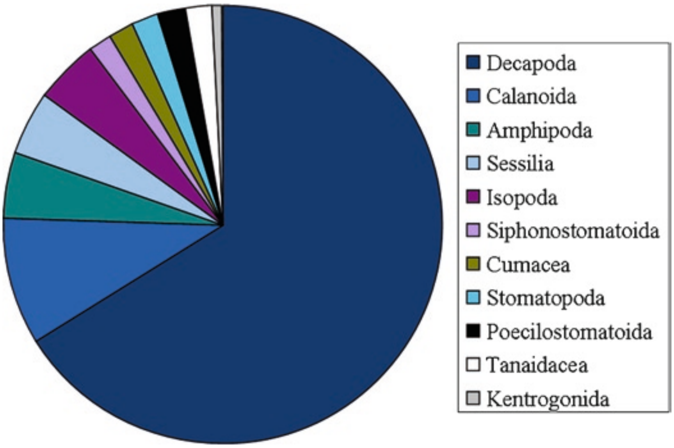

**Fig. 1** Number of alien crustaceans in the Mediterranean Sea, presented by order

new arrivals will be encountered and identified are higher. Also, the species most likely to be introduced by the predominant means of introduction (Suez Canal, vessels, mariculture) are shallow water species.

A taxonomic classification (Fig. 1) shows that the taxa most frequently recorded are Decapoda (70 species), Calanoida (10), Amphipoda, Sessilia and Isopoda (5 species each). The data are presumably most accurate for large and conspicuous species which are easily distinguished from the native biota, and those occurring along a frequently sampled or fished coasts and for which taxonomic expertise is readily available. Data are entirely absent for many of the small-sized crustacean orders such as Cyclopoida, Euphausiacea, Harpacticoida, Mysida.

Nearly four-fifths of the alien crustaceans in the Mediterranean have their native range in tropical seas (Indo-Pacific Ocean, Indian Ocean, Red Sea, pantropical) (Fig. 2). Caution should be taken when using these data, as the actual origin of the Mediterranean populations of a species widely distributed in the Indo-Pacific Ocean may be its populations in the Red Sea, the Indian or Pacific Oceans, or secondary introduction from already established populations in the Mediterranean itself. With a single exception (*Marsupenaeus japonicus*), the source populations of alien crustacean species in the Mediterranean have not been ascertained by molecular means (Tsoi et al. 2007).

As far as can be deduced (see above) the majority of alien crustaceans in the Mediterranean entered through the Suez Canal (64 species) (with 3 more species primarily introduced through the Canal and secondarily transported by vessels), followed by primarily vessel-transported aliens (31 species) (Fig. 3). The means of introduction differ greatly among the orders: whereas of the 70 alien decapods, 17 were introduced by vessels, 4 of 5 Sessilia and 3 of 5 Isopoda have been vessel-transported. Mariculture introductions (intentional and unintentional) are few.

The numbers of alien crustaceans recorded in the Mediterranean each decade over the past century have increased noticeably in the past 2 decades, reflecting probably both an increase in introductions and an interest in their study (Fig. 4).

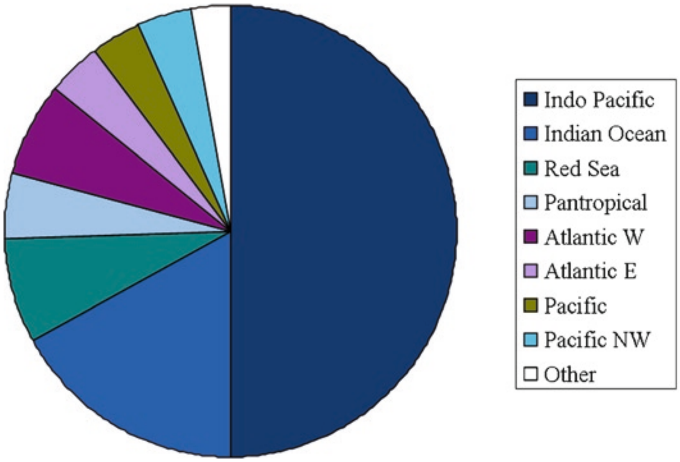

**Fig. 2** Number of alien crustaceans in the Mediterranean Sea, presented by their native range

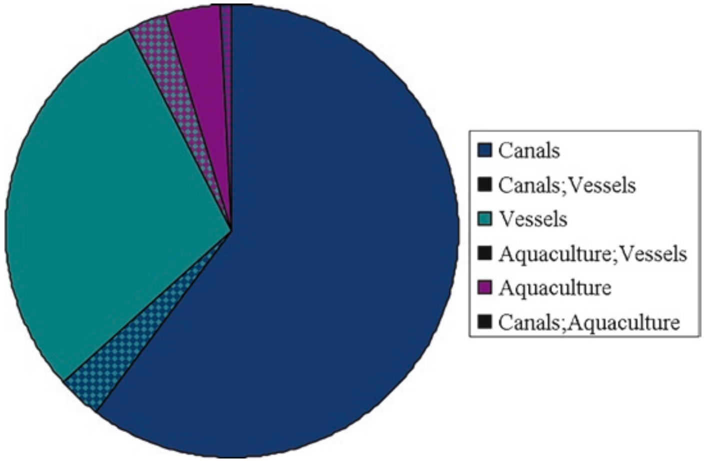

**Fig. 3** Number of alien crustaceans in the Mediterranean Sea, presented by their presumed means of introduction

Few species were recorded in the earliest decades of twentieth century. A spate of records in the 1920s reflects the publication of the results of 'The Cambridge Expedition to the Suez Canal' (see above). The 'Nasser Plan' in the 1950s doubled the Suez Canal's width and increased its navigable depth (Galil 2006b), further eroded the 'salinity barrier' of the Bitter Lakes, which allowed the introduction of increasing numbers of crustaceans. The smaller number of introductions in 1970s and 1980s may have been due to the physical barriers inserted in the Suez Canal and removed following the Egyptian-Israeli accord. The increasing role of the Mediterranean as a hub of international commercial shipping since the 1950 is reflected in the increasing number of vessel-transported aliens: 3 of 11 in the 1960s,

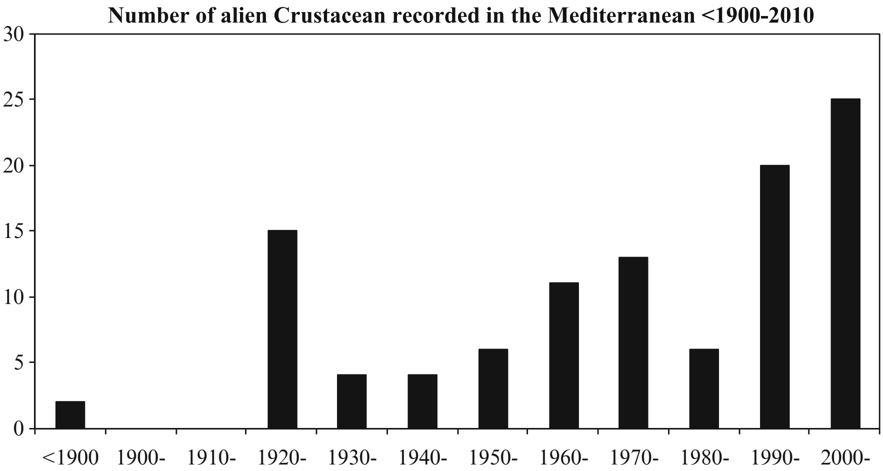

**Fig. 4** Number of alien crustaceans recorded each decade in the Mediterranean Sea, 1900–2010, presented by their presumed means of introduction

6 of 12 in the 1970s, 7 of 20 in the 1990s, and 11 of 25 alien crustaceans in the past decade. The rather sharp decline in the number of vessel-introduced crustacean records in the 1980s may be due to the closure of the Suez Canal and the impact of the Arab Oil Embargo on oil shipping and international trade that limited the number of vessels transiting the Mediterranean.

A comparison of the crustacean alien species recorded along the Mediterranean coasts of Spain and France, and an equivalent length of coast in the Levant (Port Said, Egypt to Marmaris, Turkey), shows marked differences in their numbers, origin and means of introduction (Fig. 5). There are more than four times as many alien crustaceans along the Levantine coast (78) as in the westernmost Mediterranean (16). The majority of alien crustaceans in the easternmost Mediterranean entered through the Suez Canal, whereas vessels, and mariculture are the main means of introduction in the western Mediterranean. Nearly 80% of the Levantine aliens originate in the tropical Indo-Pacific and Indian Ocean, but only 30% of the western Mediterranean aliens.

# 4 Discussion

## 4.1 *Environmental Impact*

With few exceptions, the ecological impacts of alien species on the native Mediterranean biota are poorly known (Zibrowius 1992; Boudouresque 2004). Little is known about the kaleidoscopic inter-relationships of native and alien biota in the Mediterranean Sea, hindering thorough evaluation and direct tests of competition leading to niche limitation, displacement or extirpation. The documented instances of sudden concurrent changes in abundance, where populations of native Mediterranean

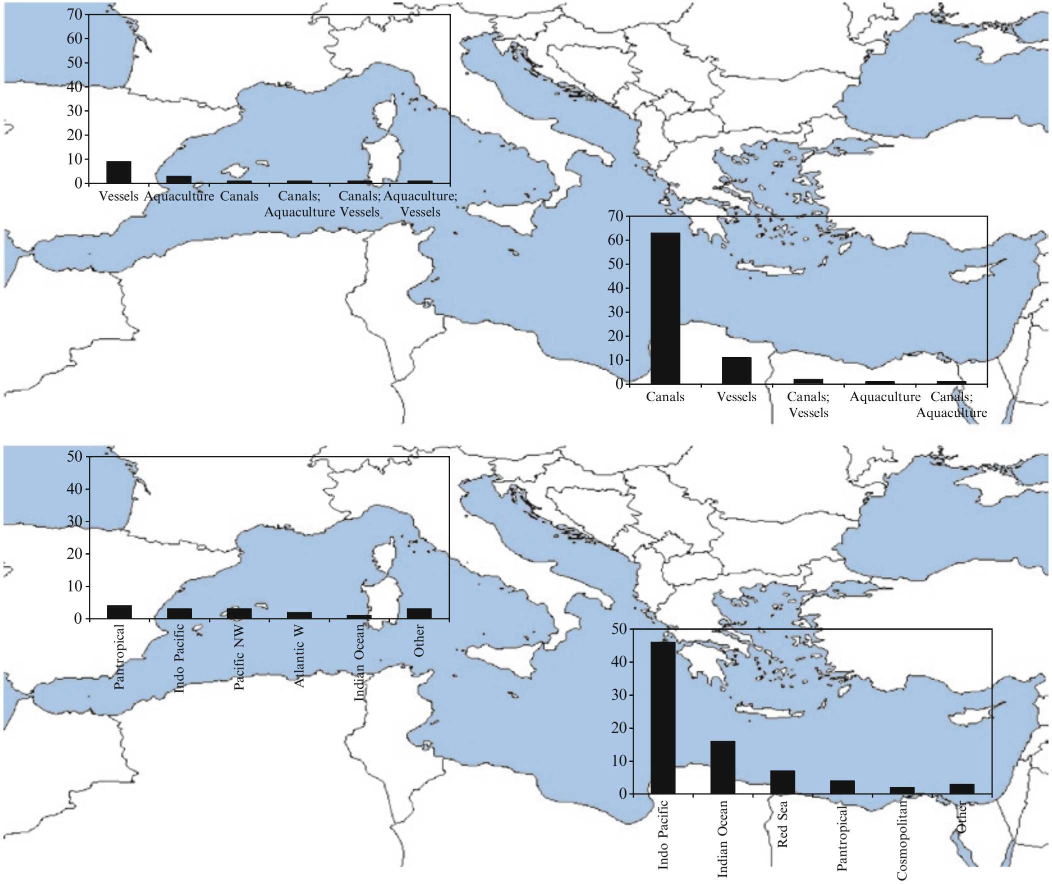

**Fig. 5** Number of alien crustaceans in the easternmost (Egypt to Turkey) and westernmost (Spain and France) Mediterranean Sea, presented by their native range and presumed means of introduction

species appear to have been wholly outcompeted or partially displaced from their habitat space following the introduction and increase in the alien populations, could be part of a profound anthropogenic alteration of the marine ecosystem through habitat destruction, pollution, and rising Mediterranean sea-water temperature. At present, with little or no experimental evidence, it is all but impossible to disentangle potential confounding factors in evaluation impacts of many (if not most) invasions. Still, a handful of invasive crustaceans have drawn the attention of scientists, for their conspicuous impacts on the native biota attributed to them.

The native penaeid prawn, *Melicertus kerathurus*, was commonly caught by trawlers along the Israeli coastal shelf on sandy or sandy mud bottoms, and supported a commercial fishery throughout the 1950s (Holthuis and Gottlieb 1958). It has since nearly disappeared, and its habitat overrun by the Erythrean penaeid prawns. Similarly, off the Turkish Mediterranean coast, Geldiay and Kocatas (1972) reported that *M. kerathurus* has been replaced by alien penaeids in fisheries catches, indeed, it no longer appears in the catch lists of the penaeid targeted bottom trawl fishery in Mersin Bay (Duruer et al. 2008). Udekem d'Acoz C d' (1999) reported that *M. japonicus* "has almost evicted the native *P. kerathurus* from the easternmost part of the Mediterranean". The presence of *M. monoceros* and *Rimapenaeus similis* in the Gulf of Gabes, Tunisia, has raised concerns over the fate of the local *M. kerathurus* fisheries (Chaouachi et al. 1998; Ben Hadj Hamida-Ben Abdallah et al. 2010). The Erythrean snapping shrimps *Alpheus inopinatus*, and *A. audouini*, are more common in the south-eastern Levantine rocky littoral than the native *A. dentipes,* and the Erythrean *A. rapacida*, is much more common than the native *A. glaber* on the muddy bottoms (Lewinsohn and Galil 1982; Galil 1986).

The Erythrean mantis shrimp, *Erugosquilla massavensis*, thrives along the Levantine coast, from Libya to Crete, and is common at depths of 20–40 m. The formerly abundant native Spottail mantis shrimp (*Squilla mantis*) that is fished commercially in shallow waters elsewhere in the Mediterranean "… has been displaced by the [Erythrean] mantis shrimp *E. massavensis* along the Levantine coast of Turkey" (Özcan et al. 2008). Off the Israeli coast the alien mantis shrimp has displaced the native one into deeper waters (between 60 and 90 m). Lewinsohn and Manning (1980) questioned "whether temperature, bottom type, or pressure from *O. massavensis*, or a combination of these is responsible for its depth distribution".

The plagusiid crab *Percnon gibbesi* is the most invasive crustacean to enter the Mediterranean: it has expanded rapidly across the sea, establishing large populations in anthropogenically impacted areas such as ports, as well as in natural habitats, within a short time of its arrival. The crab was first collected in the Mediterranean Sea in 1999 from the Balearic Islands and Sicily and its adjacent islands (Relini et al. 2000; Garcia and Reviriego 2000; Mori and Vacchi 2002). Later reports documented its dispersal northwards along the Tyrrhenian coast of Italy, along the Ionian coast of Calabria, eastwards to Greece and Turkey and southwards to Libya (Pipitone et al. 2001; Mori and Vacchi 2002; Cannicci et al. 2004; Deudero et al. 2005; Cannicci et al. 2006; Yokeş and Galil 2006a; Elkrwe et al. 2008). Despite its extensive spread and establishment success, no substantial environmental impacts have been reported even where its large populations dominate the intertidal (Deudero et al. 2005). But, that said, there are no qualitative, quantitative or experimental studies done anywhere on any potential ecological or biological changes that may have occurred after the arrival of *Percnon*.

An examination of the data of alien crustaceans in the Mediterranean does not yet support the belief that a widely spread alien species is "... more likely to affect multiple native species over large fractions of their respective ranges and drive some of them to extinction" (Ricciardi and Cohen 2007). Of the ten most widely spread species (recorded in six or more peri-Mediterranean countries), all but one present in the sea since the middle of the previous century, negative environmental impacts have been reported for three (*M. japonicus*, *M. monoceros*, *E. massavensis*). This present study emphasizes again that for most species there are simply no data of any sort on their impact, and the lack of study is often confused with the lack of impact. While invasions driving natives "to extinction", is not yet known to have occurred in the Mediterranean biota, the data do support Ricciardi and Cohen's (2007) contention that invasions will impact multiple native species. Of the nearly 1,300 specimens of decapod and stomatopod crustaceans collected by benthic trawl off the central Israeli coast at depth of 37 m, in May 2008, only two specimens were native Mediterranean species (*Goneplax rhomboides* and *Pontocaris cataphracta*) the rest of the sample consisted of Erythrean aliens: *Alpheus rapacida*, *Charybdis longicollis*, *Ixa monodi*, *Metapenaeus monoceros*, *Metapenaeopsis aegyptia*, *Myra subgranulata*, *Erugosquilla massavensis.* The haul taken at the exact same place in October 2008 consisted solely of Erythrean aliens: *A. rapacida*, *C. longicollis*, *Dorippe quadridens*, *Marsupenaeus japonicus M. monoceros*, *M. aegyptia*, *M. subgranulata*, *Penaeus semisulcatus*, *Portunus segnis*, *Trachysalambria palaestinensis*, *Clorida albolitura* and *E. massavensis.* The native decapod and stomatopod biota of the upper shelf soft sediments in the southeastern Levantine Sea has been substituted by Erythrean aliens.

Absence of natural enemies, be it competitors, predators, pathogens, or parasites, is one of the explanations given for the success of alien biota (Torchin et al. 2003), but some alien crustacean parasites have been spectacularly successful in their new habitat. The Levantine populations of the Erythrean swimming crab *C. longicollis* had been parasitized in the early 1990s by the sacculinid rhizocephalan, *Heterosaccus dollfusi* (Galil and Lützen 1995). In its second decade in the Mediterranean, the population of *H. dollfusi* seems stable: despite the high prevalence of the parasite and its injurious impact on the host reproduction, there is no noticeable reduction in the host population (Innocenti and Galil 2007, 2011). The Erythrean sacculinid had not been detected in any of the other portunid crabs, alien or native, inhabiting the Levantine sublittoral, including the congeneric *C. helleri*. However, two Erythrean alien parasitic copepods, *Mitrapus oblongus* and *Clavellisa ilishae* have been described from the fishing grounds of Alexandria, Egypt, infecting a native Mediterranean host, *Sardinella aurita* (El Rashidy and Boxshall 2009). Clearly, the substitution of a native fish for the original Erythrean host may impact on their Levantine populations.

## 4.2 Economical Impact

Some Erythrean aliens have been exploited commercially almost as soon as they entered the Suez Canal. In the early twentieth century the Suez Canal Company sought to exploit the biota in the Canal, and hired Gruvel, a fisheries expert who was familiar with the Levantine fisheries, as 'chef de mission' to identify possible commercially advantageous products. Gruvel realized the economic importance of the alien-based fisheries to the Levant "… pour les marches palestiniens et syriens, un appoint non négligeable et particulièrement intéressant, par consequent, pour l'ensemble des populations de ces deux Pays" (1936). In his report, Contribution à l'étude de la bionomie générale et de l'exploitation de la faune du Canal de Suez, Gruvel (1936) identified decapods of economic interest. Disappointed by the lack of "les grands Crustacés comestibles, comme Langoustes, Homards et Scyllares", Gruvel conceded that the crustaceans were "de beaucoup le plus intéressant".

An early Erythrean invader, the swimming crab *Portunus segnis*, was recorded from Port Said in 1898, where it soon became abundant, and by the early 1900s it was offered in the markets of Port Said, Alexandria and Haifa (Fox 1924; Calman 1927). Gruvel reported that the crab was "véritablement importante au point de vue économique" and praised it: "On sert ces crabes, bouillis ou farcis, dans à peu près tous les restaurants. Farcis et cuits au four, ils constituent un mets excellent et, en général, très apprécié" (Gruvel, 1936). The crab is abundant along the entire Egyptian Mediterranean coast, as well as along the Levantine coasts up to the Gulf of Iskenderun in southeastern Turkey. During the 1930s and 1940s the Arab fishermen of Haifa and Acre sold annually 20 tons of the species "most common in the open sea, particularly in the Acre Bay region" (Perlmutter 1956). To this day *P. segnis* is "considered … as one of the most valuable fishery resources" along the Mediterranean coast of Egypt, with catches in Bardawil lagoon alone increasing from 492 to 1,322 tons between 1995 and 2005 (Abdel Razek et al. 2006). It is popular in the Levant: "Au Liban, comme dans d'autres secteurs du Levant ... A une importance commerciale. Ce crabe ... est régulièrment et en quantité present dans les étalages des marchands " (Zibrowius and Bitar 2003). The crab is offered in many restaurants catering to the thriving tourist industry along the southern Turkish coast (Özcan et al. 2005).

The Erythrean prawns, and especially the tiger prawn, *Marsupenaeus japonicus*, have been greatly valued from the start: "C'est le plus magnifique exemplaire de crevette que nous ayons jamais rencontré, au cours de nos différentes recherches dans les Colonies." (Gruvel 1936). The species *M. japonicas, Metapenaeus monoceros* and *Penaeus semisulcatus*, are highly prized and are considered a boon to the Levantine fisheries. They compose most of the prawn catch off the Mediterranean coast of Egypt and in the Nile delta lagoons (Dowidar and Ramadan 1976; Bishara 1976). Off the Sinai coast, the proceeds from the penaeids' landings accounted for over a third of the total trawl catch taken at depths of up to 25 m; where the dominant species were *P. semisulcatus* and *M. japonicus* (Tom 1979). Off the Israeli coast *M. japonicus* and *P. semisulcatus* are highly prized and beginning in the 1970s a shrimp fishery developed. A small fleet of coastal “mini” trawlers has specialized in shrimping, bringing in a quarter of the total trawl catch volume and a third of the trawl gross income (Pisanty and Grofit 1991; Snovsky and Shapiro 1999). Off Southeastern Turkey, *P. semisulcatus*, *M. japonicus* and *Metapenaeus stebbingi* dominate the penaeid fisheries (Kumlu et al. 1999; Can et al. 2004; Duruer et al. 2008).

Gruvel (1936) noticed the Erythrean mantis shrimp *Erugosquilla massavensis* (as *Squilla massavensis*) in the local markets: “On la trouve communément, sur les marchés de Suez et d’Ismaïlia”. The species is abundant today along the Levantine coast, from Libya to Crete, but though of potential commercial importance, it has been only rarely offered on the markets of Cyprus, Israel and Turkey.

The Erythrean swimming crab, *Charybdis longicollis* is abundant and ubiquitous on sandy mud sediments at 25–60 m (occasionally to 135 m), where it may form as much as 70% of the benthic biomass (Galil 1986, 1992; Özcan et al. 2005). It is a common trawl by-catch “… considered a true pest, the fishermen complain that their nets are filled with these crabs” (Lewinsohn and Holthuis 1964). Worse, its aggressive behaviour coupled with powerful pincers interferes with sorting the catch and hampers the cleaning of the nets.

## *4.3 Establishment Success and Dispersal*

The fraction of alien species that spread following establishment is considered one of the measures of invasion success. The ‘tens rule’ postulates that one in ten of species “accidentally brought into the country” appear in the wild; one in ten of those become established; “and that one in ten of those established become a pest”, ‘pest’ defined as an alien with “high population density” (Williamson and Fitter 1996). Recently the term was reinterpreted to mean an invasive alien i.e., a species that spreads beyond its point of entry, though “not necessarily harmful” (Jeschke and Strayer 2005). Our ignorance of the ‘selector’ dynamics of the pathways involved precludes analysis of the first step in the ‘tens rule’. The scant and patchy surveys of the Levantine marine biota mean that chances of recording an ephemeral alien are rather low, barring analysis of the second step as well. However, the records are robust enough to examine what proportion of the established aliens are abundant and/or expand beyond their point of entry. To test this, the data were arranged in invasion sequence, excluding species known from a single record. Aware of the time lag between the introduction and population build up, invasion records of less than a decade were eliminated as well. The number of established crustaceans in the Mediterranean corrected for time-lag (restricting it to records before 1999) is 47; of these, 35 were recorded from three or more countries, and fully 18 alien crustaceans were recorded from five or more countries. At present this is true mostly for Erythrean aliens (with the exception of *Callinectes sapidus* and *Percnon gibbesi*) and mostly confined to the Levant. This fact highlights the particular condition of Levant biota. These figures manifest an invasion success of over 70% for crustaceans – far in excess of the ‘tens rule’, signifying that once established in the Mediterranean, they are highly likely to turn invasive. All but one of the widely-spread crustaceans entered the Mediterranean at least half a century ago through the ‘corridor’ created by the excavation of the Suez Canal. Of the three major invasion pathways, the Suez Canal is exceptional in providing the opportunity for substantial propagule pressure through continuous dispersal events of large inoculums, simultaneous movement of coevolved species, and long-duration dispersal to an environmentally compatible region.

There is no doubt that the location of the opening of the Suez Canal at the southeastern Levantine Sea directly influenced the outcome of the Erythrean Invasion. The higher SST (Nykjaer 2009), the prevailing counter clockwise coast-hugging currents and the wide shallow shelf influenced establishment success. Already in the 1950s it was suggested that the establishment of Erythrean aliens was related to a rise in SST: the sudden escalation in the populations of certain Erythrean aliens had been attributed to a rise of 1–1.5°C during the winter of 1955 (Ben Yami 1955; Chervinsky 1959; Ben Yami and Glaser 1974). Ben Tuvia (1966) contended that the thermophilic aliens require summer temperatures high enough for the reproductive processes and development of eggs, and minimum winter temperatures above their lethal limits to establish populations in the Mediterranean.

For much of the twentieth century Erythrean aliens were confined within the Levantine Sea, but the 1990s saw the breaching of the barrier. A shift in the source of the Eastern Mediterranean Deep Water occurred from the Adriatic to the southern Aegean Sea (Theocharis et al. 1992). The increased outflow of the newly formed, denser water through the Cretan Arc Straits into the eastern Mediterranean has been compensated by inflowing Levantine surface and intermediate water (Wu et al. 2000). The more extensive inflow of the warm-water Asia Minor Current along the Anatolian coastline, carrying westwards warm, salty water from the Levant, was positively correlated with the initiation of a significant increase in the number of Erythrean aliens along the Southwestern Anatolian and the southern Aegean coasts: only one of the 13 Erythrean decapod and stomatopod species now known in the Aegean Sea, *Thalamita poissonii*, was collected before 1991 (Dounas and Steudel 1994; Kevrekidis et al. 1998; Galil and Kevrekidis 2002; Yokeş and Galil 2004, 2006b; Pancucci-Papadopoulou et al. 2005, 2009; Corsini-Foka et al. 2004, 2006; Corsini-Foka and Kondilatos 2006; Kirimitzoglou et al. 2006; Özcan et al. 2008).

The last decades of the twentieth century saw pronounced thermal fluctuations and a significant increase in the average SST in the Mediterranean, and a growing concern over the “tropicalization” of its biota by the marked rise in the number, abundance and geographic expansion of thermophilic alien species, with the Levantine Sea acting as a reservoir (Galil 2009). Persistence of the warming trend would likely have a significant influence on the establishment and distribution of thermophilic species. Rising seawater temperature may change the pool of species which could establish themselves in the Mediterranean, enable the warm stenothermal species (native and alien) to expand beyond their present distributions, and may impact a suite of population characteristics (reproduction, survival) that determines interspecific interactions. Therefore, the dominance and prevalence patterns of both native and alien species may change, and provide the newly arriving thermophilic aliens with a distinct advantage over some of the native (and indeed perhaps pre-existing alien) Mediterranean biota.

## 4.4 *Management and Mismanagement*

Marine bioinvasions pose a challenge to the environmental ethics and policies of the peri-Mediterranean countries. As signatories to the Convention on Biological Diversity these countries are required to prevent the introduction of, control or eradicate alien species, which threaten ecosystems, habitats or species (Article 8(h)), and ensure that the environmental consequences of their policies that are likely to have significant adverse effects on biological diversity are taken into account (Article 14.1) (www.cbd.int/convention).

The massive "official" and "unofficial" importation of commercially important species for mariculture in the 1970s and 1980s coincided with the appearance of mariculture-introduced alien crustaceans. Segments of the industry may still resort to illegal importations: a bilaterally ablated female banana prawn, *Fenneropenaeus merguiensis*, was collected in the Bay of Iskenderun, Turkey, in late 2006 (Özcan et al. 2006). Because eyestalk ablation is commonly used in aquaculture to induce maturation of gonads, there is no doubt that specimen escaped or was released from a nearby aquaculture facility. Neither the Turkish authorities nor the Food and Agriculture Organization of the United Nations have been aware of the importation of that species. Legislation on introduction and transfers of alien species exists in some peri-Mediterranean countries, though in practice the administrative measures to control the deliberate importation of aliens and limit their dispersal are still rudimentary and seldom enforced. Nevertheless, the impact of the voluntary guidelines espoused in the successive versions of the International Council for the Exploration of the Sea (ICES) code of practice on the introductions and transfers of marine organisms (ICES-International Council for the Exploration of the Sea 2005), and the realization by the industry that the imported species may arrive with their complement of parasites and pathogens, led to institution of "zoosanitary precautions" that have already contributed to a reduction in the numbers of mariculture-associated alien species in the past decade.

A great number of alien crustaceans in the Mediterranean Sea have been vessel-introduced and vessel-dispersed (Galil 2006a). The International Maritime Organization (IMO) sponsored an international instrument to regulate ballast water management since ballast-mediated bioinvasions have caused significant economic and environmental losses. The International Convention on the Control and Management of Ships Ballast Water and Sediments, a potentially significant environmental achievement, was adopted by a Diplomatic Conference in 2004. To enter into force the convention should be ratified by 30 States, representing 35% of world merchant shipping tonnage. At present only 22 contracting states have signed on (www.imo.org), but assuming that the Convention will be ratified and implemented, the number of ballast-transported aliens may be reduced. However, hull fouling, long acknowledged as a dominant vector of transport of alien biota, is on the increase as a result of the implementation of another IMO Convention: the International Convention on the Control of Harmful Anti-Fouling Systems on Ships, which calls for a global prohibition on the application of organotin compounds, entered into force on 17.9.2008 (www.imo.org). Alternative ship coating recently introduced as a substitute to tributyltin-based antifouling paints "may not be as effective, possibly resulting in more species being transported" (Gollasch 2006). The increasing role of the Mediterranean as a hub of international commercial shipping (Dobler 2002) has been reflected in the growing number of vessel-introduced aliens in the past 20 years (Fig. 6) (Zagami et al. 2005; Abello and Hispano 2006; Zaouali et al. 2007a, b; Aydin et al. 2009; Ben Hadj Hamida-Ben Abdallah et al. 2010; Faccia et al. 2009). Unless ballast- and hull transport are strictly controlled, shipping-mediated introductions of alien species are set to continue apace.

The Suez Canal, the most prolific invasion pathway (Fig. 6), is undergoing yet further enlargement in order to maintain its market share. The current expansion will increase its depth to allow passage of vessels up to draught of 66 ft (20.1 m) by the end of 2009, and already the Suez Canal Authority is conducting feasibility studies with the aim to increase the draught to 72 ft (21.9 m) to allow passage of fully loaded VLCC and ULCC tanker classes (www.suezcanal.gov.eg). Tragically, no management option to reduce the influx of alien biota through the Suez Canal has even been discussed.

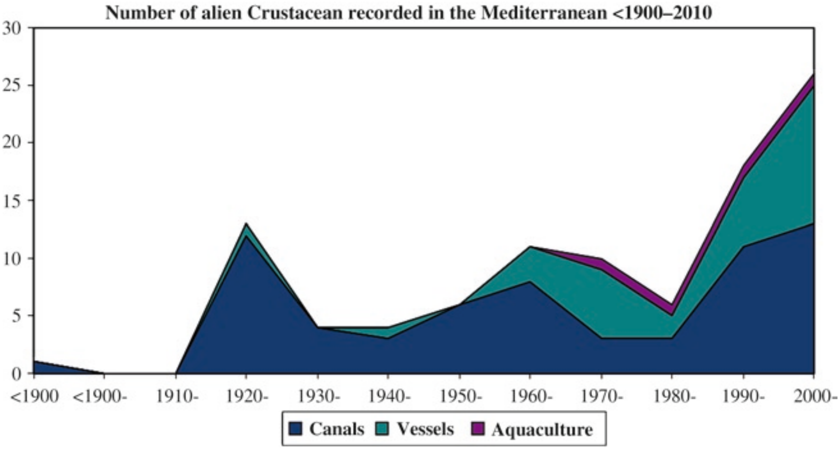

**Fig. 6** Number of alien crustaceans recorded each decade in the Mediterranean Sea, 1900–2010

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# An Incoming Flood on a Cryptic Stage: Understanding Alien Crustacean Invasions in Southeast Asia

**Darren C.J. Yeo, James T. Carlton, Serena L.M. Teo, and Peter K.L. Ng**

**Abstract** Despite being both an ancient center of trade and now one of the world's busiest ports, few marine invasions, and no alien marine or estuarine crustaceans, are reported from Singapore. This study proposes that a large number of alien species in Singapore specifically, and in Southeast Asia in general, may be overlooked, due to our lack of historical knowledge of the biota. This is illustrated with a list of 127 species of crabs that occur in Singapore but whose aboriginal distributions could have been impacted by human-mediated vectors. Biofouling, ballast water, and the ornamental and live seafood trade now serve to bring in a large number of alien species into Singapore: these, in turn, set the stage for future invasions and management concerns.

**Keywords** Marine Invasions • Alien species • Cryptogenic species • Crustacea • Cirripedia • Stomatopoda • Decapoda • Brachyura • Southeast Asia • Singapore

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# 1 Introduction

Singapore, located 137 km north of the equator at the confluence of the South China Sea and the Indian Ocean, has been an international maritime port of call since at least the 1300s (Miksic 2000), with Atlantic Ocean trading links commencing by the 1500s, and with steadily increased globalization since the early 1800s following the establishment of Singapore as a British colonial port in trade with the South Asia and East/Southeast Asia. As such, Singapore serves as a potential model system for assessing both the extent of marine invasions in tropical ecosystems and, after more than 700 years of ships transporting alien species from distant waters, the deeper antiquity of invasions as well.

Three additional modern-day factors make Singapore stand out in any discussion on the scale of historical and modern invasions of alien marine animals and plants. First, Singapore is one of the world's busiest ports, situated along one of the most heavily used international shipping routes in the world (between Europe and the Far East via the Suez Canal and the Straits of Malacca), and experiences a huge volume of shipping traffic (Kaluza et al. 2010). Second, it is a regional and international center of the freshwater and marine ornamental or aquarium trade, controlling some 22% of the world trade. Third, it is a hub for the live seafood trade, with large quantities of live marine animals brought into the island from all over the world for sale or re-export.

Despite the prevalence of these biological invasion pathways, and the antiquity of the harbour, there have been few reports of established alien marine invertebrates, let alone crustaceans, in Singapore. The challenges inherent in a study of invasions in tropical Southeast Asia are examined, and viable approaches to address these are suggested.

# 2 Pathways of Introduction

## *2.1 Shipping*

Shipping is the major carriage for 80–90% of international trade by volume (IMO 2006; UNCTAD 2009). With the advent of modern fleets, more and larger ships are travelling faster than ever before, and in recent years the number of reports of introductions of organisms to new environments through shipping vectors has increased (Ruiz et al. 2000). Singapore has long been one of the busiest ports in the world. In 2008 alone, more than 1.6 billion gross tonnage (GT) passed through Singapore's port with 131,695 vessel arrivals (MPA 2009). In addition, Singapore is a major global player in the offshore oil industry, involved in the construction and/or conversion, maintenance, repair, and retrofitting of floating oil platforms and floating production storage offloading systems. The large volume of shipping that passes through Singapore brings with it great quantities of ballast water discharge and fouling (on the hull, rudder, propeller shaft, sea chests, and other parts of vessels), both of which are recognized as among the most important pathways of marine species introduction (Fofonoff et al. 2003; Minchin and Gollasch 2003).

## 2.2 *Ornamental and Live Seafood Trade*

The ornamental and live seafood trades (involving local retail as well as import-export) are well-known pathways whereby alien marine species are entering Singapore. Local production including fisheries and aquaculture accounts for some of the marine ornamental and seafood (including crustaceans) supply. But on the whole, Singapore is much more reliant on imports than on local production for both local consumption and for export. In 2008, local production accounted for 5,141 tonnes of fish supply in Singapore compared to imports of 157,627 tonnes of fish, and exports of 44,853 tonnes (Singapore Department of Statistics 2009). The ornamental fish trade is a major industry with exports amounting close to 100 million Singapore Dollars (SGD) in 2008 (Ministry of National Development 2009). Most of the ornamentals are freshwater species, which are cultured locally or imported, whereas the ornamental marine species are almost exclusively imported wild-caught species. The live seafood trade is another growing source for potential alien marine crustacean introductions. Like ornamental species, live seafood species can also be imported into Singapore for either local consumption or re-export.

## 2.3 *Limited Knowledge of Marine Invasions in Southeast Asia*

While knowledge of the larger-bodied marine invertebrates, especially molluscs and decapods, in Southeast Asia in general, and in the South China Sea and Singapore in particular, is reasonably good, it is important to emphasize that our understanding is largely limited to taxonomic knowledge, and does not extend or translate to knowledge of faunistic history. The lack of historical baseline surveys and biodiversity records for the South China Sea combined with the poorly resolved systematics of many tropical groups (especially amongst smaller-bodied taxa) are major impediments to defining the biogeographic status of many species. Carlton (1996) defined cryptogenic species as species that are not demonstrably native or introduced, due to lack of historical records in a given area. It is therefore plausible that as a result of the increased efforts in conducting marine surveys in the South China Sea in recent years (e.g., see SH Tan and Ng 2007; SH Tan and Low 2009), many new species that have been found may in fact be cryptogenic, since they may represent either discoveries of native species or recent introductions by human-mediated means. In addition, a great many historical invasions may simply be overlooked. Shallow-water tropical marine species, especially those with wide distributions that logically would pose challenges to maintaining the gene flow needed to inhibit allopatric speciation, may in fact reflect the deep history of anthropogenic introduction via ships, centuries before the advent of marine biology (Carlton 2009). Indeed, Singapore is likely to have been along the maritime Silk Road for over 2,000 years, where Chinese merchant shipping sailed between southeastern Chinese ports in the Western Pacific Ocean and ports in the Red Sea and the Western Indian Ocean (see Jiao 2010).

## *2.4 Known Marine Introductions in Singapore*

At least two bivalve molluscs and one serpulid polychaete are known to have invaded Singapore waters. As numerous successful invasions of marine and estuarine crustaceans, including copepods, isopods, amphipods, barnacles, decapods, and many other groups, are known to have occurred around the world, it is suggested that crustacean invasions have occurred in Singapore but for the reasons noted above have been overlooked.

Thus, the Caribbean mussel *Mytilopsis sallei* (Dreissenidae) is believed to have been introduced into Singapore waters 20–30 years ago through ballast water discharge and/or fouling, and is now the dominant fouling species in artificial tidal monsoon canals (KS Tan and Morton 2006). This species is related to the invasive Ponto-Caspian zebra mussel *Dreissena polymorpha* which has invaded North America and caused major impacts there (Ricciardi et al. 1998; Connelly et al. 2007). The longer term spread and impact of *M. sallei* in natural ecosystems in Singapore is unclear since it is concentrated in artificial and polluted habitats where native biodiversity is generally low, and no major socio-economic impacts have been detected as yet (KS Tan and Morton 2006). But they may prove to be a serious competitor for native filter-feeding fouling bivalves and potentially impact coastal developments in the future. Other invasions in Singapore include the estuarine bivalve *Brachidontes striatulus* (see Morton and KS Tan 2006) and a tubeworm, *Hydroides sanctaecrucis,* which is established in Singapore fouling communities (Lewis et al. 2006). In addition, other groups recently reported fouling communities on artificial floating structures that also likely include introduced species, including marine algae (Lee et al. 2009) and sponges (Lim et al. 2009).

## *2.5 The Potential for Modern-Day Invasions*

Given the hundreds of thousands of vessels that pass through Singapore every year (MPA 2009), and the connectedness of the port, the risk of marine invasion would appear to be high, with potentially hundreds of alien crustaceans species arriving annually into the port in vessel fouling and in ballast water (Ruiz et al. 2000; Gollasch 2002; Minchin and Gollasch 2003; Drake and Lodge 2004, 2007a, b; Mineur et al. 2007; Davidson et al. 2009; Kaluza et al. 2010).

In fact, 13 species of alien brachyurans and one species of alien stomatopod were found in the fouling community of one semisubmersible oil platform being cleaned in dry dock in Singapore, which accounted for more than 50% of the number of species and more than 70% of the number of individuals in the collection (Table 1; Yeo et al. 2009). All 14 species were new records for Singapore waters (Yeo et al. 2009) and among these were two known invasive crab species:

**Table 1** Alien marine cirriped, decapod, and stomatopod species detected as biofouling on shipping in Singapore waters (Yeo et al. 2009; SLMT unpubl. data)

| Species | Family | Probable origin |
|---|---|---|
| **Cirripedia** | | |
| *Amphibalanus variegatus* | Balanidae | Indo-West Pacific |
| *Megabalanus coccopoma* | Balanidae | Eastern Pacific |
| **Decapoda: Brachyura** | | |
| gen. n., sp. n. | Acidopsidae | Unknown |
| *Glabropilumnus seminudus* | Pilumnidae | East Indo-West Pacific |
| *Pilumnus* cf. *schellenbergi* | Pilumnidae | Australia and New Guinea |
| *Pilumnus spinicarpus* | Pilumnidae | Australia |
| *Carupa tenuipes* | Portunidae | Indo-West Pacific |
| *Thalamitoides quadridens* | Portunidae | Indo-West Pacific: oceanic |
| *Chlorodiella laevissima* | Xanthidae | Indo-West Pacific: oceanic |
| *Liomera cinctimana* | Xanthidae | Indo-Pacific |
| *Liomera monticulosa* | Xanthidae | Indo-West Pacific: oceanic |
| *Liomera rubra* | Xanthidae | Indo-West Pacific: oceanic |
| *Liomera tristis* | Xanthidae | Indo-West Pacific: oceanic |
| *Platypodia tomentosa* | Xanthidae | West Pacific |
| *Pseudoliomera helleri* | Xanthidae | Indo-West Pacific: oceanic |
| *Xanthias punctatus* | Xanthidae | Indo-west central Pacific |
| **Stomatopoda** | | |
| *Gonodactylaceus randalli* | Gonodactylidae | Oceanic western Pacific and northern Australia |

*Glabropilumnus seminudus* (Pilumnidae), which is established in Hawai'i, where it is believed to have been introduced through fouling on barges arriving from Guam in the 1950s (Edmondson 1952; Coles et al. 1997; Carlton and Eldredge 2009), and *Carupa tenuipes* (Portunidae), distributed throughout the Indo-Pacific, and now an established species in the Eastern Mediterranean, having entered from the Red Sea via the Suez Canal, and spread to coastal areas off Israel, Turkey, and Greece (Galil 2004; Pancucci-Papadopoulou et al. 2009). *Carupa tenuipes* has also been reported in sea chests of ships arriving in New Zealand (Coutts and Dodgshun 2007).

Two sessile alien balanid barnacles, *Megabalanus coccopoma* and *Amphibalanus variegatus* have also been observed in the fouling communities on vessels coming into the Port of Singapore. No populations of any of these species are yet known, but since some of these species have a history of introduction elsewhere, it would not be surprising that, as more detailed surveys are carried out in the future, some will be shown to be established in Singapore waters.

A growing number of alien marine crustacean species is also being encountered in the ornamental and live seafood trades. Marine decapod crustacean species that are commonly imported into Singapore in the ornamental and live seafood trades are listed in Tables 2 and 3, respectively. These records are based on personal observations and unpublished data because the relevant government agencies do not keep detailed records of imported ornamental and live seafood crustacean species. The main differences between species that are imported through the two trades are in the size and range of native habitats of the organisms. For obvious reasons, edible crustaceans are on average many times larger than ornamental species. They also

**Table 2** Common marine decapod and stomatopod species brought into Singapore in the ornamental trade (DCJY, PKLN, pers. obs.). Most of the species are from the Philippines, Indonesia, and Sri Lanka, with some imports from Malaysia, India and Taiwan

| Species | Family |
|---|---|
| **Decapoda: Caridea** | |
| *Alpheus soror* | Alpheidae |
| *Alpheus* spp. | Alpheidae |
| *Lysmata amboinensis* | Hippolytidae |
| *Lysmata* spp. | Hippolytidae |
| *Thor amboinensis* | Hippolytidae |
| *Periclimenes* spp. | Palaemonidae |
| **Decapoda: Stenopodidea** | |
| *Stenopus hispidus* | Stenopodidae |
| **Decapoda: Astacidea** | |
| *Enoplometopus* spp. | Enoplometopidae |
| **Decapoda: Anomura** | |
| *Coenobita* spp. | Coenobitidae |
| *Calcinus* spp. | Paguridae |
| *Diogenes* spp. | Paguridae |
| **Decapoda: Brachyura** | |
| *Lybia tesselata* | Xanthidae |
| **Stomatopoda** | |
| *Odontodactylus scyllarus* | Odontodactyllidae |

**Table 3** Major marine decapod and stomatopod species brought into Singapore as live seafood (PKLN, unpublished data)

| Species | Family | Import source | Wild-caught or aquaculture |
|---|---|---|---|
| **Decapoda: Penaeoidia** | | | |
| *Fenneropenaeus merguiensis* | Penaeidae | Southeast Asia | Wild-caught and Aquaculture |
| *Litopenaeus vannamei* | Penaeidae | Southeast Asia | Aquaculture (stocks from Eastern Pacific) |
| *Penaeus monodon* | Penaeidae | Southeast Asia | Wild-caught and Aquaculture |
| **Decapoda: Astacidea** | | | |
| *Homarus americanus* | Nephropidae | Northeastern America | Wild-caught |
| **Decapoda: Achelata** | | | |
| *Jasus edwardsii* | Palinuridae | Australia | Wild-caught |
| *Panulirus femoristriga* | Palinuridae | Southeast Asia | Wild-caught |
| *Panulirus homarus* | Palinuridae | Southeast Asia | Wild-caught |
| *Panulirus longipes* | Palinuridae | Southeast Asia | Wild-caught |
| *Panulirus ornatus* | Palinuridae | Southeast Asia | Wild-caught |
| *Parribacus antarcticus* | Scyllaridae | Southeast Asia | Wild-caught |
| *Scyllarides haanii* | Scyllaridae | China, Philippines | Wild-caught |
| **Decapoda: Anomura** | | | |
| *Paralithodes camtschaticus* | Lithodidae | Japan, Russia | Wild-caught |

(continued)

**Table 3** (continued)

| Species | Family | Import source | Wild-caught or aquaculture |
|---|---|---|---|
| **Decapoda: Brachyura** | | | |
| *Cancer pagurus* | Cancridae | Scotland | Wild-caught |
| *Metacarcinus magister* | Cancridae | Northeast Pacific (Canada) | Wild-caught |
| *Chaceon albus* | Geryonidae | Western Australia | Wild-caught |
| *Pseudocarcinus gigas* | Menippidae | Western Australia | Wild-caught |
| *Hypothalassia acerba* | Hypothalassiidae | Western Australia | Wild-caught |
| *Scylla paramamosain* | Portunidae | Southeast Asia, southern China | Wild-caught |
| *Scylla olivacea* | Portunidae | Southeast Asia | Wild-caught and Aquaculture |
| *Scylla serrata* | Portunidae | Southeast Asia, Australia | Wild-caught |
| *Scylla tranquebarica* | Portunidae | Southeast Asia | Wild-caught |
| *Eriocheir hepuensis* | Varunidae | China | Wild-caught and Aquaculture |
| *Eriocheir sinensis* | Varunidae | China | Wild-caught and Aquaculture |
| **Stomatopoda** | | | |
| *Harpiosquilla raphidea* | Squillidae | Malaysia, Indonesia | Wild-caught |
| *Lysiosquilla maculata* | Lysiosquillidae | Sabah, Indonesia | Wild-caught |

generally come from a wider latitudinal range, i.e., from warm tropical waters to cold high latitude waters, whereas ornamental crustaceans tend to be mostly tropical or subtropical species (PN, DCJY, pers. obs.).

Besides the threat of imported species being introduced into Singapore waters, the growing seafood and ornamental trades pose an even more insidious problem: that of "hitchhikers" on these commercial species. Much of the seafood entering Singapore, for example, carry a host of endobiotic (which may be symbiotic or commensal) and epibiotic organisms. Most obvious are the barnacles. Such hitchhikers are common not only on crustaceans but also on live oysters (*Crassostrea* spp.) shipped mainly from Australia and New Zealand. These may include crustacean parasites, copepods and bopyrid isopods. The live seafood and ornamental fish trade also presents a means for crustacean fish parasites of all groups to be introduced into Singapore waters and infect native crustaceans.

## 3 A Cryptic Past, and a Way Ahead

The low incidence of marine invasive species in Singapore mirrors a pattern observed in major tropical ports in northern Australia, which were found to have fewer marine invasions compared to temperate ports in southern Australia and New Zealand (Hutchings et al. 2002). A hypothesis proposed to explain this pattern is that tropical communities with high connectivity, high biodiversity and low endemicity are less susceptible to invasions than more isolated temperate communities with lower biodiversity and higher endemicity (Hilliard and Raaymakers 1997; Hilliard et al. 1997 cited in Hutchings et al. 2002). Furthermore, the apparent lack of marine introductions also reflects insufficient documentation or lack of historical baseline data (Hutchings et al. 2002), the same data that are urgently needed to improve the poor knowledge of marine introductions in Singapore (BC Tan and KS Tan 2003; Yeo and Chia 2010) and in Southeast Asian seas.

As a starting point for further investigations, a list of brachyuran species that are regarded as possible cryptogenic species in Singapore (Table 4) is provided. These are species that have wide and continuous (and ostensibly natural) distributions; in addition, most are taxonomically poorly known. Twenty-seven species are highlighted as especially strong candidates as cryptogenic species based on our knowledge of their distribution and biology. These can be divided into three groups based on their occurrence/habitat preference for various fouling communities: (1) species associated with mangrove-type communities and typically occurring together with fouling barnacles, bryozoans, and mussels; (2) species associated with coral reef-type communities and typically occurring syntopically with fouling soft corals, sponges, and ascidians; and (3) species linked with fouling communities in artificial/modified marine/estuarine environments such as ports (including hard structures such as rocks, concrete areas, breakwaters and the associated mud/sand substrata of the subtidal areas).

The likely cryptogenic species candidates stand out by possessing characters such as being potentially easily transported by shipping (as fouling or in ballast water), hardiness (in being able to tolerate variations and extremes in temperature and salinity), and having the potential propensity for being relatively easily introduced and established. Add to that the ship traffic over the centuries and the connectedness of the Port of Singapore (Kaluza et al. 2010), and one could justifiably ask if any of these species are possibly native.

Several approaches can now be taken to elucidate the historical biogeography of these and many other potential cryptogenic species. Fine-grained resolution of the distribution of many species may reveal the existence of distant, isolated populations that may be the result of ship-borne transport. For example, a great many Indo-Pacific species are often said to occur from the “Red Sea to Japan,” or “Japan to Singapore,” when in fact only a portion of the range of many species may be continuous, and the end-point locations may be thousands of kilometres away from the next nearest population. Molecular studies can be of substantial value in revealing not only geographic tracks of dispersal but centers of origin, based in part upon epicenters of high haplotype richness. Careful analysis of the temporal patterns of collections, using both museum resources and recent surveys, may reveal a sequential pattern of discovery not related to the distribution of biologists or the dispersal of taxonomists.

Promulgating similar lists of cryptogenic amphipods, isopods, tanaids, cumaceans, mysids, copepods, ostracods, barnacles, shrimp, and other groups may clarify the scale of historical alteration of Southeast Asian marine biodiversity.

**Table 4** Potential cryptogenic brachyuran species occurring in Singapore waters (present study)

| Species | Family | Remarks |
|---|---|---|
| *Baruna trigranulum*[a] | Camptandriidae | Mangrove-type communities; found on barnacle clumps and fouling communities |
| *Paracleistostoma depressum*[a] | Camptandriidae | Artificial/modified environments; a small species that lives in subtidal mud in human-impacted areas |
| *Calappa hepatica* | Calappidae | |
| *Carpilius maculatus* | Carpiliidae | |
| *Neodorippe callida* | Dorippidae | |
| *Dromidiopsis indica* | Dromiidae | |
| *Lauridromia dehaani* | Dromiidae | |
| *Lewindromia unidentata*[a] | Dromiidae | Coral reef-type communities; associated with sponges; small-sized and can be found in fouling on artificial platforms |
| *Hyastenus aries* | Epialtidae | |
| *Hyastenus diacanthus*[a] | Epialtidae | Coral reef-type communities; in fouling communities in reef edge areas |
| *Hyastenus hilgendorfi* | Epialtidae | |
| *Hyastenus sebae* | Epialtidae | |
| *Hyastenus whitei* | Epialtidae | |
| *Menaethius monoceros*[a] | Epialtidae | Coral reef-type communities; lives among algae and clumps of sponges; easily transported |
| *Phalangipus longipes* | Epialtidae | |
| *Tylocarcinus styx* | Epialtidae | |
| *Eucrate alcocki* | Euryplacidae | |
| *Eucrate tripunctata* | Euryplacidae | |
| *Trissoplax dentata*[a] | Euryplacidae | Artificial/modified environments; a small species that lives in subtidal mud in human-impacted areas |
| *Galene bispinosa* | Galenidae | |
| *Halimede ochtodes* | Galenidae | |
| *Grapsus albolineatus*[a] | Grapsidae | Artificial/modified environments; in reef-edge areas with rocks in human-impacted areas |
| *Metopograpsus frontalis*[a] | Grapsidae | Artificial/modified environments; frequents vertical structures, e.g., jetty pilings |
| *Metopograpsus latifrons* | Grapsidae | |
| *Metopograpsus messor* | Grapsidae | |
| *Metopograpsus oceanicus* | Grapsidae | |
| *Pachygrapsus transversus*[a] | Grapsidae | Coral reef-type communities and artificial/modified environments; common on fouling areas; small |
| *Pachygrapsus minutus*[a] | Grapsidae | Coral reef-type communities and artificial/modified environments; common on fouling areas; small |
| *Halicarcinus coralicola* | Hymenosomatidae | |

(continued)

**Table 4** (continued)

| Species | Family | Remarks |
|---|---|---|
| *Trigonoplax unguiformis* | Hymenosomatidae | |
| *Achaeus lacertosus* | Inachidae | |
| *Camposcia retusa* | Inachidae | |
| *Oncinopus araneus* | Inachidae | |
| *Arcania gracilis* | Leucosiidae | |
| *Ixa cylindrus* | Leucosiidae | |
| *Lyphira heterograna* | Leucosiidae | |
| *Seulocia vittata* | Leucosiidae | |
| *Micippa philyra*[a] | Majidae | Coral reef-type communities; in reef areas; common on reef-associated fouling platforms |
| *Micippa platipes*[a] | Majidae | Coral reef-type communities; in reef areas; common on reef-associated fouling platforms |
| *Schizophrys aspera*[a] | Majidae | Coral reef-type communities; in reef areas; common on reef-associated fouling platforms |
| *Schizophrys dama*[a] | Majidae | Coral reef-type communities; in reef areas; common on reef-associated fouling platforms |
| *Tiarinia gracilis* | Majidae | |
| *Ashtoret lunaris* | Matutidae | |
| *Matuta planipes* | Matutidae | |
| *Matuta victor* | Matutidae | |
| *Menippe rumphii*[a] | Menippidae | Artificial/modified environments; commonly under rocks in open areas and on man-made structures like breakwaters |
| *Myomenippe hardwickii*[a] | Menippidae | Mangrove-type communities; a hardy species with young commonly associated with mussel and barnacle clumps |
| *Sphaerozius nitidus*[a] | Menippidae | Coral reef-type communities and artificial/modified environments; also found on barnacles and fouling clumps in oceanic waters |
| *Ocypode ceratophthalmus* | Ocypodidae | |
| *Ocypode cordimanus* | Ocypodidae | |
| *Epixanthus frontalis*[a] | Oziidae | Artificial/modified environments; commonly under rocks in open areas and on man-made structures like breakwaters |
| *Ozius guttatus*[a] | Oziidae | Artificial/modified environments; commonly under rocks in open areas and on man-made structures like breakwaters |
| *Ozius rugulosus* | Oziidae | |
| *Ozius tuberculosus* | Oziidae | |
| *Daldorfia horrida* | Parthenopidae | |
| *Cryptopodia fornicata* | Parthenopidae | |
| *Enoplolambrus carenatus* | Parthenopidae | |

(continued)

**Table 4** (continued)

| Species | Family | Remarks |
|---|---|---|
| *Enoplolambrus pransor* | Parthenopidae | |
| *Parthenope longimanus* | Parthenopidae | |
| *Rhinolambrus contrarius* | Parthenopidae | |
| *Rhinolambrus pelagicus* | Parthenopidae | |
| *Actumnus elegans* | Pilumnidae | |
| *Actumnus squamosus* | Pilumnidae | |
| *Actumnus setifer* | Pilumnidae | |
| *Benthopanope eucratoides*[a] | Pilumnidae | Artificial/modified environments; a small species found in mangrove areas and edges, but common in man-made muddy-rocky areas, e.g., near wharfs |
| *Glabropilumnus laevimanus* | Pilumnidae | |
| *Heteropanope glabra*[a] | Pilumnidae | Artificial/modified environments; a small species found in mangrove areas and edges, but common in man-made muddy-rocky areas, e.g., near wharfs |
| *Pilumnus longicornis*[a] | Pilumnidae | Coral reef-type communities; in reef areas; common on reef-associated fouling platforms |
| *Pilumnus vespertilio* | Pilumnidae | |
| *Rhizopa gracilipes* | Pilumnidae | Artificial/modified environments; found in subtidal muddy areas impacted by man like in ports |
| *Vellumnus labyrinthicus* | Pilumnidae | |
| *Arcotheres coarctatus* | Pinnotheridae | |
| *Plagusia squamosa*[a] | Plagusiidae | Coral reef-type communities and artificial/ modified environments; common on fouling areas |
| *Podophthalmus vigil* | Portunidae | |
| *Charybdis affinis* | Portunidae | |
| *Charybdis anisodon* | Portunidae | |
| *Charybdis feriata* | Portunidae | |
| *Charybdis granulata* | Portunidae | |
| *Charybdis hellerii* | Portunidae | |
| *Charybdis miles* | Portunidae | |
| *Charybdis natator* | Portunidae | |
| *Charybdis truncata* | Portunidae | |
| *Portunus gladiator* | Portunidae | |
| *Portunus hastatoides* | Portunidae | |
| *Portunus pelagicus* | Portunidae | |
| *Portunus sanguinolentus* | Portunidae | |
| *Thalamita admete*[a] | Portunidae | Coral reef-type communities; in reef areas; common on reef-associated fouling platforms |
| *Thalamita crenata* | Portunidae | |
| *Thalamita danae* | Portunidae | |
| *Thalamita picta* | Portunidae | |
| *Thalamita sima* | Portunidae | |

(continued)

**Table 4** (continued)

| Species | Family | Remarks |
|---|---|---|
| *Thalamita spinimana* | Portunidae | |
| *Clistocoeloma merguiense* | Sesarmidae | |
| *Episesarma mederi* | Sesarmidae | |
| *Metasesarma obesum* | Sesarmidae | |
| *Nanosesarma minutum* | Sesarmidae | Mangrove-type communities and artificial/modified environments; small |
| *Parasesarma leptosoma* | Sesarmidae | |
| *Parasesarma plicatum* | Sesarmidae | |
| *Perisesarma eumolpe* | Sesarmidae | |
| *Perisesarma fasciatum* | Sesarmidae | |
| *Pseudosesarma edwardsii* | Sesarmidae | |
| *Selatium brockii* | Sesarmidae | |
| *Tiomanium indicum* | Sesarmidae | |
| *Tanaocheles bidentata* | Tanaochelidae | |
| *Metaplax crenulata* | Varunidae | |
| *Metaplax elegans* | Varunidae | |
| *Thalassograpsus harpax* | Varunidae | |
| *Ptychognathus barbatus* | Varunidae | |
| *Actaea areolata* | Xanthidae | |
| *Actaea savignii* | Xanthidae | |
| *Actaeodes hirsutissimus* | Xanthidae | |
| *Actaeodes mutatus* | Xanthidae | |
| *Atergatis floridus* | Xanthidae | |
| *Atergatis integerrimus* | Xanthidae | |
| *Chlorodiella nigra* | Xanthidae | |
| *Cyclodius ungulatus* | Xanthidae | |
| *Etisus anaglyptus* | Xanthidae | |
| *Etisus dentatus* | Xanthidae | |
| *Etisus laevimanus* | Xanthidae | |
| *Gaillardiellus orientalis* | Xanthidae | |
| *Leptodius exaratus*[a] | Xanthidae | Artificial/modified environments; in reef-edge areas with small rocks in human-impacted areas |
| *Leptodius gracilis* | Xanthidae | |
| *Leptodius sanguineus*[a] | Xanthidae | Artificial/modified environments; in reef-edge areas with small rocks in human-impacted areas |
| *Liomera tristis* | Xanthidae | |
| *Liomera venosa* | Xanthidae | |
| *Paractaea rufopunctata rufopunctata* | Xanthidae | |
| *Pilodius granulatus*[a] | Xanthidae | Artificial/modified environments; in reef-edge areas with small rocks in human-impacted areas |

[a] Particularly strong candidates for cryptogenic species

## 4 Invasion Management and Policy

The globalization of trade has also meant that alien crustaceans now have the means to disperse across international boundaries in unexpected and potentially uncontrollable ways. The nature of free trade also means that the control of these organisms will be extremely difficult. This is especially so for high-value food items such as crabs, lobsters, and shrimp.

Singapore's status as a global hub of shipping and trade, and its location along major shipping routes at the crossroads between biogeographical regions (HTW Tan et al. 2010; Kaluza et al. 2010), makes the country vulnerable as the first point of introduction for invasive species entering the tropical Southeast Asian region (Hutchings et al. 2002), and beyond. Busy ports are vulnerable to stepping stone invasions, whereby organisms may transfer from one vessel to another (Apte et al. 2000; Floerl et al. 2009). This scenario is possibly illustrated by the establishment in New Zealand of the Japanese swimming crab, *Charybdis japonica* (Portunidae), which is native to subtropical to temperate East Asia (Wee and Ng 1995; Smith et al. 2003). It is believed that the species spread first into Southeast Asia, and was from there transported and introduced to New Zealand either through ballast water discharge or fouling (PKLN, unpublished data).

Evidence suggests that as a result of heavy shipping through Southeast Asia, many alien species are entering into tropical Southeast Asia and some have likely become established in ports. While at present there are few examples of marine invasives in tropical Southeast Asia, the evidence suggests that this is an artefact of knowledge rather than an ecological reality. Southeast Asia's seas have an unprecedented high density of ecologically sensitive coastal regions with high biodiversity which overlaps with an area with the highest density of shipping routes in the world. More studies are urgently needed to understand the mechanisms whereby introduced species established in disturbed harbours may become invasive, to prevent environmental impact to the many sensitive ecosystems present in tropical Asia. Understanding of these mechanisms would be especially important for biodiversity conservation, social economics and protection of human health, in face of longer term environmental changes due to rapid coastal urbanization as well as global climate change impacts in the region. Having in place a broader regulatory and legal framework to prevent accidental invasions will be a *sine qua non* of long-term environmental management.

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# Alien Marine Crustaceans of Japan: A Preliminary Assessment

**Wataru Doi, Seiichi Watanabe, and James T. Carlton**

**Abstract** Although invasions may have commenced in the 1500s, our record of invasions of alien marine and estuarine species in Japan begins largely in the 1930s. We expand the previous inventory of 10 alien species to 31 alien and cryptogenic species, underscoring that this, too, may be a striking underestimate. Most of the marine crustacean invasions into Japan have occurred along the Pacific coast; a number of alien crustaceans form abundant populations in urbanized bays near international ports. The specific geographic sources of most invasions are not known; studies have clarified the origins of the barnacle *Balanus glandula* (from America), but hybridization or low genetic divergence has inhibited clarification of the exact source of the crab *Carcinus* and the barnacle *Megabalanus coccopoma.* The biogeographic origins of the alien crustacean fauna in Japan include the North Atlantic and North and South Pacific oceans. We cannot distinguish between ship fouling and ballast water as vectors for most species; this said, it is probable that ship fouling has been a major contributor to the arrival of alien barnacles. No species are yet known to have been introduced solely by ballast water, but this may be an artifact of the lack of collections and identification of potential ballast-only taxa (planktonic copepods, cladocerans, and mysids). Other vectors include importations from China and Korea of shellfish for stocking, crabs for farming, and of live bait; all of these may lead to the introduction of novel genetic stocks and of associated species. There are few studies that have examined the ecological and economic impact of alien crustaceans. The barnacle *Amphibalanus amphitrite* appears to

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be competitively superior to native barnacles and has a negative impact on their densities. Alien crabs inhabit communities established by alien barnacles and mussels (which serve as their prey); these “alien communities” occur, for example, in the inner areas of Tokyo Bay. The European crab *Carcinus* appears to be declining in some regions while the American crab *Pyromaia* is increasing. The economic cost to the power industry, shipping, aquaculture and fisheries for clearing the biofouling associated with alien barnacles and other alien fouling organisms is probably severely underestimated. Although the Invasive Alien Species Act was passed in Japan in 2005, it did not refer to alien marine organisms. Consequently, preventing the introduction of alien marine species into Japan, or their subsequent dispersal along its coastline, is proving difficult to enforce.

## 1 Introduction

Alien marine and brackish-water crustaceans (among many other taxa) presumably first began arriving on the shores, bays and estuaries of Japan in the 1500s and 1600s. After initial contact in 1542, Japanese maritime connections with Europe and South-East Asia were intermittent for the next 75 years. In 1616 Japan began to close its harbours to all foreign countries and a period of isolationism commenced. During the ensuing *sakoku* centuries this incoming tide of alien marine species was presumably much reduced or non-existent until maritime trading with the outside world resumed in the 1850s at the time of the Meiji restoration. Thus while alien crustaceans had arrived and likely established populations by the early 1600s, and then from the 1850s and on, we have little insight into the nature and diversity of invasions prior to the twentieth century. Systematic descriptions of the Japanese fauna, including crustaceans, were begun only towards the end of the *sakoku* period by Kaempfer, Thunberg, and Von Siebold (Holthuis 1967). Our present record of marine alien species in Japan commences largely only in the 1930s, as a result of the absence of sufficient early collections and the lack of trained taxonomists.

Interest in Japanese alien marine and estuarine crustaceans dates back some 60 years when Hiatt (1948) concluded that the North American crab *Pachygrapsus crassipes* had been introduced to Japan. In the 1960s, Kawahara (1963) and Utinomi (1960, 1966) recorded the alien barnacles known from Japanese waters. Arakawa (1980) summarized data concerning marine invertebrate invasions, as did later papers by Otani (2002, 2004, 2009), Iwasaki (2004, 2005, 2006a, b, 2007a, b, 2009), Iwasaki et al. (2004a, b) and Kimura et al. (2004). With few exceptions (Otani 2006, Otani et al., 2007; Iwasaki 2006b) most of these contributions have been in Japanese.

We present here a preliminary re-assessment of the alien marine and brackish-water crustaceans of Japan, in part by expanding our purview to smaller-size taxa (such as copepods and amphipods) and by broadening the arena of potentially cryptogenic species.

While of no small interest in terms of invasion ecology, we do not formally treat here species that are now "naturally" immigrating from southern waters into Japan due to ocean warming. For example, we note that the barnacle *Tetraclita japonica formosana*, found on the Pacific coast of Honshu (southern part of Kii and Boso Peninsula) appears to be a recent arrival from Okinawa, and its presence in Japan may represent a poleward range shift driven by warming (Tsang et al. 2008). Similarly, the portunid crab *Charybdis lucifera*, found along the Pacific coasts of Honshu and Shikoku (from Chiba to Kochi) (Norman et al. 1998; Nabeshima and Fukui 1999), has possibly moved north, dispersed as larvae with the Kuroshio Current, although Nabeshima and Fukui (1999) note that a record of *C. lucifera* in Osaka Bay may be related to shipping.

## 2 A Preliminary Inventory: Established Alien Crustaceans

The establishment of ten alien crustacean species was summarized by Iwasaki et al. (2004b) and Iwasaki (2007a). These included six species of barnacles (*Amphibalanus amphitrite*, *A. eburneus*, *A. improvisus*, *A. zhujiangensis*, *Balanus glandula* and *Megabalanus coccopoma*), three crabs (*Pyromaia tuberculata*, *Carcinus aestuarii* × *C. maenas* hybrids, and *Rhithropanopeus harrisii*), and one isopod (*Paracerceis sculpta*). All were introduced via ship fouling and/or ballast water (Ariyama and Otani 2004; Kado 2006; Otani 2006; Iseda et al. 2007; Yamaguchi 2009).

To these 10 species we add 6 alien and 15 cryptogenic species, in order to begin to illustrate the potential depth and breadth of alien crustacean invasions that have occurred in Japanese waters (Table 1, Fig. 1). We caution that the current assessment should not be taken as a final or accurate census of non-native crustaceans in Japan: Carlton (2009) has reviewed a broad arena of historical, taxonomic, and biogeographical challenges that have lead to a serious underestimation of the diversity of marine and estuarine aliens in most areas of the world.

Most of the marine invasions into Japan have occurred along the Pacific coast (Iwasaki et al. 2004a, b), and are located in the vicinity of major international ports such as Tokyo, Yokohama, Nagoya, Osaka and Kobe. The populations of the crabs *Carcinus aestuarii* × *maenas* and *Pyromaia tuberculata* and the isopod *Paracerceis sculpta* are only found in the inner bays of international megaports such as Tokyo Bay, Ise Bay and Osaka Bay.

*Barnacles* We treat five species of alien barnacles below, under temporal trends. The titan acorn barnacle *Megabalanus coccopoma*, a native of the tropical eastern Pacific, was recently distinguished from the native species *M. rosa* and *M. volcano* using mitochondrial DNA barcoding (Yamaguchi 2009; Yamaguchi et al. 2009). The earliest collection date in Japan is 2000. *Megabalanus coccopoma* was found at Shimoda and Senjoujiki on the Izu Peninsula; at Toushima, Tanabe Bay on the Kii Peninsula, and from the hulls of two ships in dry-docked at Kobe Port, Hyogo and Mizushima Port, Okayama. An additional geographic survey found that

**Table 1** Introduced and cryptogenic marine and estuarine crustaceans of Japan

| Vectors | | Regions | | Date | | Status | |
|---|---|---|---|---|---|---|---|
| SF | Ship fouling | NE | Northeast | NYD | Date not yet determined | I | Introduced |
| SB | Ship boring, including shipworm commensals | NW | Northwest | | | C | Cryptogenic |
| | | E | East | | | | |
| BW | Ballast water | IO/SP | Indo-Pacific / South Pacific | | | | |
| BS | Solid ballast (rocks, sand) | | | | | | |

| Species | Status | First recorded date in Japan | Native to | Vector | Reference |
|---|---|---|---|---|---|
| **Copepoda** | | | | | |
| *Teredicola typica* Wilson, 1942 | I | 1971 | IO/SP | SB | Humes and Turner (1972); Carlton and Eldredge (2009) |
| *Pachypygus gibber* (Thorell, 1859) | I | 1960 | NE Atlantic | SF | Ooishi (1961, 1962, 1963) |
| *Doropygus elegans* Ooishi, 1963 | C | 1962 | NE Atlantic? | SF | Ooishi (1963) |
| **Cirripedia** | | | | | |
| *Amphibalanus amphitrite* (Darwin, 1854) | I | 1933 | IO/SP | SF/BW | Miyazaki (1938, as *Balanus amphitrite communis*, a synonym: Henry and McLaughlin, 1975); Iwasaki et al. (2004b); Iwasaki (2007a) |
| *Amphibalanus eburneus* (Gould, 1841 ) | I | 1950 | NW Atlantic | SF/BW | Iwasaki et al. (2004b); Iwasaki (2007a) |
| *Amphibalanus improvisus* (Darwin, 1854) | I | 1952 | NW Atlantic | SF/BW | Iwasaki et al. (2004b); Iwasaki (2007a) |
| *Amphibalanus zhujiangensis* (Ren, 1989) | I | 1997 | NW Pacific (South China Sea) | SF/BW | Puspasari et al. (2002); Yamaguchi (2009) |
| *Amphibalanus reticulatus* (Utinomi, 1967) | C | 1934 | IO/SP? | SF/BW | Hiro (1938); Utinomi (1949, 1967, 1970); Iwasaki et al. (2004b); Yamaguchi (2009) |

| | | | | | |
|---|---|---|---|---|---|
| *Balanus glandula* Darwin, 1854 | I | 2000 | NE Pacific | SF/BW | Kado (2003); Iwasaki et al. (2004b); Kado (2006); Geller et al. (2008) |
| *Megabalanus coccopoma* (Darwin, 1854) | I | 2000 | Tropical E Pacific | SF/BW | Yamaguchi (2009); Yamaguchi et al. (2009) |
| **Isopoda** | | | | | |
| *Limnoria tripunctata* Menzies, 1951 | C | 1943 | IO/SP? | SB/BW | Shiino (1944, as *L. lignorum*); Menzies (1954) |
| *Limnoria indica* Becker and Kampf, 1958 | C | <1975 | IO/SP? | SB/BW | Kühne (1975); Cookson (1991) |
| *Limnoria multipunctata* Menzies, 1957 | C | <1975 | IO/SP? | SB/BW | Kühne (1976); Cookson (1991) |
| *Paralimnoria andrewsi* (Calman, 1910) | C | 1943 | IO/SP? | SB/BW | Shiino (1944, 1951); Kühne (1976); Carlton and Eldredge (2009) |
| *Paracerceis sculpta* (Holmes, 1904) | I | 1986 | NE Pacific | SF/BW | Ariyama and Otani (2004), who note that *P. japonica* Nunomura, 1998 is this species; Iwasaki (2007a) |
| **Tanaidacea** | | | | | |
| *Sinelobus* "*stanfordi* (Richardson, 1901)" | C | <1938 | Unknown | SF/BW | Miyadi (1938); Nunomura (1995); Saito and Higashi (2000); van Haaren and Soors (2009) |
| **Amphipoda** | | | | | |
| *Monocorophium acherusicum* (Costa, 1857) | I | 1955 | NW Atlantic | SF/BW | Irie (1956); Nagata (1960); Hirayama (1995) |
| *Monocorophium insidiosum* (Crawford, 1937) | I | 1955 | NW Atlantic | SF/BW | Nagata (1960, 1965); Onbe (1966); Hirayama (1984) |
| *Jassa marmorata* Holmes, 1903 | I | NYD (1930s?; see text) | NW Atlantic | SF/BW | Conlan (1990); Sano et al., 2003 |
| *Jassa slatteryi* Conlan, 1990 | I | NYD | NE Pacific | SF/BW | Conlan (1990); Sano et al., 2003 |
| *Ampithoe valida* Smith, 1873 | C | NYD | NW Atlantic? | SF/BW | Bousfield (1973); Chapman (2007); H. Ariyama (pers. comm.) |

(continued)

**Table 1** (continued)

| Species | Status | First recorded date in Japan | Native to | Vector | Reference |
|---|---|---|---|---|---|
| *Melita nitida* Smith, 1873 | C | NYD | NW Atlantic? | SF/BW | Yamato (1987); Jarrett and Bousfield (1996); Faasse and van Moorsel (2003); Chapman (2007) |
| *Leucothoe alata* Barnard, 1959 | C | NYD | Unknown | SF | Chapman (2007) |
| *Leucothoe spinicarpa* Abildgaard, 1789 | C | NYD | Unknown | SF | Chapman (2007) |
| *Platorchestia platensis* Kröyer, 1845 ( = *Orchestia platensis*) | C | 1897 | Atlantic? | BS | Iwasa (1939); Ruffo (1949); Morino (1975, 1978); Spicer and Janas (2006) |
| *Caprella equilibra* Say, 1818 | C | 1890 | Unknown | SF/BW | Mayer (1903); Takeuchi (1999) |
| *Caprella penantis* Leach, 1814 | C | Ca. 1890? | Unknown | SF/BW | Mayer (1903); Takeuchi (1999) |
| *Caprella scaura* Templeton,1836 | C | 1875 | Unknown | SF/BW | Mayer (1890, 1903); Takeuchi (1999); Martinez and Adarraga (2008) |
| **Decapoda** | | | | | |
| *Pyromaia tuberculata* (Lockington, 1877) | I | 1970 | NE Pacific | SF/BW | Iwasaki et al. (2004b); Doi et al. (2009c) |
| *Carcinus aestuarii* Nardo, 1847 × *Carcinus maenas* (Linnaeus, 1758) | I | 1984 | NE Atlantic, Mediterranean | SF/BW | Sakai (1986); Iwasaki et al. (2004b); Darling et al. (2008); Doi et al. (2009c) |
| *Rhithropanopeus harrisii* (Gould, 1841) | I | 2006 | NW Atlantic | SF/BW | Iseda et al. (2007); Iwasaki (2007b); Doi et al. (2009c) |

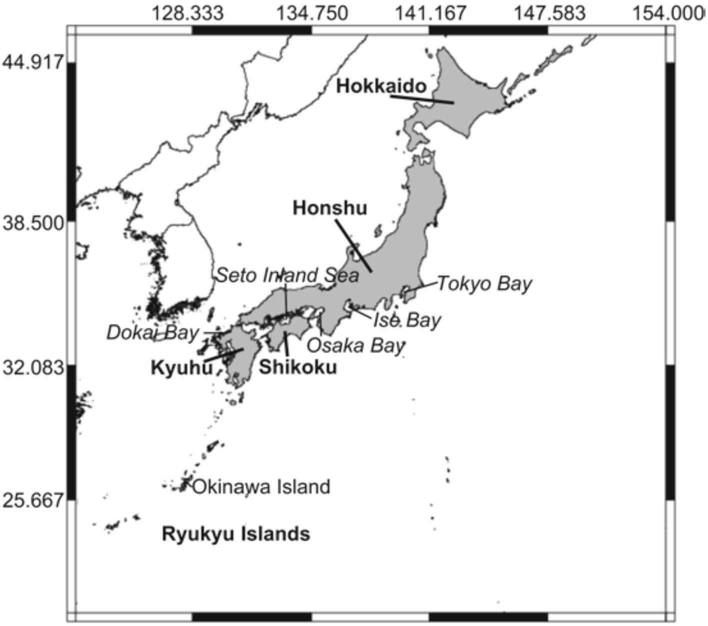

**Fig. 1** Map of Japan showing selected locations where alien marine crustaceans are established. Four major enclosed coastal areas support international ports: Tokyo Bay has the Port of Tokyo and Yokohama; Ise Bay has the Port of Nagoya; Osaka Bay has the Port of Osaka, and Seto Inland Sea has the Port of Kobe

*M. coccopoma* also occurred in Tokyo Bay; at Chigasaki in Sagami Bay, and Choshi on the northeast of the Boso Peninsula in central Honshu.

*Copepods* Humes and Turner (1972) found the clausiid copepod *Teredicola typica* living in the mantle cavity of the teredinid shipworm *Lyrodus pedicellatus* at Takahama, Fukui in 1971; Carlton and Eldredge (2009) review the literature and distribution of this species, which is likely native to the southern hemisphere. The European notodelphyoid copepod *Pachypygus gibber*, parasitic in the pharyngeal cavity of solitary ascidians, was recorded from Tanabe Bay, Wakayama and Oomishima, Ehime and Motoya Bay, Mie by Ooishi (1961), and from Kesennuma, Miyagi by Ooishi (1963) in 1960 and 1962. The hosts of *P. gibber* were *Styela plicata* and *Cnemidocarpa areolata* (both native to Japan) and the introduced North Atlantic ascidian *Ciona intestinalis* (Ooishi 1961, 1963). This alien copepod was probably introduced to Japan with *Ciona*. While there appear to be no further reports of these species, we have no reason to believe that they are not still present in Japanese waters.

*Amphipods* The North Atlantic corophiid amphipod *Monocorophium acherusicum* was first found in Ariake-kai in 1955 (Irie 1956) and in Mihama Bay, Seto Inland Sea, from 1955 to 1957 (Nagata 1960). This species is commonly found along the Japanese coast (Hirayama 1995). *Monocorophium insidiosum*, also from the North Atlantic, was collected from Mihama Bay together with *M. acherusicum* (Nagata 1960), and from a mooring buoy near Fukuyama Harbour, from 1955 to 1956 (Onbe 1966). Conlan (1990) recorded the tube dwelling North Atlantic amphipod *Jassa marmorata* from Oshoro Bay (Sea of Japan) and Akkeshi Bay in Hokkaido; while no dates of collection are yet available for this material, we note that Gurjanova (1938) had recorded *J. marmorata* from the Sea of Japan no later than the 1930s. Sano et al. (2003) report it from drifting seaweed in 1994 off the Tohoku coast in northern Japan. Although these three amphipods are commonly found in Japanese coastal waters (Ishimaru 1994), there are no historical data on their history of introduction, range expansions or population dynamics. Exploration of pre-1950s amphipod collections or archived fouling material from Japan would be instructive in this regard.

The Northeast Pacific *Jassa slatteryi* is known in the Western Pacific from two Japanese bays, Tanabe Bay, Wakayama Prefecture, and Akkeshi Bay, Hokkaido (Conlan, 1990) and from Korea (Conlan 1990; Jeong et al. 2007), and has been collected from vessel fouling (Lim and Park 2006). Sano et al. (2003) further report it from drifting seaweed in 1994 off the Tohoku coast in northern Japan. It has also been introduced to the southern hemisphere (Robinson et al. 2005; Mead et al. 2011), and thus shows a proclivity to being ship-dispersed. We regard it as introduced to Japan and Korea.

## 3 Cryptogenic Crustaceans

There are potentially scores of Japanese crustaceans that could be considered cryptogenic. We offer a few examples here.

*Copepods* The endocommensal copepod *Doropygus elegans* was described from Japan and is known only in the introduced ascidian *Ciona intestinalis* (Ooishi 1963), a species native to the North Atlantic Ocean. We consider it cryptogenic as it may have been acquired by *Ciona* from a native Japanese ascidian (although not yet reported in any native host).

*Barnacles* The recognition of *Amphibalanus reticulatus* as introduced to the Hawaiian fauna (Carlton and Eldredge 2009) raises questions about its history in the North Pacific, and we thus place it in the cryptogenic category for Japan, where it was previously regarded as native. *Amphibalanus reticulatus* is distributed primarily in the Indian Ocean, South Pacific, and Indo-Pacific, with distant outlier populations in Japan and in the Hawaiian Islands. Its closest morphological relatives are *Amphibalanus variegatus* and *Amphibalanus amphitrite*, whose distributions are also both centred in the Indian Ocean and South Pacific. Utinomi (1967: 217) recorded a first date of 1934 for Japan, and Utinomi (1970: 220) noted that *A. reticulatus* may owe its wide distribution to ship-mediated transport. Early confusion about its native status in Japan may arise from the fact that *Balanus reticulatus* was first *named* from Japan, but as a nomen novum, not as a new species.

*Tanaids* We regard a species of *Sinelobus* in Japanese fouling communities as cryptogenic. This and the same or similar taxa are referred to as *Sinelobus stanfordi* around the world, but this name is widely regarded as a yet-to-be-resolved species complex (references in Table 1).

*Isopods* The wood-boring isopod, or gribble, *Limnoria tripunctata* was first collected in 1943 in Misaki, Japan (Shiino 1944, as *L. lignorum*), although it may have been present for decades if not centuries. Its distribution in Japan remains poorly known. The assignment of Shiino's Misaki record to *L. tripunctata* was made by Menzies (1954: 380, Table 4, in reference to Shiino, 1951, cited therein as 1950). Beckman and Menzies (1960) later indicated that Mawatari's (1950) *L. lignorum* was also *L. tripunctata.* In neither case is it clear that Menzies examined actual material, although Menzies and Shiino were in communication by 1950 (Shiino 1951: 333), and it is possible that Shiino provided specimens to Menzies. It is not clear, therefore, which of Shiino's 1951 records of *L. lignorum* are *L. tripunctata* or *L. lignorum*, which also occurs in Japan (Cookson 1991). Quayle (1965b: 7) notes that wood from an oyster-producing location in Sendai, Japan, "contained only *Limnoria tripunctata*"; Quayle (1965a) proposed that *L. tripunctata* was native to Japan and was introduced to British Columbia in the wooden crates that were used to transport Japanese oysters to North America. Three additional wood-boring limnoriids have been reported from Japanese waters (Table 1): *Limnoria indica* and *Limnoria multipunctata*, both from the Ryukyu Islands, and *Paralimnoria andrewsi* from Misaki and Tanabe Bay (Carlton and Eldredge 2009, specifically suggested that the latter species may be an introduction to Japan). Although all four of these wood-boring species have without doubt been widely dispersed by ships, their origins remains unclear, and we thus regard them as cryptogenic in Japan. Shiino (1951) commented that the unusual disjunct distribution of *P. andrewsi* "appears to provide additional support for the view that the distribution of *Limnoria* may be affected more by the navigation routes of wooden ships than by the specificity of the environment".

*Amphipods* The North Atlantic amphipods *Ampithoe valida* and *Melita nitida* have been reported by a number of workers from Japan (Table 1). However, there are more than ten species of *Ampithoe* in Japan, and while *A. valida* is regarded as introduced to the northeast Pacific Ocean (Chapman 2007), *A. valida* has not been verified from Japan (H. Ariyama, pers. comm.). Several authors regard the Japanese species *Melita setiflagella* as identical to *Melita nitida* (Jarrett and Bousfield 1996; Faasse and van Moorsel 2003; Chapman 2007), and thus introduced to Japan. However, most Japanese researchers retain *M. setiflagella* as a valid species and consequently we treat it here as cryptogenic.

The amphipods *Leucothoe alata* and *L. spinicarpa* are considered to be potentially introduced with their ascidian hosts (Chapman 2007); they are considered cryptogenic in Japan until further taxonomic and biogeographic work on Japanese material can be done.

The global distribution of the amphipod *Platorchestia platensis* (= *Orchestia platensis*; reviewed in Spicer and Janas 2006), may represent a mixture of introduced populations and undescribed species. Many species of maritime talitrids were historically dispersed in "solid" or "dry" ballast of early sailing vessels. Ruffo (1949), fide Spicer and Janas (2006), recorded *P. platensis* from Japan from material collected in 1897–1899. It may be an introduced species, but until further evidence is collected, it is here considered cryptogenic (see also Morino 1975, 1978).

Three cosmopolitan caprellids, *Caprella equilibra*, *C. penantis* and *C. scaura* were recorded from Japan in the nineteenth century (Takeuchi 1999). Martinez and Adarraga (2008) suggest *C. scaura* is native to the western Indian Ocean, but we conservatively retain it here as cryptogenic. Mayer (1890), under the name *Caprella scaura* forma *diceros*, refers to 1875 *HMS Challenger* specimens from Japan; were *C. scaura* shown to be non-native to the North Pacific Ocean, this would render this amphipod as one of the earliest recorded crustacean introductions in Japan.

## 4 Intercepted and Bait Species

The Manila clam *Ruditapes philippinarum* (= *Venerupis philippinarum*) was imported from China and North Korea and seeded in suitable mud flats in Japanese waters in order to enhance the reduced domestic stock and recreational shellfish gathering. The leucosiid crab *Philyra pisum* and the parasitic pea crab *Pinnotheres sinensis* were found in 2002 and 1993, respectively in the sacks of clams imported from China or North Korea (Ito 1993; Okoshi 2004). Although these two crabs are also native to Japan the unintentional introduction of individuals from foreign populations could potentially lead to the release of novel genetic stocks and thus hybridization with native populations.

The shore crab *Hemigrapsus takanoi* is imported from China and sold as live fish bait for angling in fishing goods stores (Doi et al. unpublished data). Although *H. takanoi* is native to Japan, this is clearly an introduction of an alien population and thus potentially an inoculation of novel genetic stocks (Iwasaki 2006b).

## 5 Crustaceans Imported for Research or Farming

Since at least the early twentieth century alien decapods have been intentionally imported by Japanese marine laboratories and fisheries institutes for aquaculture or research purposes (Maruyama et al. 1987; Iwasaki 2006b; 2007a). None of these species are reported as established in the wild in Japan. For example, 47 individuals of the prawn *Penaeus chinensis* imported from the Yellow Sea for farming were intentionally released in 1967 along the east coast of Kyushu (Maruyama et al. 1987). Several specimens of the North American lobster *Homarus americanus,* reared in the Hokkaido Fisheries Experimental Institute, escaped in 1914 (Maruyama et al. 1987). Watabe (1993) reported the finding of a 24.9 cm living *Homarus americanus* in Sagami Bay.

The Chinese mitten crab *Eriocheir sinensis* has been commercially reared in fallow rice fields in northern Honshu (e.g., Yamagata and Fukushima Prefectures) since 1999 (Takeda and Koizumi 2005; Iwasaki 2006b, 2007a). Although two adult female specimens were captured in Odaiba in 2004 (see below), there were no reports of escapees from the Honshu area.

## 6 Non-established Species

Three alien crabs were previously recorded in Japanese waters. Three specimens of the North American Atlantic *Callinectes sapidus* (blue crab) were found in Lake Hamana in 1975 (Sakai 1976) and another specimen was found in 1991 (Hasegawa 1992); one specimen was also found in Osaka Bay in 1984 (Ariyama 1985). A single male of the North American Pacific *Metacarcinus magister* (= *Cancer magister*, the Dungeness crab) was collected in a small-beam trawl off Kushiro, Pacific coast of Hokkaido in 1979 (Abe 1981). Both of these well-known edible crabs were transported by shipping (Abe 1981; Iwasaki 2007a). In November 2004, two mature females of the Asian *Eriocheir sinensis* (Chinese mitten crab) were found on a sandy subtidal bottom off Odaiba in Tokyo Bay (Takeda and Koizumi 2005). Although this crab is farmed in northern Japan, the source of these specimens remains unclear: they may have been farm escapees, imports from China, or shipping-transported.

## 7 Species Removed from Further Consideration

We remove from further consideration at this time a number of species that were previously considered as possible aliens in the Japanese fauna.

*Copepods* The copepod *Centropages maigo*, described in 2005 from Shimizu, Shizuoka, was thought to be a possible ballast water introduction to Japan from the Indo-West Pacific (Ohtsuka et al. 2005). Ohtsuka et al. (2007) later concluded that this copepod was “likely” a native Japanese species because it was recorded from three medium-size international ports (Shimizu, Tomakomai and Hakodate) but not from major international ports such as Tokyo, Osaka, or Kobe, where large amounts of foreign ballast water are discharged. The authors further suggested *C. maigo* and *C. sinensis* may have speciated during the glacial period from a common Western Pacific ancestor.

*Barnacles* The barnacle *Amphibalanus variegatus* was recorded from Okayama and Yamaguchi in western Honshu and Fukuoka, Nagasaki and Kumamoto, Kyushu province during the 1930s and 1960s by Hiro (1938) and Utinomi (1949, 1967, 1970) and *Amphibalanus venustus* was reported from the Sea of Japan coastline at Wakasa Bay in 1967 by Yasuda (1970) and Sado Island in 1968 by Utinomi (1970). These two barnacles have not been generally recorded since the 1970s and their establishment is considered as unlikely (Iwasaki et al. 2004b; Yamaguchi 2009). However, Horikoshi and Okamoto (2005, 2007) collected ten individuals of *A. variegatus* attached to floating buoys in Tokyo Bay during 2004–2005, but the existence of a breeding population in the area has not been confirmed (Iwasaki 2006a).

Further, molecular studies of *A. variegatus* revealed a genetic differentiation between Japanese and Australian populations (Yamaguchi 2009), and thus the Japanese population was tentatively recognized as *Amphibalanus* aff. *variegatus* and as a probable native species (Yamaguchi 2009).

The barnacles *Megabalanus zebra* and *M. tintinnabulum* were recorded, without detailed description, from the hull of a petroleum tanker traveling between Japan and the Middle East, and from artificial structures off Okinawa (Yamaguchi Yamaguchi 1986). Two specimens of *M. zebra* were reported in the collection of Ph. F. Von Siebold, but their date and locality remain unknown (Yamaguchi and Baba 1993). Otani et al. (2007) found *M. tintinnabulum* fouling the propeller, post-rudders and bows of two 50,000 DWT class bulkers operating between Osaka Bay and Australia/Indonesia. Yamaguchi (2009) omitted both of these species from his updated list of alien Japanese barnacles.

*Amphipods* The Atlantic brackish water amphipod *Apocorophium acutum* was recorded in 2002 in a brackish water lake at Nakaumi, western Honshu (Yamauchi et al. 2006). This is the only record from Japan and according to H. Ariyama (pers. comm.), who identified the specimens, their identification remains uncertain.

*Isopods* Brusca et al. (2007) stated that the Northeastern Pacific isopod *Synidotea harfordi* was "introduced to Japan". Gurjanova (1936) recorded *S. harfordi* from Russia in the Sea of Japan; Menzies and Miller (1972), noting Gurjanova's record, suggested that *S. harfordi* was native to both the Western and Eastern Pacific. Kussakin (1982), however, re-examined Gurjanova's specimens of *S. harfordi*, and identified them as the native Asian species *Synidotea laevidorsalis*. Later, Moore (2004) listed *S. harfordi* from the "Sea of Japan" without citing Kussakin's work. We conclude that reports of *S. harfordi* from Japanese waters are without foundation.

Hewitt et al. (2004) reported that the Northeastern Pacific isopod *Cirolana harfordi* was introduced to Japan. This record probably refers to *C. harfordi japonica*, a subspecies which has now been given full species status.

*Crabs* Hiatt (1948) argued that the Northeastern Pacific grapsid crab *Pachygrapsus crassipes* may have been introduced to Japan as zoeae in the ballast tanks of ships coming from California. The isolated nature of this population in Japan and lack of pre-1890 reports appeared to make this a logical conclusion. However, Cassone and Boulding (2006) have shown that Asian *P. crassipes* are genetically distinct and likely colonized Japan more than 800,000 years ago.

## 8 Temporal Trends

As noted earlier, our resolution of recognized marine bioinvasions in Japan does not precede the 1930s, reflecting the challenges in resolving the history of the Japanese marine biota prior to the mid-twentieth century. Two species, the barnacle *Amphibalanus amphitrite* and the amphipod *Jassa marmorata* were, or may have been, present by the 1930s (Table 1). After that, the invasion record re-commences in the 1950s, with the advent of more detailed explorations after World War II. Examination of the first records of cryptogenic species is insightful (Table 1): here we find additional 1930s records as well as nineteenth century records, which suggest that invasions were likely occurring, as expected, long ago.

## 9 Range Expansion from Initial Introductions

Several alien crustaceans that were presumed to be introduced within the last 10 years initially dispersed locally around their area of initial introduction. Examples include the isopod *Paracerceis sculpta* in Osaka Bay (Ariyama and Otani 2004), the barnacle *Amphibalanus zhujiangensis* on Okinawa Island (Yamaguchi 2009) and the crab *Rhithropanopeus harrisii* in Ise Bay (Iseda et al. 2007). Iwasaki et al. (2004b) analyzed the distribution pattern and range expansion of eight alien marine species introduced into Japan including the barnacles *A. amphitrite*, *A. eburneus*, *A. improvisus* and the crab *Carcinus*, using data obtaining from a questionnaire survey. The average speed of dispersal for *A. improvisus* and *C. aestuarii* was estimated to be 13.9 and 24.7 km year$^{-1}$, respectively.

The time of first discovery of several species of established alien marine crustaceans can be divided into three broad periods: (1) ~1950, (2) 1970–1980 and (3) 2000~. Three species of established barnacles, *A. amphitrite*, *A. eburneus*, and *A. improvisus* were introduced before (*A. amphitrite*) and/or around 1950 and have since expanded their distribution around the main islands of Japan (Iwasaki et al. 2004a). We discuss below the expansion history of these three species, other species of barnacles, and crabs.

*Amphibalanus amphitrite* (Fig. 2) The earliest occurrence of *A. amphitrite* in Japan was reported from Kanazawa Oyster Farm (Kanagawa Prefecture) in 1933 by Miyazaki (1938). Hiro (1937, 1938) reported *A. amphitrite* from Misaki (Kanagawa), Shirahama (Wakayama), Kure (Hiroshima), Sasebo (Nagasaki) and Maizuru (Kyoto). When first recognized *A. amphitrite* already occurred along the Japanese coast adjacent to the Pacific Ocean, Sea of Japan and East China Sea, indicating either simultaneous invasion in separate ports or rapid range expansion via domestic shipping (Iwasaki et al. 2004b). Its introduction may have occurred in hull fouling from Hawaii via the Philippines. Initially *A. amphitrite* was more abundant in Japanese military ports such as Kure and Sasebo, and was found only on vessel surfaces below the water line and on experimental plates (Hiro 1938). During the 1940s–1960s *A. amphitrite* was recorded from Tokyo Bay, Ago Bay (Mie), Osaka Bay, and the western coastline of Kyushu and Hakodate, Hokkaido. The distribution expanded to southern regions of Hokkaido in the north and southern areas of Kyushu by the 1980s (Iwasaki et al. 2004b).

*Amphibalanus eburneus* (Fig. 3) The earliest record of *A. eburneus* is from Yokosuka, Kanagawa in 1950 (Henry and McLaughlin 1975). During the 1960s, the geographical distribution of *A. eburneus* rapidly expanded to the ports and inner

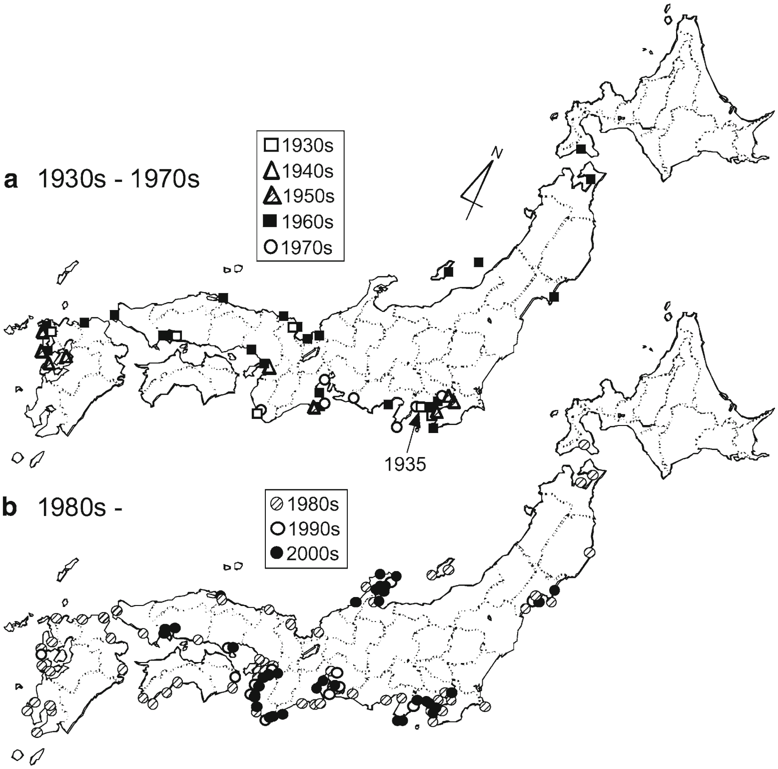

**Fig. 2** Distribution and timing of collections of *Amphibalanus amphitrite* in Japan. In Figs. 2–6, the Satsunan, Ryukyu, and Ogasawara Islands are excluded from the maps because of the lack of information. The year and site of the first record are indicated by an arrow (Figs. 2–5 from Iwasaki et al. 2004a © The Japanese Association of Benthology)

bay areas of the Pacific Ocean such as Yokosuka, Shimizu and Kagoshima, Sea of Japan (i.e., Kamo, Sado, Tsuruga, Wakasa, Maizuru and Hakata), the Seto Inland Sea at Aioi, Kure and Hiroshima, and East China Sea including the Ports of Sasebo and Nagasaki (Iwasaki et al. 2004b). During the 1980s *A. eburneus* was reported from all of mainland Japan except for Hokkaido and Okinawa (Otani 2002). There remains a lack of information regarding the initial establishment of *A. eburneus* on the mainland (Iwasaki et al. 2004a).

*Amphibalanus improvisus* (Fig. 4) This barnacle was first recorded in Ago Bay, Mie in 1952 with subsequent reports from the Pacific coasts of central Honshu at Lake Hamana, Atsumi Peninsula, Mikawa Bay, Ise Bay, Kumano-Nada Sea, Kii Channel and Osaka Bay (Iwasaki et al. 2004b). During the 1960s, *A. improvisus* expanded to Ibaraki in the north and Kyushu in the south on the Pacific side of Japan and was first noted from Wakasa Bay, Nakaumi and Lake Shinzi along the Sea of Japan coastline. During the 1970s the distribution expanded from Aomori to Niigata and the northern part of Honshu, being more or less completed by the 1980s (Iwasaki et al. 2004b).

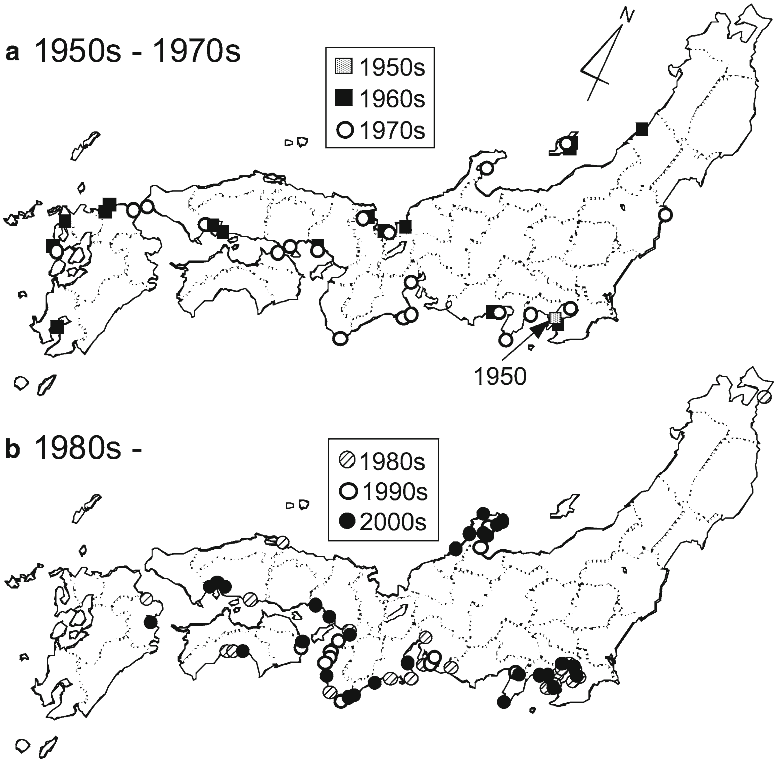

**Fig. 3** Distribution and timing of collections of *Amphibalanus eburneus* in Japan

*Amphibalanus zhujiangensis* The first Japanese record of *A. zhujiangensis* was from two individuals found on test panels in the Gushikawa River, Okinawa Island in 1997. This species was previously known only from the type locality, Zhujian River in Hong Kong (Puspasari et al. 2002; Yamaguchi 2009). In March 2009 many *A. zhujiangensis* were found at Gushikawa on natural rock substratum (Yamaguchi 2009). Yamaguchi (2009) further reported *A. zhujiangensis* from northern Sulawesi, Indonesia and the Northern Territory, Australia.

*Balanus glandula* The Northeastern Pacific acorn barnacle *B. glandula* was first found in 2000 in Ofunato Bay, Iwate Prefecture in northern Honshu (Kado 2003) where it had established dense populations over the entire littoral zone. Kado (2003) suggested that *B. glandula* may have been introduced as early as the 1960s but long overlooked. When it was first discovered *B. glandula* already occurred along the Pacific coast of northern Japan between 38° 30’ and 42° 40’ N (Geller et al. 2008). “By 2005, gravid barnacles were present at high densities at Kushiro and Katsurakoi on Hokkaido, the northernmost island of Japan, where it had been absent in 2000. Thus, *B. glandula* (had) reached its present northern and western endpoints at 43° 00’ N and 144° 26’ E within 5 years” (Geller et al. 2008). *Balanus glandula* has successfully colonized the littoral zone, especially in large commercial ports and at locations considerably distant from these ports.

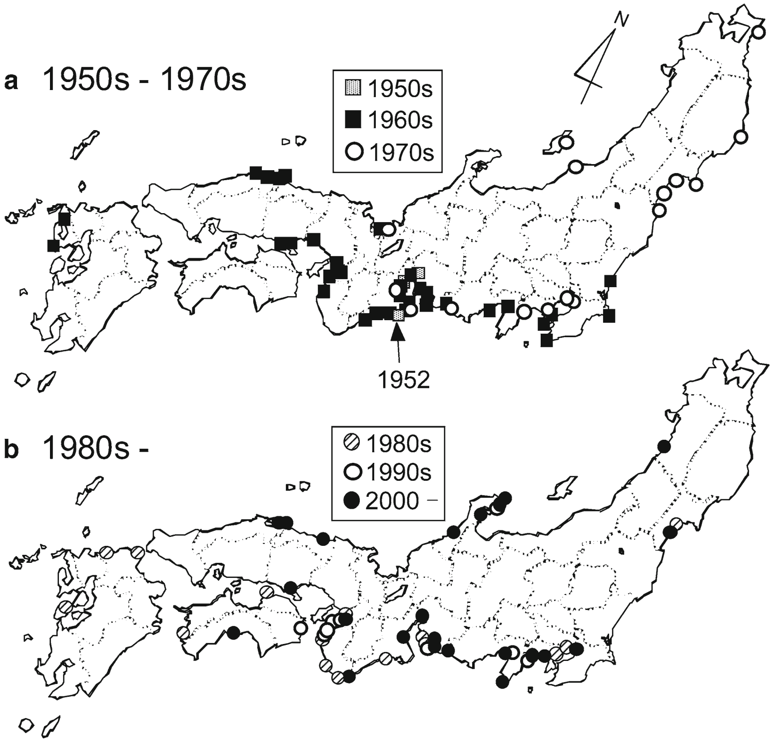

**Fig. 4** Distribution and timing of collections of *Amphibalanus improvisus* in Japan

The current Japanese distribution of *B. glandula* is Hokkaido-northern Honshu and of *A. zhujiangensis*, Okinawa Island (Kado 2006; Yamaguchi 2009). Being cold and warm-water barnacles, their potential range is limited to Northern and Southern Japan, respectively.

*Pyromaia tuberculata* (Fig. 5) This Northeastern Pacific crab was first found in 1970 off Jogashima Island and Aburatsubo Bay on the Miura Peninsula; Yokosuka, Odawara, and in Tokyo Bay. At the time of discovery, *P. tuberculata* had already established dense population in Tokyo Bay (Furota and Furuse 1988) and had become the dominant species in benthic assemblages on subtidal sandy-mud bottoms in the inner part of the bay. Furota and Furuse (1988) inferred that the introduction occurred in the 1960s, based upon personal communications from local fishermen, and from its absence in bottom trawl samples in 1954–1955 (Kubo and Asada 1957). In 1971–1973, *P. tuberculata* was recorded in Uraga Channel, Sagami Bay and Ise Bay and Tokyo Bay. In the late 1970s, *P. tuberculata* was observed in Osaka Bay, Miyajima in Hiroshima and Hakata, and by the 1980s *P. tuberculata* had expanded to the central part of Honshu and Seto Inland Sea. It also was recorded in Suruga Bay, Lake Hamana, Mikawa Bay, Nagoya Port, Shima Peninsula, Otsu (Hyogo), Yuya Bay and Hakata Bay. *Pyromaia tuberculata* was found in

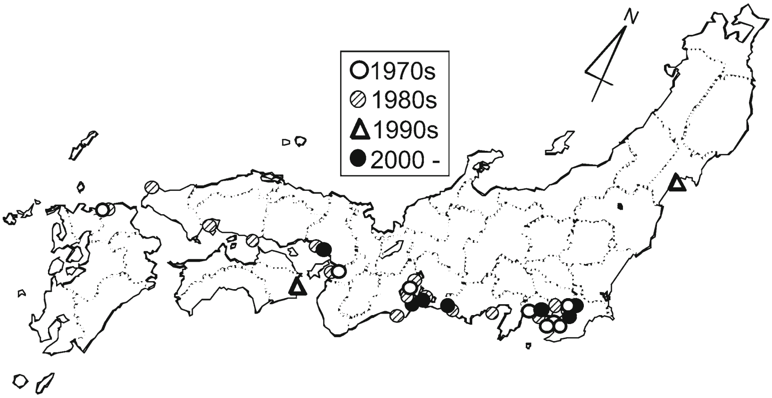

**Fig. 5** Distribution and timing of collections of *Pyromaia tuberculata* in Japan

Komatsujima Port in Tokushima (Shikoku) in the 1990s and in Sendai Bay (northern Honshu), Tokyo Bay, Enoshima in Kanagawa, Lake Hamana, Mikawa Bay in the 2000s (Iwasaki et al. 2004b).

*Carcinus maenas* × *C. aestuarii hybrids* (Fig. 6) The Mediterranean green crab *Carcinus aestuarii*, identified initially by its morphology (Sakai 1986), was first found in 1984 at Futtsu and Yokohama in Tokyo Bay. Recent molecular genetic work has demonstrated that the Japanese population represents hybrids between *C. aestuarii* and the European *C. maenas* (Darling et al. 2008). *Carcinus* was not recorded again until the 1990s. Since then, *Carcinus*'s distribution began to expand across Tokyo Bay; it became particularly dense in the inner most part of the Bay in 1994. At the same time *Carcinus* was found in Osaka and Dokai Bays in northern Kyushu. In the former bay, the pattern of range expansion was similar to that of Tokyo Bay. *Carcinus* spread within Osaka Bay and to the eastern Seto Inland Sea and showed high population densities (Nabeshima 2007). In 2001–2002, the crab occurred in Suruga Bay, Lake Hamana and Ise Bay. *Carcinus* is still restricted to inner bay areas near metropolitan cities, even though more than 25 years have passed since it was first found.

## 10 Population Fluctuations

No long term studies of the population dynamics of alien crustaceans have been undertaken in Japan. With few exceptions, only intermittent and qualitative data are available.

The biological attributes of the Tokyo Bay populations of *Carcinus* have been monitored since their population peak in 1994. Monthly sampling from 1994 to 2005 in Keihin Canal, Tokyo, has shown considerable variation and an apparent decline since 2000 (Doi et al. unpublished). The size frequency distribution has become narrower in range and shifted to smaller sized individuals, the size at sexual maturity has decreased, and spawning and recruitment occur later in the year (Doi et al. 2009a). The causes of these changes are unknown but they suggest a decrease in population fitness for the green crab in Tokyo Bay.

In the 1980s to early 1990s *Pyromaia tuberculata* occurred in low density populations predominately in the inner part of Tokyo Bay. Small numbers of mature individuals were reported from the central and outer part of the bay, correlated with predation by demersal fishes and by other benthic organisms

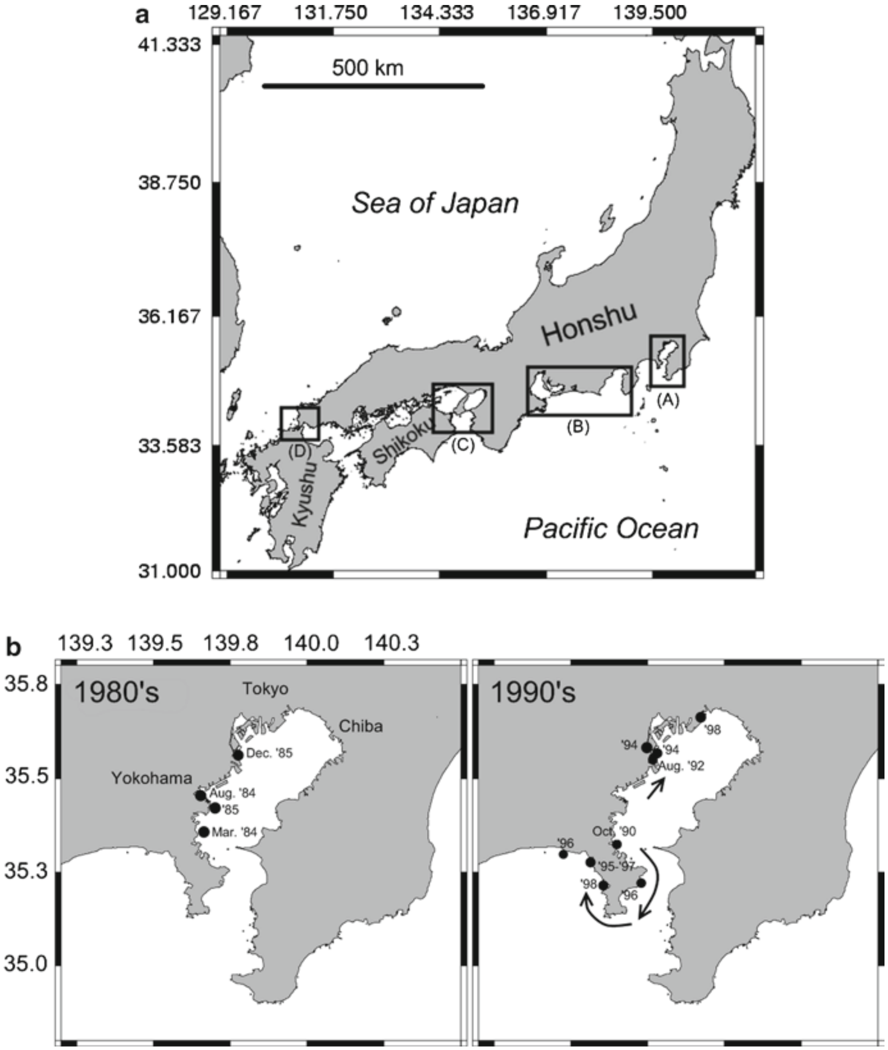

**Fig. 6** Distribution and timing of collections of *Carcinus* in Japan: (**a**) overview of major sites; (**b**) Tokyo Bay, (**c**) Suruga and Ise Bay, (**d**) Osaka Bay and Eastern Seto Inland Sea, and (**e**) Dokai Bay (Watanabe 1997; Kitano and Imai 2002; Chen et al. 2003; Iwasaki et al. 2004a; Nabeshima 2007)

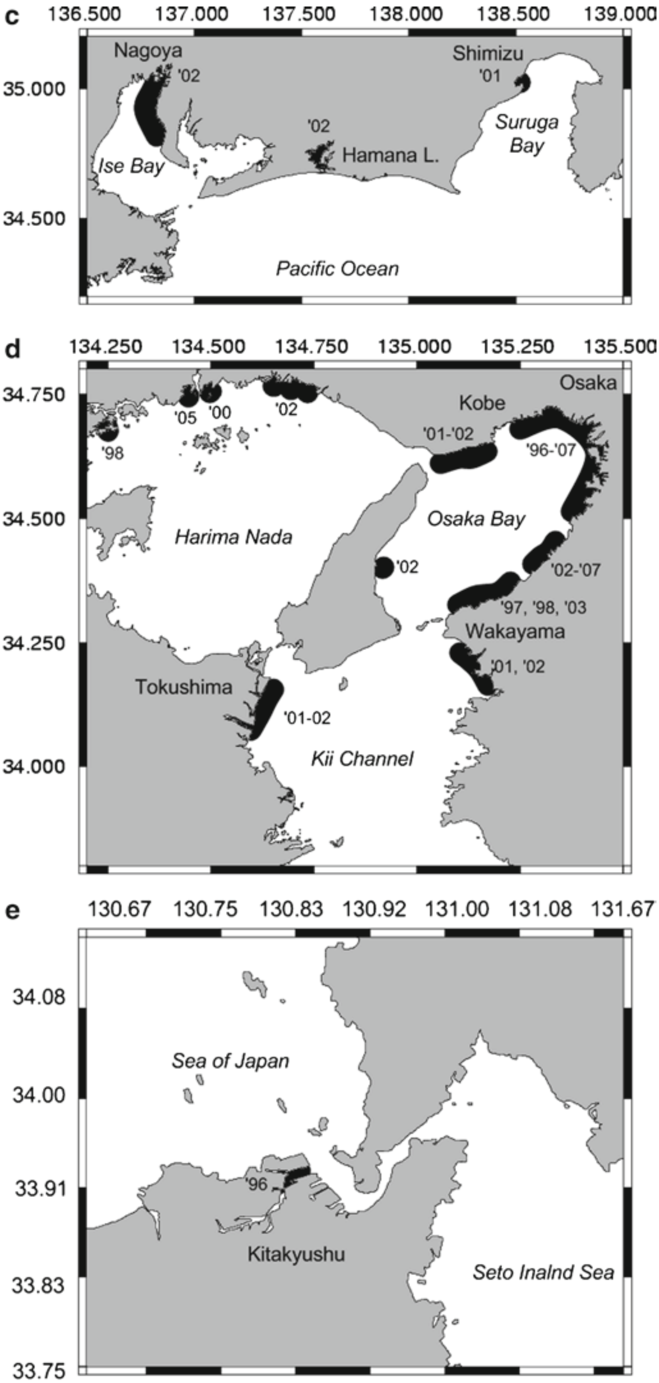

**Fig. 6** (continued)

**Table 2** Crab species composition of (A) bottom trawl samples (2002–2006) and (B) dredge samples (2004–2006) in the central and outer part of Tokyo Bay, respectively (Doi et al. unpublished data)

(A) Bottom trawl samples

| Rank | Crab species | No. individuals |
|---|---|---|
| 1 | *Pyromaia tuberculata* | 2,902 |
| 2 | *Carcinoplax vestita* | 745 |
| 3 | *Charybdis bimaculata* | 496 |
| 4 | *Pugettia incisa* | 108 |
| 5 | *Portunus hastatoides* | 75 |
| – | Other native species ($n=22$) | 176 |
| – | Total | 4,502 |

(B) Dredge samples

| Rank | Crab species | No. individuals |
|---|---|---|
| 1 | *Pyromaia tuberculata* | 1,359 |
| 2 | *Charybdis bimaculata* | 35 |
| 3 | *Pugettia incisa* | 6 |
| 4 | *Tritodynamia rathbunae* | 6 |
| 5 | *Enoplolambrus laciniatus* | 5 |
| – | Other native species ($n=18$) | 27 |
| – | Total | 1,438 |

(Okoshi and Furota 1997). Bottom trawl surveys conducted in the central part of Tokyo Bay during 2002–2006 (Table 2A) and dredge surveys conducted in the outer part of the Bay during 2004–2006 (Table 2B) have shown a dramatic increase in the population with *P. tuberculata* accounting for 64.5% and 94.5% of the samples by number of individuals.

## 11 Biogeographic Patterns: Donor-Recipient Relationships

Otani (2006) suggested that the source region of many unintentionally introduced organisms in Japanese waters is the Northeast Pacific and the East Asian Seas. We note that the *source* region (the actual source of the specific donor populations of alien species that were introduced to Japan) may be different than the species origin.

Several studies have attempted to clarify actual source regions using molecular genetic data. Geller et al. (2008) confirmed through mtDNA analysis that the likely sources for the initial invasion of the barnacle *Balanus glandula* to northern Japan were Alaska and Vancouver. However, the source population and thus the donor-recipient relationship in the crab *Carcinus* (Darling et al. 2008) and the barnacle *Megabalanus coccopoma* (Yamaguchi et al. 2009) could not be clarified using DNA, due to hybridization (for *Carcinus*) and low genetic divergence among native and introduced populations (for *Megabalanus*).

The biogeographic origins of the alien crustacean fauna in Japan include both Atlantic and Pacific theatres. Of the 16 introduced species treated here, 8 are from the North Atlantic Ocean, 4 are from the northeast Pacific (the west coast of North America), and 1 each is from the northwest Pacific (South China Sea) and the tropical eastern Pacific. Only 2 species are from the Indian Ocean/South-Pacific. Of the 15 cryptogenic species, 4 may be from the North Atlantic, and 5 may be from the Indian Ocean/South Pacific, the latter thus potentially filling in the apparently low representation of species from that broad region in the Japanese alien fauna (the origin of an additional 6 cryptogenic species is, not surprisingly, not yet known).

## 12 Vectors

It is often a challenge, in the absence of direct evidence, to distinguish between vessel fouling (on hulls, sea chests, and other vessel surfaces) and ballast water and sediments as invasion vectors (Fofonoff et al. 2003; Otani 2002, 2004). For example, the amphipod *Monocorophium acherusicum* is found in ballast tanks (Gollasch et al. 2000), but also in fouling: over 136,000 individuals, including ovigerous females, fouled a barge on the subantarctic Macquarie Island (Lewis et al. 2006). For 14 of the 16 alien Crustacea, we cannot distinguish between ship fouling and ballast water (Table 1), the more so because the larvae, juveniles, and/or adults of all 14 of these taxa are potentially transportable by both ship fouling and ballast water (Carlton 1985; Carlton and Geller 1993). For the 15 cryptogenic species, we cannot distinguish ballast water from fouling for fully half of the species (Table 1). The exceptions for both introduced and cryptogenic taxa are commensals (copepods and amphipods) of ascidians associated with hull fouling. No species are yet known to be have introduced into Japan solely by ballast water, but this may be an artifact of the lack of discovery and proper identification of potential ballast-only taxa (such as planktonic copepods, cladocerans, and mysids).

This said, it is probable that ship fouling has been a major contributor to the arrival of alien barnacles in Japan (Otani et al. 2007). Based on direct observations, the hulls of bulk carriers are considered to be the most likely vector for the introduction and dispersal of *Megabalanus cocopoma* (Yamaguchi 2009; Yamaguchi et al. 2009). Fouling on cargo vessels transporting lumber from the northwest coast of the United States of America was the likely vector for the introductions of *Balanus glandula* (Kado 2003). Since adult specimens of the European green crab *Carcinus maenas* were found in sea chests (Coutts et al. 2003), this was judged to be the primary vector for the introduction of *Carcinus* into Japan (Otani 2004, 2006).

Other vectors, however, have been or remain in play. Solid ballast may have brought shore-dwelling talitrids (and maritime insects) to Japan in the nineteenth or earlier centuries. In the days of wooden ships, shipworms and their commensals were likely introduced (one of these appears to be the copepod *Teredicola typica*), as may have been a number of species of wood-boring gribbles (which, however, can continue to be transported by ballast water).

In modern times, shellfish importations and aquaculture operations are active potential vectors. Unintentional introductions could potentially occur with imported clams. Each year between 40,000 and 70,000 t of Manila clams (*Ruditapes* *philippinarum*) are imported from China and North Korea and released into Japanese coastal waters. The imported clam bags include crustaceans (such as the crabs noted earlier, and the hermit crab *Pagurus* sp.), gastropods (e.g., the naticid (moon snail) *Glossaulax didyma*) and bivalves (e.g., the ark shell *Scapharca kagoshimensis*) (Okoshi 2004). The culture of the Chinese mitten crab *Eriocheir sinensis* in fallow rice fields risks unintentional release into the wild.

## 13 Domestic Dispersal

Relative to domestic (intranational) translocations and dispersal, Arakawa (1980) suggested that the vector for the domestic expansion of the barnacle *A. eburneus* was the transportation of cultured oysters from Hiroshima for farming along the coast of the Sea of Japan. The presence of reproducing individuals of *Balanus glandula* on fenders of tugboats suggests dispersal via barges and tugboats from ports heavily settled by *B. glandula* to new locations in Japan (Kado and Nanba 2006). The Sagami Bay population of the crab *Pyromaia tuberculata* probably originated in the adjacent Tokyo Bay, from where it likely spread through larval dispersal, but its presence in areas farther away from Tokyo Bay is likely due to domestic shipping, as the species is found among sessile organisms on hard substrates (Furota 1988). The post-introduction movement of *Carcinus* included range expansion through larval dispersal within closed bays, as well as possible translocation via coastal shipping from domestic donor areas.

## 14 Ecological Impacts

With the exception of several species of barnacles and brachyuran crabs, the ecological impacts of alien crustacean in Japan have not been studied.

Iwasaki (2006a) and Yamaguchi (2009) suggested that the predominance of alien barnacles such as *Amphibalanus amphitrite* on hard substrata has lead to a significant decrease in the population density of native barnacles in enclosed bays. Mori (2006), in a field experiment, demonstrated that *A. amphitrite* is competitively superior to the native barnacles *Chthamalus challengeri* and *Fistulobalanus albicostatus*: recruits of *A. amphitrite* replaced native juvenile barnacles though interference (by covering and exfoliation). In Tokyo Bay, the cryptogenic barnacle *Amphibalanus reticulatus* was more common than alien *A. amphitrite* on buoys between 1973 and 1975 (Kajihara 1977). *Amphibalanus reticulatus* was not observed in the 1990s, whereas *A. amphitrite* occurred frequently in the intertidal of Yokohama and Tokyo ports (Kajihara 1994), becoming the most dominant barnacle there (Yamaguchi 1989). Its dominance limits the native barnacle *Chthamalus challengeri* to the upper intertidal zone through competition for suitable habitat for settlement (Furuse and Furota 1985). Kado and Nanba (2006) state that, "On exposed rocky shores, to which *B. glandula* had just started to expand its distribution, the species was starting to compete for space with two temperate-subtropical endemics, *Tetraclita japonica* and *Chthamalus challengeri* in the mid and upper littoral fringe, and with a sub-arctic endemic, *Semibalanus cariosus* in the mid and lower littoral zone".

*Amphibalanus amphitrite* and *A. improvisus* foul the exoskeleton of the native crab *Hemigrapsus sanguineus* (Niwa et al. 2001), possibly impeding its mobility.

Stomach content analysis showed that *Carcinus* spp. in Tokyo Bay is omnivorous and preys preferentially on alien mussels (Chen et al. 2004). Doi et al. (2009b) showed that the optimal-sized prey for *Carcinus* and the co-occurring native crab *Hemigrapsus takanoi* is similar, suggesting a potential for food competition between the two species, but no field studies were carried out to test for actual ecological interactions or impacts.

The alien crab *Rhithropanopeus harrisii* lives in the mats formed by the barnacle *Amphibalanus eburneus* and alien mussels (Iseda et al. 2007). Alien crabs consume alien barnacles and use them as refuges. It is unknown whether the mats of *A. eburneus* provide similar refuge for native species.

The metropolitan ports where alien barnacles and crabs are abundant are severely impacted by physical (such as reclamation and dredging), chemical (occurrence of eutrophication-related hypoxia and/or acidification) and biological (establishment of alien species) alterations. In the inner part of an urban bay such as Tokyo Bay, man made structures (e.g., concrete revetments) cover much of the coastline and support alien mussels and barnacles and other alien sessile invasions. In these highly urbanized and altered systems, it may be difficult to evaluate the ecological and environmental impact of alien species on the native biota.

## 15 Economic Impacts

The cost of preventative measures to stem the introduction of marine alien species to Japan has not been assessed (Otani 2006).

*Amphibalanus amphitrite*, *A. improvisus*, and *A. eburneus* are known fouling organisms, blocking water cooling intakes in power stations (Iwasaki 2006a). However, it has been suggested that the larger native barnacles *Megabalanus rosa* and *M. volcano* have caused most of the operational problems at Japanese power plants (Yamashita and Kamiya 2006). Biofouling increases the cost of shipping (Miyajima 1974), of aquaculture (oysters, pearls, algae) and of fisheries employing nets (Miyajima 1974). However, the specific economic impact of fouling alien barnacles is not clearly understood because experiments have included other sessile alien organisms such as the mussel *Mytilus galloprovincialis*. It is difficult to quantify the economic cost due to alien barnacles but it is not small (Arakawa 1974, 1980; Iwasaki 2006a). The economic impacts of other alien crustaceans have not been studied in Japan.

## 16 Management

The Japanese government and its agencies do not gather data on the marine alien species found within its territorial waters and have no contingency plan for countermeasures against their introduction and expansion (Iwasaki 2005, 2006a). The Invasive Alien Species Act of June 2005 designated invasive alien species and prohibited their farming, importation or handling. However, this act did not include marine invasive species (Iwasaki 2004, 2007b). The Ministry of the Environment published a watch list of aliens, including three marine crustacean species (*Carcinus maenas*, *Carcinus aestuarii*, and *Amphibalanus amphitrite*), warning against their release into the wild (http://www.env.go.jp/nature/intro/1outline/caution/index.html), although, as reviewed here, hybrids of the former two species, and the latter species, are already established in Japan. These Japanese statutes are insufficient because they address only a limited number of species already known for their negative economic and ecological impacts. This approach should be replaced by precautionary risk management, imposing a general ban on introductions of alien species except those that have been assessed and approved (Takahashi 2006; Iwasaki 2007b).

A marine alien species established in the wild is almost always impossible to eradicate. The only effective and cost-effective measures are those that prevent the importation of a species through painstaking control of its vectors (Iwasaki 2006b, 2009). Otani (2009) suggested that ship fouling management should include (1) efficacious antifouling paints that are frequently applied, (2) dry-docking support strips whose position should be changed during each docking, (3) frequent removal of hull fouling, and (4) shorter port turn-around times.

Okoshi (2009) proposed that imported clams should be strictly quarantined, and that the pathway between the source (production area) and the target (release area) be more vigilantly documented by introducing a tracing system. Local clam fisheries and recreational shellfish gathering should be reorganized as to be less reliant on the importation of foreign clams (e.g., seed production based on local clam population). Quarantine control should be introduced for importation of live fishery products and bait (Iwasaki 2006a).

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# Aliens in the Antipodes: Non-indigenous Marine Crustaceans of New Zealand and Australia

**Shane T. Ahyong and Serena L. Wilkens**

**Abstract** New Zealand and Australia have a relatively short history of European colonisation, going back little more than two centuries. Otherwise, the first human settlement in the region dates back to less than 1,000 years (New Zealand) and 40,000 years (Australia). Although alien species no doubt arrived with the first human settlers, the bulk of marine species alien to Antipodean shores have arrived in the last 200 years. The geographically isolated positions of New Zealand and Australia, relative to major population centres in the northern hemisphere, has made the region one of the last to be reached by European exploration of past centuries. Thus, Australia and New Zealand have a relatively short history of marine invasion. This study surveys the current state of knowledge of alien Crustacea in the Antipodes. To date, 112 and 41 alien or cryptogenic marine crustacean species have been recorded from New Zealand and Australia waters, respectively, of which 28 and 38 are established. In addition, three alien chelicerate species have been recorded from New Zealand. The majority of these probably arrived as stowaways amongst hull fouling and solid ship ballast (in the earliest days). Others have arrived as larvae in ballast water or have been deliberately introduced. Whereas the environmental impact of many alien Crustacea remains unknown, some species have become important pests.

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## 1 Introduction

Biological invasions have had a long recorded history in the northern hemisphere, particularly in connection with European seafaring, exploration and colonisation. In contrast, New Zealand and Australia have a relatively short history of European colonisation that dates back little more than two centuries. The first human settlement in the region dates back to less than 1,000 years in New Zealand with the arrival of Māori from elsewhere in the southwest Pacific, and 40,000 years in Australia, with the arrival of people now known as the Australian Aborigines. Some alien species probably arrived with the earliest human settlers, but the bulk of marine species alien to Antipodean shores have arrived in the last 200 years. The isolated positions of New Zealand and Australia, relative to major human population centres in the northern hemisphere, has made the region one of the last to be reached by European exploration of past centuries. Moreover, the biota of New Zealand and Australia (especially Southern Australia) has evolved in isolation or semi-isolation from northern hemisphere biotas. Thus, Antipodean shores might even be considered by some to have special environmental values making marine biosecurity even more critical. Regardless, Australian and New Zealand shorelines have received numerous alien species in historical time, especially in major ports such as Auckland and Wellington harbours in New Zealand, or Port Botany and Port Phillip Bay in Australia (Pollard and Pethebridge 2002a; Hewitt et al. 2004a).

Marine arthropods (most of which are crustaceans) are significant invaders in marine systems (Ashton et al. 2007a), accounting for 28% of reports in marine coastal communities in North America (Ruiz et al. 2000), and 56% of faunal species found in ballast tanks in Europe (Gollasch 2002). In New Zealand and Australia, the majority of these probably arrived as stowaways amongst hull fouling and solid ship ballast. Others have arrived as larvae in ship ballast water, some as rafters or in flotsam, and others accidentally or deliberately introduced through fisheries and aquaculture practices. The most recent attempt to summarize the alien marine fauna of New Zealand reported 148 species of which 31 are crustaceans (Cranfield et al. 1998). Sliwa et al. (2009) listed 132 species in Australian waters of which 25 are crustaceans. Here, the current state of knowledge of alien Crustacea in the Antipodes is surveyed. For completeness, the few records of alien marine chelicerates are also included together with brief comments on the introductions and translocations of freshwater crustaceans in the region.

## 2 Inventory

To date, 112 and 41 alien or cryptogenic crustacean species have been detected in New Zealand and Australian waters, respectively, whether via accidental or deliberate introduction, and whether established or not (Tables 1 and 2). Hull-intercepts and deliberate introductions have been included for completeness. Many vessels entering New Zealand and Australian ports, especially commercial, follow regular circuits between the same ports and generally carry repeated suites of species correlating with their regions of operation. Thus, knowledge of species presently known from

**Table 1** Alien (non-indigenous) and cryptogenic marine crustacea detected in New Zealand waters

| Higher taxon | Family | Species | Date of first record or introduction | Citation | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
| DECAPODA | Alpheidae | *Alpheus parasocialis* | 2007 | Williams et al. (2008) | NIS | + | | E Australia |
| | Cancridae | *Cancer pagurus*[a] | 1907–1913 | Thomson and Anderton (1921) | NIS | | | E Atlantic |
| | Cancridae | *Glebocarcinus amphioetus* | 2003 | Brockerhoff and McLay (2008) | NIS | | ? | NW Pacific |
| | Cancridae | *Romaleon gibbosulum* | 2001 | Brockerhoff and McLay (2008) | NIS | | ? | NW Pacific |
| | Galatheidae | *Galathea spinosorostris* | 2007 | Williams et al. (2008) | NIS | + | | Tropical Pacific |
| | Goneplacidae | *Ser fukiensis* | 2005 | NIWA/MAFBNZ | NIS | + | | South China Sea |
| | Grapsidae | *Pachygrapsus laevimanus* | 2007 | Williams et al. (2008) | NIS | + | | Tropical Pacific |
| | Grapsidae | *Pachygrapsus minutus* | 2005 | NIWA/MAFBNZ | C | + | | Indo-West Pacific |
| | Grapsidae | *Pachygrapsus transversus* | 2006 | NIWA/MAFBNZ | NIS | + | | Atlantic, E Pacific |
| | Hippolytidae | *Lysmata vittata* | 2006 | Ahyong (2010a) | C | | + | Indo-West Pacific |
| | Inachoididae | *Pyromaia tuberculata* | 1975 | Webber and Wear (1981) | NIS | + | + | E Pacific |
| | Majidae | *Schizophroida hilensis* | 2007 | Williams et al. (2008) | NIS | + | | Tropical Indo-West Pacific |
| | Majidae | *Schizophrys aspera* | 2000–2004 | Coutts and Dodgshun (2007) | NIS | + | | Tropical Indo-West Pacific |
| | Menippidae | *Myomenippe hardwickii* | 2005 | NIWA/MAFBNZ | NIS | + | | SE Asia |

(continued)

**Table 1** (continued)

| Higher taxon | Family | Species | Date of first record or introduction | Citation | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
|  | Menippidae | *Sphaerozius nitidus* | 2006 | NIWA/MAFBNZ | NIS | + |  | Tropical Indo-West Pacific |
|  | Nephropidae | *Homarus gammarus*[a] | 1906/1913 | Thomson and Anderton (1921) | NIS |  |  | NE Atlantic |
|  | Ocypodidae | *Ocypode pallidula* | 2001 | McLay (2009) | NIS |  | ? | Tropical Indo-West Pacific |
|  | Paguridae | *Hachijopagurus rubrimaculata* | 2007 | Williams et al. (2008) | NIS | + |  | Southern Japan |
|  | Panopeidae | *Acantholobulus pacificus* | 2006 | NIWA/MAFBNZ | NIS | + |  | E Pacific |
|  | Penaeidae | *Metapenaeus bennettae* | 2009 | NIWA/MAFBNZ | NIS |  | + | E Australia |
|  | Penaeidae | *Melicertus plebejus*[a] | 1892, 1894 | Thomson (1922) (as *Peneaus canaliculatus*) | NIS |  |  | E Australia |
|  | Pilumnidae | *Actumnus setifer* | 2007 | Williams et al. (2008) | NIS | + |  | Tropical Indo-West Pacific |
|  | Pilumnidae | *Pilumnus minutus* | 2005 | NIWA/MAFBNZ | NIS | + |  | Tropical Indo-West Pacific |
|  | Portunidae | *Charybdis japonica* | Pre-2000 | Webber (2001) | NIS |  | + | Central or NE Pacific |
|  | Portunidae | *Charybdis hellerii* | 2000–2004 | Coutts and Dodgshun (2007) | NIS | + |  | Tropical Indo-West Pacific |
|  | Portunidae | *Carupa tenuipes* | 2000–2004 | Coutts and Dodgshun (2007) | NIS | + |  | Tropical Indo-West Pacific |
|  | Sesarmidae | *Nanosesarma minutum* | 2005 | NIWA/MAFBNZ | NIS | + |  | Tropical Indo-West Pacific |

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|---|---|---|---|---|---|---|---|---|
| AMPHIPODA | Caprellidae | *Caprella californica* | 2005 | NIWA/MAFBNZ | NIS | + | | E Pacific |
| | Caprellidae | *Caprella equilibra* | Pre 1879 | McCain (1969) | C | + | + | Cosmopolitan |
| | Caprellidae | *Caprella penantis* | Pre 1878 | McCain and Steinberg (1970) | C | + | + | Cosmopolitan |
| | Caprellidae | *Caprella mutica* | 2002 | Inglis et al. (2005) | NIS | + | + | NW Pacific |
| | Cheluridae | *Chelura terebrans* | Pre 1914 | Chilton (1919) | C | + | + | Cosmopolitan |
| | Corophiidae | *Apocorophium acutum* | 1880 | Poore and Storey (1999) | NIS | + | + | NE Atlantic |
| | Corophiidae | *Crassicorophium bonnellii* | 2004 | Inglis et al. (2006a) | NIS | | + | NE, NW Atlantic |
| | Corophiidae | *Laticorophium baconi* | 2006 | NIWA/MAFBNZ | NIS | + | | E Pacific |
| | Corophiidae | *Monocorophium acherusicum* | 1880 | Chilton (1921) as *C. crassicorne* | NIS | | + | NE Atlantic |
| | Corophiidae | *Paracorophium brisbanensis* | 2000/2002 | Stevens et al. (2002) | NIS | | + | Australia |
| | Ischyroceridae | *Ericthonius brasiliensis* | 2005 | NIWA/MAFBNZ | C | + | | Cosmopolitan |
| | Ischyroceridae | *Ericthonius pugnax* | 1914 | Inglis et al. (2005) | NIS | | + | SE Asia |
| | Ischyroceridae | *Jassa marmorata* | Pre 1990 | Conlan (1990) | NIS | + | + | NE Atlantic |
| | Ischyroceridae | *Jassa slatteryi* | Pre 1990 | Conlan (1990) | NIS | | + | NE Pacific |
| | Ischyroceridae | *Jassa staudei* | 2004 | Inglis et al. (2006b) | NIS | | + | E Pacific |
| | Melitidae | *Elasmopus rapax* | 2000–2004 | Coutts and Dodgshun (2007) | NIS | + | | Central or NE Pacific |
| | Melitidae | *Mallacoota insignis* | 2007 | Williams et al. (2008) | NIS | + | | Tropical Indo-West Pacific |
| | Melitidae | *Melita matilda* | 2002 | Inglis et al. (2006a) | NIS | | + | Southern Australia |
| | Stenothoidae | *Stenothoe gallensis* | 2000–2004 | Coutts and Dodgshun (2007) | NIS | + | + | Tropical cosmopolitan |
| | Stenothoidae | *Stenothoe valida* | Pre 1910 | Ledoyer (1986) | C | | + | Atlantic Ocean |

(continued)

**Table 1** (continued)

| Higher taxon | Family | Species | Date of first record or introduction | Citation | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
| ISOPODA | Cirolanidae | *Cirolana harfordi* | 2005 | NIWA/MAFBNZ | NIS | + | | N Pacific |
| | Cirolanidae | *Cirolana willeyi* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| | Limnoriidae | *Limnoria rugosissima* | Pre 1991 | Cookson (1991) | NIS | | + | Southern Australia |
| | Limnoriidae | *Limnoria tripunctata* | Pre 1964 | McQuire (1964) | NIS | | + | Tropical Cosmopolitan |
| | Sphaeromatidae | *Cilicaeopsis whiteleggei* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| | Sphaeromatidae | *Cymodoce tuberculata* | 1910 | Chilton (1919) | NIS | + | | Australia |
| | Sphaeromatidae | *Dynoides amblysinus* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| | Sphaeromatidae | *Dynoides dentisinus* | 2005 | NIWA/MAFBNZ | NIS | + | | NW Pacific |
| | Sphaeromatidae | *Ischyromene* sp. | 2003 | Montelli and Lewis (2008) | C | + | | Not known |
| | Sphaeromatidae | *Paracerceis sculpta* | 2005 | NIWA/MAFBNZ | NIS | + | | NE Pacific |
| | Sphaeromatidae | *Sphaeroma walkeri* | 2005 | NIWA/MAFBNZ | NIS | + | | Indian Ocean |
| TANAIDACEA | Tanaidae | *Pancoloides moverleyi* | 2007 | NIWA/MAFBNZ | NIS | + | | Tasmania |
| | Tanaidae | *Zeuxo mooneyi* | 2007 | NIWA/MAFBNZ | NIS | + | | Tasmania |
| STOMATOPODA | Squillidae | *Oratosquilla oratoria* | 2008 | Ahyong (2010b) | NIS | | + | NW Pacific |

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|---|---|---|---|---|---|---|---|---|
| CIRRIPEDIA | Austrobalanidae | *Austrominius covertus* | 2005 | NIWA/MAFBNZ | NIS | + | | E Australia |
| | Archaeobalanidae | *Chirona amaryllis* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| | Archaeobalanidae | *Chirona tenuis* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| | Balanidae | *Austromegabalanus cylindricus* | 2007 | NIWA/MAFBNZ | NIS | + | | SW Indian Ocean |
| | Balanidae | *Austromegabalanus nigrescens* | 2005 | Hosie and Ahyong (2008) | NIS | + | + | Australia |
| | Balanidae | *Austromegabalanus psittacus* | Pre 2006 | Hosie and Ahyong (2008) | NIS | | + | South America |
| | Balanidae | *Amphibalanus amphitrite* | 1960 | Foster (1978) | NIS | + | + | Indo-West Pacific |
| | Balanidae | *Amphibalanus improvisus* | 1975 | Foster and Willan (1979) | NIS | + | + | W Atlantic |
| | Balanidae | *Amphibalanus reticulatus* | 1975 | Foster and Willan (1979) | NIS | + | + | Indo-Pacific |
| | Balanidae | *Amphibalanus uliginosus* | 2005 | NIWA/MAFBNZ | NIS | + | | Southern Japan to India |
| | Balanidae | *Amphibalanus venustus* | Post 1998 | NIWA/MAFBNZ | NIS | + | | SW Atlantic |
| | Balanidae | *Amphibalanus zhujiangensis* | 2005 | NIWA/MAFBNZ | NIS | + | | NW Pacific |
| | Balanidae | *Balanus rostratus* | 2006 | NIWA/MAFBNZ | NIS | + | | N Pacific |
| | Balanidae | *Fistulobalanus albicostatus* | 1975 | Foster and Willan (1979) | NIS | + | | Tropical Indo-West Pacific |
| | Balanidae | *Fistulobalanus dentivarians* | 2006 | NIWA/MAFBNZ | NIS | + | | E Pacific |

(continued)

**Table 1** (continued)

| Higher taxon | Family | Species | Date of first record or introduction | Citation | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
|  | Balanidae | *Fistulobalanus kondakovi* | 2005 | NIWA/MAFBNZ | NIS | + |  | Tropical Indo-West Pacific |
|  | Balanidae | *Fistulobalanus pallidus* | 2005 | NIWA/MAFBNZ | NIS | + |  | Tropical Cosmopolitan |
|  | Balanidae | *Megabalanus californicus* | 2005 | NIWA/MAFBNZ | NIS | + |  | E Pacific |
|  | Balanidae | *Megabalanus coccopoma* | 2005 | NIWA/MAFBNZ | NIS | + |  | E Pacific |
|  | Balanidae | *Megabalanus crispatus* | 2005 | NIWA/MAFBNZ | NIS | + |  | Unknown |
|  | Balanidae | *Megabalanus occator* | 2005 | NIWA/MAFBNZ | NIS | + |  | Tropical Indo-West Pacific |
|  | Balanidae | *Megabalanus peninsularis* | 2005 | NIWA/MAFBNZ | NIS | + |  | E Pacific |
|  | Balanidae | *Megabalanus rosa* | 1975 | Foster and Willan (1979) | NIS | + |  | NW Pacific |
|  | Balanidae | *Megabalanus tintinnabulum* | 2005 | NIWA/MAFBNZ | NIS | + |  | E Atlantic |
|  | Balanidae | *Megabalanus cf tintinnabulum* | 2005 | NIWA/MAFBNZ | NIS | + |  | Cosmopolitan |
|  | Balanidae | *Megabalanus tulipiformis* | 2005 | NIWA/MAFBNZ | NIS | + |  | E Atlantic |
|  | Balanidae | *Megabalanus vinaceus* | 2006 | NIWA/MAFBNZ | NIS | + |  | SW Atlantic |
|  | Balanidae | *Megabalanus volcano* | 1975 | Foster and Willan (1979) | NIS | + |  | Tropical Indo-West Pacific |
|  | Balanidae | *Megabalanus zebra* | 1975 | Foster and Willan (1979) | NIS | + |  | Indo-West Pacific, SW Atlantic |

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|---|---|---|---|---|---|---|---|
| Balanidae | *Perforatus perforatus* | 2006 | NIWA/MAFBNZ | NIS | + | | E, W Atlantic |
| Chthamalidae | *Chthamalus challengeri* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| Chthamalidae | *Chthamalus dalli* | 2005 | NIWA/MAFBNZ | NIS | + | | N Pacific |
| Chthamalidae | *Chthamalus fissus* | 2006 | NIWA/MAFBNZ | NIS | + | | E Pacific |
| Chthamalidae | *Chthamalus fragilis* | 2005 | NIWA/MAFBNZ | NIS | + | | Atlantic Ocean |
| Chthamalidae | *Chthamalus moro* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| Chthamalidae | *Chthamalus panamensis* | 2006 | NIWA/MAFBNZ | NIS | + | | E Pacific |
| Chthamalidae | *Chthamalus sinensis* | 2005 | NIWA/MAFBNZ | NIS | + | | NW Pacific |
| Chthamalidae | *Euraphia calcareobasis* | 2005 | NIWA/MAFBNZ | NIS | + | | Central Pacific |
| Chthamalidae | *Pseudoctomeris sulcata* | 2005 | NIWA/MAFBNZ | NIS | + | | NW Pacific |
| Lepadidae | *Lepas anserifera* | 1975 | Foster and Willan (1979) | C | + | | Cosmopolitan |
| Lepadidae | *Lepas hilli* | 1910 | Chilton (1911) | C | + | | Cosmopolitan |
| Tetraclitidae | *Austrobalanus imperator* | 2005 | NIWA/MAFBNZ | NIS | + | | Eastern Australia |
| Tetraclitidae | *Newmanella radiata* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical W Atlantic |
| Tetraclitidae | *Tesseropora wireni* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| Tetraclitidae | *Tetraclita coerulescens* | 2005 | NIWA/MAFBNZ | NIS | + | | Central Pacific |
| Tetraclitidae | *Tesseropora rosea* | 2005 | NIWA/MAFBNZ | C | + | + | SW Pacific |
| Tetraclitidae | *Tetraclita squamosa* | 2005 | NIWA/MAFBNZ | NIS | + | | Southern China |

(continued)

**Table 1** (continued)

| Higher taxon | Family | Species | Date of first record or introduction | Citation | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
| | Tetraclitidae | *Tetraclita japonica* | 1975 | Foster and Willan (1979) | NIS | + | | NW Pacific |
| | Tetraclitidae | *Tetraclitella multicostata* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |
| | Tetraclitidae | *Tetraclitella pilsbryi* | 2006 | NIWA/MAFBNZ | NIS | + | | NW Pacific |
| OSTRACODA | Loxoconchidae | *Loxoconcha parvifoveata* | 1960s | Eagar (1999) | NIS | + | + | Southern Australia |
| CHELICERATA | Limulidae | *Carcinoscorpius rotundicauda* | 1910 | Chilton (1911) | NIS | | | Tropical Indo-West Pacific |
| | Limulidae | *Limulus polyphemus* | 1940 | Powell (1949) | NIS | | | W Atlantic |
| | Phoxichilidiidae | *Endeis flaccida* | 2005 | NIWA/MAFBNZ | NIS | + | | Tropical Indo-West Pacific |

Abbreviations: *NIS* non-indigenous, *C* cryptogenic, *?* uncertain

Records based on specimens collected under funding by the Ministry of Agriculture and Forestry/Biosecurity New Zealand and southern Australia held in the NIWA Biosecurity collection are indicated by NIWA/MAFBNZ

Deliberate introductions indicated(a). Species established within New Zealand are indicated, as are species that have been detected in hull fouling in New Zealand

**Table 2** Alien (non-indigenous) and cryptogenic marine Crustacea detected in Australian waters

| Higher taxon | Family | Species | Date of first record or introduction | Reference | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
| DECAPODA | Cancridae | *Metacarcinus novaezelandiae* | 1880 | McNeill and Ward (1930) | NIS |  | + | New Zealand |
|  | Carcinidae | *Carcinus maenas* | Pre 1900 | Fulton and Grant (1900, 1902) | NIS | + | + | NE Atlantic |
|  | Hymenosomatidae | *Halicarcinus innominatus* | 1926 | Dartnell (1969) | NIS |  | + | New Zealand |
|  | Inachoididae | *Pyromaia tuberculata* | 1978 | Morgan (1990) | NIS |  | + | E Pacific |
|  | Palaemonidae | *Palaemon macrodactylus* | 1970s | Buckworth (1979) | NIS |  | + | NW Pacific |
|  | Porcellanidae | *Petrolisthes elongatus* | 1912 | King (1997) | NIS |  | + | New Zealand |
|  | Portunidae | *Charybdis japonica* | 2000 | Smith et al. (2003) | NIS |  |  | SE, NE Asia |
| AMPHIPODA | Caprellidae | *Caprella acanthogaster* | 1993 | Guerra-Garcia and Takeuchi (2004) | NIS | + | + | NW Pacific |
|  | Caprellidae | *Caprella californica* | 2002 | AMBS (2002) | NIS | + | + | E Pacific |
|  | Caprellidae | *Caprella danilevskii* | 1879 | Guerra-García and Takeuchi (2004) | C |  | + | Cosmopolitan |
|  | Caprellidae | *Caprella equilibra* | 1879 | Haswell (1885) | C | + | + | Cosmopolitan |
|  | Caprellidae | *Caprella penantis* | 1878 | McCain and Steinberg (1970) | C | + | + | Cosmopolitan |
|  | Caprellidae | *Caprella scaura* | Pre 1885 | Haswell (1885) | C |  | + | Western Indian Ocean |

(continued)

**Table 2** (continued)

| Higher taxon | Family | Species | Date of first record or introduction | Reference | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
| | Caprellidae | *Paracaprella pusilla* | 2003 | Montelli and Lewis (2008) | NIS | + | + | Cosmopolitan |
| | Corophiidae | *Apocorophium acutum* | 1937 | Pollard and Pethebridge (2002b) | NIS | | + | NE Atlantic |
| | Corophiidae | *Crassicorophium bonnellii* | 1995 | Lemmens et al. (1996) | NIS | + | + | NE Atlantic |
| | Corophiidae | *Laticorophium baconi* | 1996 | Storey (1996) | NIS | | + | E Pacific |
| | Corophiidae | *Monocorophium acherusicum* | Pre 1921 | Chilton (1921) as *C. crassicorne* | NIS | + | + | NE Atlantic |
| | Corophiidae | *Monocorophium insidiosum* | 1973 | Storey (1996) | NIS | | + | NE Atlantic |
| | Corophiidae | *Monocorophium sextonae* | 1995 | Poore and Storey (1999); Hurley (1954) | NIS | | + | New Zealand |
| | Dexaminidae | *Paradexamine pacifica* | pre 1909 | Pollard and Pethebridge (2002b) | NIS | | + | New Zealand |
| | Liljeborgiidae | *Liljeborgia cf dellavallei* | 2000 | Pollard and Pethebridge (2002b) | NIS | | + | E Atlantic |
| | Melitidae | *Elasmopus rapax* | 1884 | Hughes and Lowry (2010) | NIS | | + | Central or NE Pacific |
| | Ischyroceridae | *Jassa marmorata* | 1879 | Storey (1996) | NIS | + | + | NE Atlantic |
| | Stenothoidae | *Stenothoe valida* | Pre 1924 | Chilton (1924) | C | | + | E, W Atlantic |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| ISOPODA | Cirolanidae | *Cirolana harfordi* | 1972 | Bruce (1986) | NIS | | + | NE Pacific |
| | Cirolanidae | *Eurylana arcuata* | 1925 | Bowman et al. (1981) | NIS | + | + | Australia |
| | Sphaeromatidae | *Paracerceis sculpta* | 1975 | Harrison and Holdich (1982b) | NIS | + | + | NE Pacific |
| | Sphaeromatidae | *Paradella dianae* | 1971 | Harrison and Holdich (1982a) | NIS | + | + | NE Pacific |
| | Sphaeromatidae | *Pseudosphaeroma* sp. | 1984 | Bruce and Wetzer (2008) | C | | + | Not known |
| | Sphaeromatidae | *Sphaeroma serratum* | 1980 | Holdich and Harrison (1983) | NIS | + | + | NE Atlantic |
| | Sphaeromatidae | *Sphaeroma walkeri* | 1924 | Baker (1928) | NIS | + | + | Indian Ocean |
| TANAIDACEA | Tanaidae | *Tanais dulongi* | 1970s | Sieg (1980) | NIS | + | + | E Atlantic |
| MYSIDACEA | Mysidae | *Neomysis japonica* | 1977 | Hutchings (1983) | NIS | | + | NW Pacific |
| STOMATOPODA | Squillidae | *Oratosquilla oratoria* | 1985 | Ahyong (2001) | NIS | + | + | NW Pacific |
| CIRRIPEDIA | Balanidae | *Amphibalanus improvisus* | 1940s | Bishop (1951) | NIS | + | | W Atlantic |
| | Balanidae | *Amphibalanus reticulatus* | Pre 1979 | Lewis (1979) | NIS | | + | Indo-Pacific |
| | Balanidae | *Megabalanus volcano* | 1953 | Allen (1953) | NIS | + | | Tropical Indo Pacific |

(continued)

**Table 2** (continued)

| Higher taxon | Family | Species | Date of first record or introduction | Reference | Status | Fouling | Established | Probable native range |
|---|---|---|---|---|---|---|---|---|
| | Balanidae | *Megabalanus rosa* | 1953 | Jones (1987) | NIS | + | + | NE Pacific |
| | Balanidae | *Megabalanus tintinnabulum* | 1949 | Jones (1987) | NIS | + | + | E Atlantic |
| | Balanidae | *Megabalanus zebra* | 2000 | Pollard and Pethebridge (2002a) | NIS | | + | Indo-Pacific, SE Atlantic |
| | Balanidae | *Notomegabalanus algicola* | 1943 | Allen (1953) | NIS | + | + | SW Indian Ocean |

Abbreviations: *NIS* non-indigenous, *C* cryptogenic

Species established within Australia are indicated, as are species that have been detected in hull fouling in Australia hull-intercepts or ballast water, but as yet not established, is useful as a potential indicator of species with increased risk of successful introduction. Many species are clearly identifiable as either native or alien, but where knowledge is insufficient, the ‘grey zone’ of cryptogenics arises (Sliwa et al. 2009; Hayden et al. 2009). For each species, a date of first record or estimated first arrival and a reference to this has been provided. Many of the New Zealand records are new reports based on specimens collected by various projects funded by the Ministry of Agriculture and Forestry Biosecurity New Zealand (MAFBNZ) and held in the biosecurity collection of the National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand. These records are identified as NIWA/MAFBNZ. For each species, the probable native range is given, and an indication as to whether the species is known to be established and whether or not it has been collected from hull fouling. Cryptogenic versus alien status is given. For the list, alien species are regarded as those that do not naturally occur around mainland New Zealand or Australia (including Tasmania). That is, distant territorial waters are not included, such as Christmas Island (Australia), or the Kermadec Islands (New Zealand). For example, the spider crab *Schizophroida hilensis*, which was found in hull fouling off North Island, New Zealand, is currently marked as alien, even though it occurs naturally to the far north in the Kermadec Islands, which remain in New Zealand territorial waters.

The taxonomic breakdown is shown in Tables 1 and 2 for New Zealand and Australia, respectively. Forty-one alien or cryptogenic crustacean species are recorded from Australia with amphipods (17), decapods (7), isopods (7) and cirripedes (7) dominating; a single tanaidacean, mysid and stomatopod are also known. In total, 14% are cryptogenic; half (51%) have been detected in hull or vessel fouling in Australia. At 115, the number of alien or cryptogenic species of arthropod (112 Crustacea; 3 Chelicerata) recorded from New Zealand is almost triple that of Australia. The taxonomic composition differs from that of Australia with the dominant taxa being cirripedes (50) and decapods (27), followed by amphipods (20) and isopods (11). Two alien species of tanaid, one ostracod and one stomatopod are recorded. In addition to Crustacea, three alien chelicerate species have been recorded from New Zealand (Table 1) but none are established. Of the 115 marine arthropod species recorded, 9% are cryptogenic and the majority (80%) occur in fouling assemblages. At first glance, the absolute and proportional differences between alien/cryptogenic crustacean species recorded respectively from New Zealand and Australia are staggering. New Zealand has the unenviable distinction of having one of the highest rates of terrestrial feral incursion in the world; is it also following suit in the marine realm? Closer inspection of the numbers reveals a different picture. The New Zealand totals are dominated by cirripedes, which are the primary Crustacea recorded from vessel hulls. Of these, many have been sampled on vessels berthed in ports, but are not yet known to be established. If only established species are considered, 38 species are recorded from Australia (16% cryptogenic) compared to 29 species (18% cryptogenic) from New Zealand. Invasive crustaceans that have drawn the most attention in New Zealand and in Australia are *Carcinus maenas* (Carcinidae), *Charybdis japonica* (Portunidae), *Pyromaia tuberculata* (Inachoididae), and *Caprella mutica* (Caprellidae).

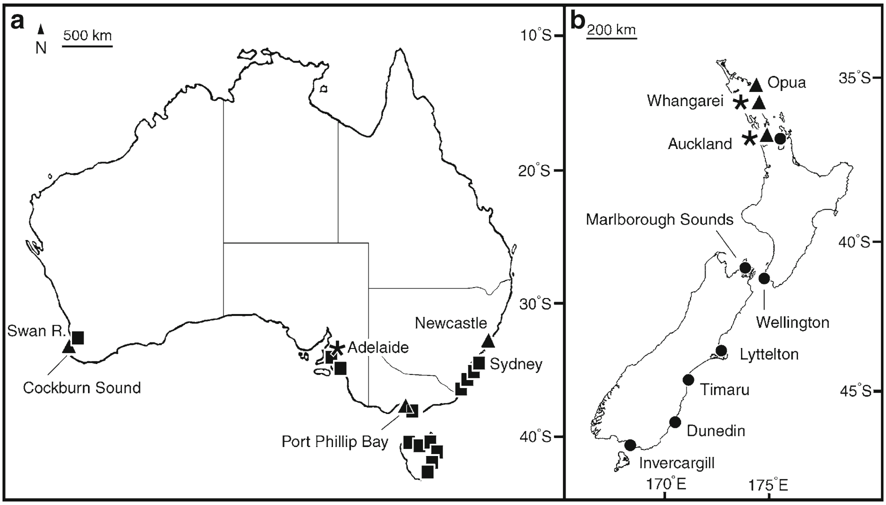

**Fig. 1** Map of (**a**) Australia and (**b**) New Zealand, showing reported localities of *Carcinus maenas* (■), *Charybdis japonica* (*), *Pyromaia tuberculata* (▲), and *Caprella mutica* (●). Note that *C. maenas* is apparently no longer present in the Swan River, Western Australia, nor is *Charybdis japonica* near Adelaide, South Australia. Records of *C. mutica* from Invercargill, Dunedin, and Auckland are from vessel hull fouling only

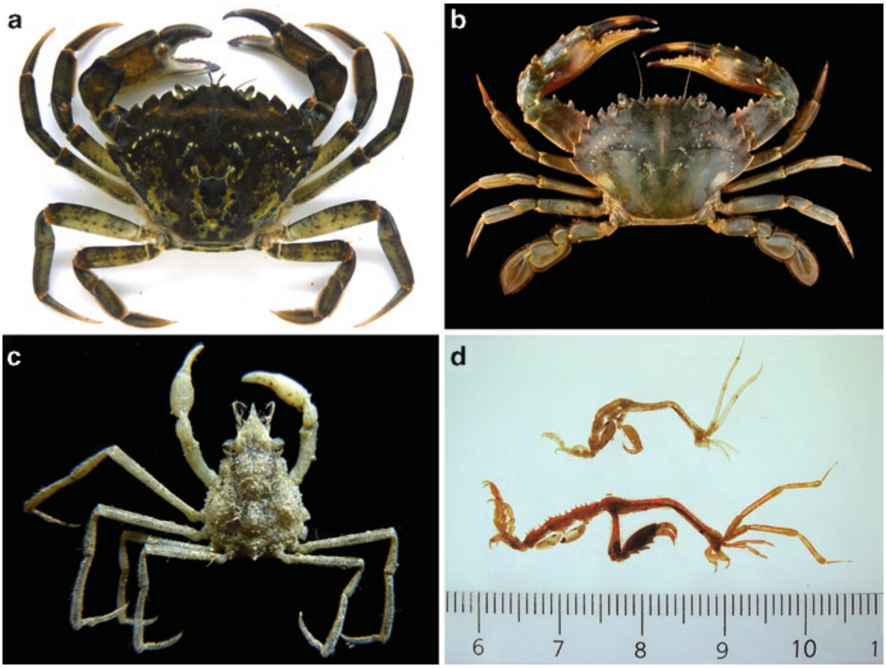

**Plate 1** (**a**) *Carcinus maenas*, Victoria, Australia. (**b**) *Charybdis japonica*, Waitemata Harbour, New Zealand. (**c**) *Pyromaia tuberculata*, Kaipara Harbour, New Zealand. (**d**) *Caprella mutica* (*lower*), *Caprella equilibra* (*upper*), Pelorus Sound, Marlborough Sounds, New Zealand (Photos: (**a**)–(**c**), S. Ahyong; (**d**), C. Woods)

## 2.1 *Carcinus maenas* (Linnaeus, 1758): European Shore Crab

The European shore crab or green crab (Fig. 1a; Plate 1a) is possibly the best-known invasive crustacean worldwide (Carlton and Cohen 2003). This species is recognised by the IUCN as being amongst the top one hundred worst bioinvasives (Lowe et al. 2000). It is regarded as a high-risk species worldwide, and in Australia, is subject of a National Control Plan (Australian Government 2008). *Carcinus maenas* is native to the Atlantic coast of Europe and North Africa, from Norway to Mauritania, including the British Isles (Clark 1986). The crab was introduced to the western Atlantic (first reported in 1817) and is now established on the east and west coasts of North America, South Africa, Japan, Patagonia, and Australia (Hidalgo et al. 2005). In Australia, *C. maenas* established in Port Phillip Bay before 1900 (possibly as early as the 1850s) and is believed to have arrived in hull fouling or in solid ballast discarded by timber ships (Fulton and Grant 1900, 1902). *Carcinus maenas* has also been present in New South Wales, as far north as Sydney since before 1900 (Ahyong 2005). A single specimen was collected in the Swan River estuary, Perth, in 1965, but the species has not since been found anywhere in Western Australia (McDonald and Wells 2009). In South Australia, *C. maenas* was first detected in Port Adelaide in 1976, and then in the Coorong in 1986 (Zeidler 1978, 1988). The most recent range expansion of *C. maenas* in Australia was to Tasmania, where it was first detected in 1993 in Georges Bay on the northeast coast (Gardner et al. 1994). It is now abundant along the north and east coasts of Tasmania at least as far south as Bruny Island (Proctor and Thresher 1997). Analysis of prevailing oceanographic conditions and size-frequency data of specimens collected at or near the time of first detection suggests that *C. maenas* may have been present in Tasmania for 2–4 years prior (Thresher et al. 2003). At present, *C. maenas* ranges from New South Wales (Sydney region) south to Victoria, Tasmania and South Australia. It is not currently found in New Zealand.

Within its native range, *C. maenas* occurs in estuarine and fully-marine habitats on mud, sand, rock and seagrass and marsh beds, typically in upper intertidal to shallow subtidal zone, but down to at least 62 m (Clark 1986). In Australia, the habitats of *C. maenas* are similar to those in its native range. The biology of *C. maenas* has been extensively studied in Europe and North America, both as a model organism, and also as an invasive species (see Cohen et al. 1995; Thresher 1997; Behrens Yamada 2001). Suffice it to say, its wide physiological tolerances, non-specialist habitat or dietary requirements, and high fecundity make *C. maenas* an ideal invasive species. In parts of North America, *C. maenas* is known to have significant impact and has proven destructive in shellfish beds and on rocky reefs (Behrens Yamada 2001), though its ecology and impacts in Australia remain to be quantified. In most parts of its Australian range, skates and rays, along with large, aggressive brachyuran predators, such as *Portunus armatus* (formerly *P. pelagicus* in Australia) are common. In Tasmania, the aforementioned predators are uncommon or absent, and this is where *C. maenas* may have the most significant impact. Large male *C. maenas* are more significant predators of juvenile native bivalves (*Katelysia scalarina*) than are native crabs such as *Paragrapsus gaimardii* (see Walton 1997), and survival of juvenile blue mussels (*Mytilus edulis planulatus*) outside of the range of *C. maenas*, was significantly higher than within (Mackinnon 1997). *Carcinus maenas* is known to prey on other native crabs and Ruiz and Rodriguez (1997) found a strong negative correlation between presence of *C. maenas* and abundance of three common native shore crabs. Thus, preliminary data suggest that *C. maenas* has the potential to significantly impact native bivalve and crab populations in Tasmania. Direct impacts on commercial oyster and mussel fisheries, however, are not yet apparent, possibly because oysters and blue mussel are farmed in Tasmania "off the bottom". Oysters are grown in plastic mesh baskets on racks standing about a metre above the substrate, and mussels are grown on long-lines in mid-water, which are generally out of reach of foraging crabs (Proctor 1997).

*Carcinus maenas* has been established in Australia for so long and over such a wide range that eradication is effectively impossible using current management tools. Use of rhizocephalan parasites, such as *Sacculina carcini* and *Portunion meanadis*, that 'castrate' male crabs, or parasitic Nemertea that feed on brooded eggs have been investigated by several workers around the world and appear have good potential (Kuris 1997; Behrens Yamada 2001). Thresher (1996) specifically explored possibilities for use of *S. carcini* in the Australian context, with the most important concerns being the degree of parasite specificity and its potential impact on native crabs. Considerably more research is required before such biological controls can be applied. Recently, European workers made important progress using of female sex pheromones, identified as uridine diphosphate, to target and trap male *C. maenas* theoretically leading to a destabilised and rapidly declining wild population (Hardege et al. 2009).

## 2.2 *Charybdis japonica* (A. Milne-Edwards, 1861): Asian Paddle Crab

*Charybdis japonica* (Fig. 1a, b; Plate 1b) is native to eastern Asia, including coastal regions of China, Japan, Korea, Taiwan and Malaysia. It is aggressive and active, with generalist dietary requirements, and favours low-energy intertidal and shallow sublittoral habitats including seagrass beds, sand and mud flats and embayments (Hu and An 1998). *Charybdis japonica* was first detected in New Zealand and Australia in September and December 2000, respectively (Smith et al. 2003). In Australia, a single adult male was captured in the Port River, Adelaide, South Australia. No further specimens have been collected from South Australia, and it appears that the species is not established there. In New Zealand, the first specimens were collected from the Waitemata Harbour, Auckland, and it is now widespread through the Auckland region including the Tamaki and Weiti estuaries, and more recently Whangarei Harbour (Gust and Inglis 2006). *Charybdis japonica* probably arrived in New Zealand as larvae in ballast water. Although various crabs, including *Charybdis* species have been found in sea chests or ballast tanks as adults or juveniles (e.g., Coutts and Dodgshun 2007 for *C. hellerii*, Gollasch, 2002 for *C. feriata*), the absence of specific parasites in New Zealand *C. japonica* is consistent with larval, rather than adult, introduction (Miller et al. 2006). Additionally, about 17% of international vessels visiting the Port of Auckland in 1999 arrived from ports within the native range of *C. japonica*, accounting for about half of the ballast water discharged into that port (Inglis 2001).

As might be expected for a species of *Charybdis*, New Zealand *C. japonica* occurs in estuarine habitats and embayments on soft level substrates. Currently, little is known about the biology of *C. japonica* in New Zealand and studies are currently underway by local universities and other research institutes in order to assess and mitigate its impacts. Population-genetic studies of *C. japonica* in New Zealand indicate an initial bottleneck at colonisation with only small-scale changes in allele frequencies between 2002 and 2007, and circumstantial evidence of a secondary invasion (Tooman 2009). Preliminary analysis of habitat use in New Zealand estuaries, in combination with environmental parameters from its native range, suggests that *C. japonica* could survive in estuaries throughout much of New Zealand, though it is unclear if reproductive populations could be maintained in each case (Gust and Inglis 2006). At present, the relatively wide but still limited range of *C. japonica* in New Zealand makes eradication feasible, though probably not for long. Attempts to control *C. japonica* via standard traditional baited trapping has not proven very effective (Golder Associates 2008), and investigations are currently underway into species-specific sex pheromones to increase trap yields and destabilise populations. Just as *C. hellerii* has proven destructive after introduction to the various Atlantic localities (Dineen et al. 2001), *C. japonica* has the potential to negatively impact estuarine communities in New Zealand by competition with, and predation on, native species.

### 2.3 *Pyromaia tuberculata* (Lockington, 1877): Fire Crab

The fire crab, *Pyromaia tuberculata* (Fig. 1a, b; Plate 1c), is native to the Pacific coast of North America, but has spread over the last 40 years to Japan, Brazil, Argentina, Southern Australia and New Zealand, probably as larvae in ballast water (Poore 2004). *Pyromaia tuberculata* appears to have arrived in Australia within the last three decades, where it was first collected in 1978 from Cockburn Sound, Western Australia (Morgan 1990). The species has since been reported from Port Phillip Bay, Victoria, where it has been present since at least 1990 (Poore and Storey 1999), and in 1996, from eastern Australia, off Newcastle, New South Wales (Ahyong 2005). The first New Zealand records of *P. tuberculata* are from the Auckland area (the Hauraki Gulf and Firth of Thames) in 1975 (Cranfield et al. 1998). *Pyromaia tuberculata* has since been detected in Kaipara and Manukau harbours in the Auckland region (2006; NIWA/MAFBNZ data), Whangarei (2002; Inglis et al. 2006c) and Opua (2006; NIWA/MAFBNZ data). Within its natural range, *P. tuberculata* occurs in a variety of habitats including rocky reefs amongst seaweeds, wharf pilings, under rocks, among sponges and other fouling, and also on sand/mud sediments. It usually lives in shallow water but may occur down to 650 m (Brockerhoff and McLay 2008). A feature of *P. tuberculata* contributing to its success as an invasive species is its ability to colonise disturbed, organically polluted habitats such as maritime ports (Furota and Furuse 1988). It can tolerate hypoxic conditions and its high fecundity and short generational cycle (approximately 40 days) further enhance its ability to rapidly expand into new habitats (Furota 1996a, b). In the organically polluted waters of Tokyo Bay, Japan, *P. tuberculata* has become firmly established. Juvenile crabs are able to survive summer hypoxic conditions, quickly recruit after the summer hypoxia recovers, reach maturity and breed. Many native benthic species in the same habitat are killed during the hypoxic summer season, leaving available habitat and resources for *P. tuberculata* to utilise (Furota 1988, 1990). The ecological impacts of invasive *P. tuberculata* have been studied only indirectly in Port Phillip Bay where it is locally abundant at depths below 12 m and has become an important food source for demersal fish (Parry et al. 1995). It is widespread and abundant throughout much of Port Phillip Bay and is now among the 20 most important linkages in the Port Phillip Bay foodweb (Officer and Parry 1997). The abundance of *P. tuberculata* in Phillip Bay has possibly promoted expansion of the spiky globefish into deeper water (Hobday et al. 1999). Thus, within decades of its first introduction, *P. tuberculata* may have contributed to changes in fish community structure in Port Phillip Bay. Nothing is known of the ecology of *P. tuberculata* in Northern New Zealand, but it too is probably an important prey item for demersal fish.

### 2.4 *Caprella mutica* (Schurin, 1935): Japanese Skeleton Shrimp

*Caprella mutica* (Fig. 1b; Plate 1d) is one of the larger caprellid amphipods, reaching 50 mm in length. It is native to temperate northeastern Asia but over the last 40 years, *C. mutica* has spread throughout the Northern Hemisphere, starting with Humboldt Bay on the west coast of North America in the 1970s, with subsequent populations establishing in Europe and the east coast of North America via multiple invasions (Ashton et al. 2007b, 2008). In 2002, *C. mutica* was identified from Timaru, South Island, New Zealand; the first southern hemisphere location (Woods et al. 2008). The established New Zealand range presently includes Timaru (first record February 2002), Lyttelton Harbour (April 2006), Pelorus Sound in the Marlborough Sounds (May 2007) and Wellington Harbour (November 2007) (Woods et al. 2008; NIWA/MAFBNZ data). In addition, *C. mutica* has also been collected from vessel hulls in Auckland, Dunedin and Invercargill in 2006 (NIWA/MAFBNZ data), though it is apparently not yet established in those ports. Although Timaru was the first site of discovery, *C. mutica* was probably first introduced at Lyttelton (Willis et al. 2009). In its native habitat, *C. mutica* is associated with attached macroalgae and near-bottom drifting seaweeds including *Sargassum* spp. (Ashton et al. 2007b). Outside of its native range *C. mutica* is commonly associated with human activities and predominantly found in ports and harbours, oilrigs and aquaculture facilities where it densely colonises nets, mooring ropes and buoys (Willis et al. 2004). In New Zealand, *C. mutica* is common on hull fouling, often on wharf piles and is especially abundant on suspended mussel-culture lines.

Although *C. mutica* is native to the Northeastern Pacific, population-genetic studies indicate that the New Zealand population is probably derived from Atlantic populations (Willis et al. 2009).

The impact of *C. mutica* in New Zealand is as yet unknown, though it could displace smaller, less abundant native caprellids and deplete resources through rapid reproduction, high population density, and aggressive behaviour. As with other invasive populations of *C. mutica* around the world, population densities in New Zealand are higher than in its native habitat. Populations sampled in New Zealand by Willis et al. (2009) almost always exceeded 10,000 individuals $m^{-2}$ and were as high as 1,84,800 $m^{-2}$. Moreover, populations of *C. mutica* in its native range and in Europe experience a winter decline in abundance and reproduction (probably related to low water temperature), unlike New Zealand populations, which show no such decline and are reproductive year-round, making further range expansion highly likely (Willis et al. 2009). *Caprella mutica* can be a major dietary component of the New Zealand seahorse *Hippocampus abdominalis* (see Woods et al. 2008), warranting further study of its role in food webs and community structuring.

## 3 Temporal Trends

Alien species have arrived in New Zealand and Australian waters since at least the 18th century. Twenty-seven alien species of Crustacea have become established in New Zealand, with only 4 confirmed as established prior to the 1940s. The majority have probably become established since about 1980 onwards. Excluding the deliberate but unsuccessful fisheries introductions (see Sect. 5.2), at least 81 alien marine crustacean species have been detected in New Zealand waters, which are not yet known to be established. Most of these have been collected from vessel hulls in the last decade as a result of New Zealand government biosecurity programmes. Of the 38 alien/cryptogenic marine arthropods (all crustaceans) established in Australia, a quarter had become established by 1943, with the remainder believed to have become established since the 1970s. The difficulties in pinpointing dates of first arrival and subsequent establishment notwithstanding, the estimates for a large proportion of alien Crustacea in both New Zealand and Australia broadly correlate with increasing volumes of maritime traffic associated with international trade (and certainly also with increased biosecurity surveillance). Moreover, as a general trend, the origin of invaders follows the dominant source of maritime traffic, with the earliest invasive species originating from European Atlantic waters, and more recent arrivals originating from the Northwestern Pacific (Hayden et al. 2009).

The absolute differences in known established alien marine arthropods between New Zealand and Australia (29 versus 38) and non-established aliens (83 vs. 2) are noteworthy. In view of the considerable difference in coastline length and higher volume of maritime traffic to Australia, the lower numbers of alien crustaceans detected in Australia probably reflects differences in surveillance processes between the two countries. In Australia, between about 1995 and 2004, baseline surveys of 42 marine ports were conducted in order to estimate presence and distribution of alien species (Sliwa et al. 2009). These surveys followed standard CRIMP (Centre for Research into Invasive Marine Pests) protocols developed by Hewitt and Martin (1996, 2001). Between 2000 and 2008, 20 New Zealand ports were also surveyed one or more times, in addition to extensive surveys of vessel hulls (e.g., Inglis et al. 2006a, b, c, 2008). The New Zealand port surveys followed modified CRIMP protocols (Hewitt and Martin 1996, 2001; Gust et al. 2001), but were also geared towards generating baseline knowledge of overall species composition. The Australian port surveys focused more on target species rather than identifying all species sampled (Sliwa et al. 2009). In the New Zealand case, however, samples were all identified to species where possible. Additionally, since 2006, MAF Biosecurity New Zealand has funded the National Institute of Water and Atmospheric Research (NIWA) to provide species-level identifications and collection management of all marine biosecurity specimens through the Marine Invasives Taxonomic Service (Gould and Ahyong 2008). This has provided an extensive (although almost certainly incomplete) inventory of native and alien species present in New Zealand ports. Thus, the apparent anomalies between numbers of detected aliens in Australia and New Zealand probably reflect different survey approaches and goals.

## 4 Biogeographic Patterns

The alien crustacean ‘fauna’ in Australian and New Zealand waters does not show strong biogeographic trends, though the majority of established aliens in New Zealand and Australian ports originate in the Australasian region. This more or less reflects the pattern of maritime traffic, of which a large volume is now from East and Southeast Asia. The most recent introduction is the Northwestern Pacific crab, *Charybdis japonica,* now established in the Auckland area. Other temperate-water species from outside the region, such as the European Green Crab, *Carcinus maenas* and eastern Pacific Fire crab, *Pyromaia tuberculata*, have also established themselves in Australia and/or New Zealand (for *P. tuberculata*). *Carcinus maenas* arrived in Australia from Europe more than a century ago, and *P. tuberculata*, although native to the west coast of America, arrived in Australia and New Zealand in the 1970s, probably via Japan. Not surprisingly, several species have been successfully ‘exchanged’ between New Zealand and Australia. The indigenous New Zealand species, *Petrolisthes elongatus* (Porcellanidae), *Metacarcinus novaezelandiae* (Cancridae) and *Halicarcinus innominatus* (Hymenosomatidae), were introduced to southern Australia in the late 1800s or early 1900s. Similarly, the isopod *Eurylana arcuata* (Cirolanidae), amphipods *Melita matilda* (Melitidae) and *Paracorophium brisbanensis* (Corophiidae), and barnacle *Austromegabalanus nigrescens* (Balanidae) have been introduced to New Zealand from Australia. Some Australian and New Zealand crustaceans have also travelled further a field, such as the barnacle *Austrominius modestus* (Austrobalanidae), now established in the North Atlantic. Many other alien Crustacea in Australian and New Zealand waters are common in fouling communities around the world, including corophiidean amphipods and numerous barnacles, which had gone around the world even before Charles Darwin took an interest.

# 5 Main Pathways

The isolated position of New Zealand in the temperate Southwestern Pacific means that incremental range expansions by species from neighbouring regions are unlikely and that the primary vectors for invasive Crustacea are hull fouling and ballast water associated with shipping and other marine craft, such as oil platforms and barges. This is also true for Australia. Australia has a considerably longer coastline and spans a greater latitudinal range (~35°) than the New Zealand mainland (~15°), having close northern neighbours in Indonesia and Papua New Guinea. The tropical marine fauna of far northern Australia and southern Indonesia, that of the Arafura and Timor seas, is largely shared, so invasive species in northern Australia will probably originate from elsewhere, as in the case of the Caribbean black striped mussel (*Mytilopsis saillei*) detected and eradicated in Port Darwin (CRIMP 2001). Most of the major Australian maritime ports, however, correspond to major population centres in subtropical eastern or temperate southern Australia, such as Brisbane, the Sydney region (Port Jackson, Port Botany and Port Kembla), Melbourne (Port Phillip Bay), Hobart, Adelaide and Perth. As with New Zealand, Australia is also effectively isolated geographically, and the most likely invasion pathways for marine crustaceans in Australia are via international shipping. Marine species have probably been dispersed via shipping from time immemorial, but the advent of container shipping in the 1960s along with significant overall increases in international maritime traffic has markedly increased the importance of shipping as a means of marine species introductions (Carlton 1985). Although shipping comes to New Zealand and Australia from all around the world, the primary trade routes involve a northerly circuit through East Asia and Southeast Asia, and a trans-Pacific circuit to the west coast of America, with the former contributing the largest volume of traffic and potential invasive species. Both of these routes include both tropical and temperate water ports, increasing the suite of potential invasive species that could be carried.

## *5.1 Ballast and Hull Fouling*

The primary vectors associated with shipping are ballast water and hull fouling. Ballast water is an important vector for transporting crustaceans into new environments, particularly as pelagic larvae, and has been widely studied (e.g., Drake et al. 2005). In addition to pelagic organisms, ballast water also includes sediments that accumulate within, including associated biota or propagules. Ballast water is uploaded in a foreign port and variously discharged depending on the stabilisation and amount of cargo on a vessel. Owing to the high reliance on international shipping for trade, Australia and New Zealand are vulnerable to ballast-water introductions. The type and direction of trade is significant for risk assessment of ballast water. Australia is a net exporter of raw materials such as coal, iron ore, grain and wood-chips. Thus, the majority of bulk carriers, about half from Japan, enter Australian ports in ballast, discharging large volumes of ballast water prior to loading. Kerr (1994) estimated that about 160 million tonnes of ballast water are discharged annually into Australian ports. In New Zealand, a significant volume of shipping traffic also originates from East Asia, with an estimated 4.4 million tonnes of ballast water discharged in 2002 (Wotton and Hewitt 2004), the presumed vector of *Charybdis japonica* into New Zealand (Gust and Inglis 2006).

In addition to water as ballast, solid ballast has historically been used in vessels for stabilisation during transit. Dry or semi-dry ballast included rocks, sand, wood and other substrata collected from near shore, which may include local species. Subsequent disposal of solid ballast in port introduced new species into the environment, as is probably the case for *Carcinus maenas* in Australia more than a century ago (Fulton and Grant 1902).

Hull fouling is a long-recognised dispersal vector, operating since the earliest days of shipping, and is possibly the most significant vector for marine species introduction to Australia and New Zealand (Cranfield et al. 1998). Some types of bulk carriers and container vessels are under strong commercial pressure to maximise speed to minimise transit times providing strong incentives for regular defouling. These high-speed merchant vessels, with good maintenance schedules, usually have reduced levels of external fouling, but sea chests and internal structures nevertheless consistently harbour fouling assemblages (Dodgshun and Coutts 2003). Twenty-seven percent (41/150) of species in a recent survey of sea chests from 42 vessels in New Zealand were Crustacea, of which at least 7 species were alien (Coutts and Dodgshun 2007). Slower-moving vessels, such as pleasure craft, some fishing vessels, barges, pontoons and oil drilling platforms present a greater risk, because of the much higher levels of fouling often present (Hewitt et al. 2004b). In this context, floating oil-drilling platforms and rigs, which spend long periods in situ and otherwise move at slow speed, provide a large surface area and complex substrate for settlement, and are a significant potential source of alien species. Whole epibenthic communities can effectively be translocated (Yeo et al. 2009), providing a large input of propagules. Within a diverse fouling assemblage on the Maui oil platform moored off New Zealand in the 1970s, Foster and Willan (1979) found 6 of 12 species of barnacles to be alien. Similarly, in a recent survey of a barge destined for Macquarie Island from Tasmania, more than half of crustacean species that could be positively identified were native to neither the source nor destination, including extremely high densities of the known invasive amphipods *Monocorophium ascherusicum* (Corophiidae) and *Jassa marmorata* (Ischyroceridae) (see Lewis et al. 2006).

Other sources of fouling assemblages include floating wrecks and structures. A floating wreck recently intercepted off northern New Zealand was found to include nine Crustacean species not known from mainland New Zealand (Williams et al. 2008). As expected, the bulk of alien crustaceans detected in New Zealand and Australia have been from some type of vessel fouling.

Half or more of the alien/cryptogenic crustacean species detected in Australia and New Zealand so far have been found in fouling (Tables 1 and 2).

### *5.2 Deliberate Introductions: Fisheries, Aquaculture and Aquarium Trade*

Fisheries, aquaculture and trade practises have resulted in the unintentional and also deliberate introductions of a number of Crustacea in both New Zealand and Australia. Deliberate introductions include species imported or translocated for aquaculture, fisheries and/or ornamental purposes. Unintentional or accidental introductions typically occur with livestock escapees, or incidentally when alien species are carried on aquaculture gear such as floats, ropes or cages, for instance.

In New Zealand, attempted introductions of edible crustaceans go back at least to the late 1800s through the efforts of various Acclimatisation Societies. In 1894, the Otago Acclimatisation Society attempted to introduce the Australian Eastern King Prawn *Melicertus plebejus* (as *Penaeus canaliculatus*: Penaeidae) from Australia into Dunedin Harbour (Thomson 1922). In 1892, the Wellington Acclimatisation Society released *M. plebejus* into Nelson harbour (Thomson and Anderton 1921). Both attempts were ill-conceived and, not surprisingly, unsuccessful. However, in addition to the more amateurish attempts to introduce potential fishery species by local New Zealand societies, more substantial efforts and better-planned efforts were made to 'create' new fisheries. In 1904, the Portobello Hatchery and Marine Station was established, principally to assist in naturalising potential fishery species. Between 1905 and 1918, the Portobello hatchery bred and attempted to naturalise the European lobster (*Homarus gammarus*: Nephropidae) and edible crab (*Cancer pagurus*: Cancridae). Substantial numbers of larvae were hatched and released, but without due consideration of regional hydrodynamics. Neither species became established. More recently, in the 1980s and 1990s, a short-term attempt was made to farm the marine prawn *Fenneropenaeus chinensis* (Penaeidae) and the Australian freshwater crayfish, the Smooth Marron, *Cherax cainii* (Parastacidae), in North Island, New Zealand; neither venture was successful, and brood-stock was destroyed. It is not clear, however, if all New Zealand marron populations have yet been eradicated, with sporadic reports of marron being found in farm dams or ponds (MAF 2005). At present, the only alien crustacean being farmed in New Zealand is the tropical freshwater shrimp, *Macrobrachium rosenbergii* (Palaemonidae), which is under intensive aquaculture at a facility near Lake Taupo, North Island. The warm-water requirement of *M. rosenbergii* means that the species is unlikely to establish in the wild.

As in New Zealand, local acclimatisation societies were active in parts of Australia, and although even monkeys were brought to Tasmania, Crustacea were not targeted.

Deliberate crustacean introductions for fishery purposes have not succeeded in New Zealand or Australia, but several successful introductions have accidentally occurred when translocating other fishery species. The indigenous New Zealand decapods *Petrolisthes elongatus*, *Halicarinus innominatus*, and *Metacarcinus novaezelandiae*, now well established in southeastern Australia, were most likely introduced accidentally to Tasmania amongst Foveaux Strait oysters transported there between 1900 and 1935 (Dartnell 1969), though King (1997) favoured solid ship ballast as the likely vector for *P. elongatus*. *Caprella mutica* is believed to have been translocated to the Pacific and Atlantic coasts of North America either as a result of numerous independent cross-oceanic introductions with oyster spat, or from small-scale transport following its first introduction (Cook et al. 2007), though it probably arrived in New Zealand on fouling or in ballast water.

Within Australia, translocations of freshwater crayfish have been cause for concern. Fortunately, Australia has not experienced the problem of foreign invasive crayfish as has been documented elsewhere in the world (Holdich 1999; Gherardi 2007), but translocations within the country have been problematical. Three species dominate Australian freshwater crayfish aquaculture, all Parastacidae: the yabby (*Cherax destructor*), the red-claw (*Cherax quadricarinatus*) and the smooth marron (*Cherax cainii*). All three species are also sold in small numbers for the aquarium trade, but the vast bulk of production is for human consumption. The yabby and red-claw dominate crayfish aquaculture in eastern Australia, and the smooth marron in the west. The red-claw has been translocated worldwide where it has often become feral (Ahyong and Yeo 2007). The yabby has been translocated to Western Australia and Tasmania where it may displace local species. The smooth marron, native to southwestern Australia is widely farmed and has been translocated in Australia; it has itself become a threat to the geographically restricted hairy marron (*Cherax tenuimanus*). The impacts of crayfish introductions into Western Australia are reviewed in detail by Lynnas et al. (2007).

## *5.3 Aquarium Trade Imports*

The worldwide aquarium trade is a multi-billion dollar industry (Wabnitz et al. 2003), that is growing by US$14 million annually (Padilla and Williams 2004). Aquarium-trade introductions are well documented around the world for marine and freshwater species, mainly fish (e.g., Whitfield et al. 2002). In Australia and New Zealand, however, especially for Crustacea, the role of the aquarium trade as a vector for alien species introductions is currently negligible compared to other vectors. This stems primarily from the longstanding prohibition on live invertebrate imports into Australia, and the highly restricted list of allowable invertebrate imports into New Zealand. In New Zealand, the coral reef shrimps *Lysmata amboinensis*, *L. debelius*, *Perclimenes brevicarpalis* and *Stenopus hispidus* are the only Crustacea currently approved for live import under the *Import Health Standard for Ornamental Fish and Marine Invertebrates from all Countries*, dated 21 March 2007.

## 6 Ecological and Economic Impacts

Invasive species have been identified as among the top threats to native biodiversity and impacts of invasive Crustacea have been documented around the world, for example, *Carcinus maenas* worldwide (Behrens Yamada 2001), *Paralithodes camtschaticus* in the northeastern Atlantic (Jorgensen and Primicerio 2007), and *Eriocheir sinensis* in Europe (Bentley 2010). Unfortunately, ecological impacts of alien Crustacea in New Zealand and Australia are not well quantified, though based on current research, few appear to be ecologically or economically problematical. Known impacts of the most significant invasive species in the Antipodes, *Carcinus maenas*, *Pyromaia tuberculata*, *Charybdis japonica*, and *Caprella mutica*, are discussed above under the profiles of those species.

Economic impacts derive from direct ecological changes induced by invasions, such as loss of fisheries or expensive defouling or eradication operations, as well as public funding channelled into biosecurity management and infrastructure. To date, *Carcinus maenas* has not significantly impacted fisheries in Australia, though the value of fisheries potentially at stake are currently valued at over AUD $25 million per year (ABARE 2007). Relative to elsewhere in the world, there appears to be a greater concern about invasive species in Australia and New Zealand, and this has resulted in significant public spending to protect national interests (Hewitt et al. 2004b).

Whereas invasive species seldom benefit habitat or economy, they are occasionally an economic plus. In Australia, sometime around the mid-1980s, the Japanese Mantis Shrimp (*Oratosquilla oratoria*) was introduced to Sydney Harbour, probably via ballast water (Ahyong 2001). It rapidly became established in the estuaries of the Sydney region and, since the early 1990s, *O. oratoria* has been commercially harvested. It appears to be most common in impacted, low diversity habitats, though its ecological impacts have not been studied. *Oratosquilla oratoria* was detected in New Zealand waters (Kapiara Harbour) for the first time in April 2010, where it probably arrived as larvae in ballast water. It is apparently established, and has probably been present at Kaipara since at least 2008 judging by the large size of specimens captured. The impact of *O. oratoria* in New Zealand is not presently known.

## 7 Management and the Future

The biosecurity systems in New Zealand and Australia are generally similar, being based around (1) border control, (2) import health standards, (3) post-entry quarantine, (4) surveillance, and (5) pest management (Hayden and Whyte 2003). In both cases, the primary controls are held by central government, though Australia has the added complexity of individual State and Territory jurisdictions, and pest management in New Zealand is also handled by Regional Councils. In Australia, a national framework is achieved through the *National System for the Prevention and Management of Marine Pest Incursions*, an intergovernmental agreement (Federal/State/Territory) coordinated by the federal Department of Agriculture, Forestry and Fisheries (DAFF). In New Zealand, exclusion and management of introduced species is governed by the Biosecurity Act 1993 and the Hazardous Substances and New Organisms Act 1996, and administered by MAF Biosecurity New Zealand (Hewitt et al. 2009).

Because the major invasion pathways for invasive Crustacea are ballast water and fouling, and because well-established marine invasive species are usually impossible to eradicate, border and pre-border control is even more critical as the primary line of defence (Hayden et al. 2009). Unfortunately, water-tight border controls in the marine context are extremely difficult to maintain. Policies in New Zealand and Australia promote offshore ballast-water exchange to reduce the risk of transporting invasive species to ports. Australia currently also uses a risk-based decision support system to determine when vessels from international ports are required to undertake a ballast-water exchange. The rationale for determining exchange depends on the presence/absence of identified invasive species in either the origin or destination ports (Dunstan and Bax 2008).

Developed protocols regulate ballast-water discharge in New Zealand and Australia, but the state of risk assessment and management of hull fouling is less mature. In New Zealand, an Import Health Standard (IHS) has yet to be established for fouled hulls or sea chests. Regulations are certainly in place that prohibit hull cleaning and dumping of foreign fouling in New Zealand waters, but the risks associated with fouled vessels entering New Zealand are yet to be robustly and routinely assessed. MAF Biosecurity New Zealand is currently undertaking a comprehensive and detailed assessment of the risks associated with hull fouling on all vessel types entering New Zealand (Hayden et al. 2009). Similarly, Australia is yet to develop a comprehensive framework for mitigating risks posed by hull fouling. That marine invasive species continue to arrive and establish in New Zealand and Australian ports indicates that current marine border and pre-border controls are not sufficiently effective.

Although the challenges in preventing arrival and establishment of invasives are significant, the challenges of detection are no less important. Robust sampling protocols have already been developed to detect alien species (Hewitt and Martin 1996, 2001). However, recognising them is another matter. From a biosecurity perspective, the relative isolation of Australia and New Zealand has advantages – invasive species are unlikely to easily arrive by natural means, especially in the case of New Zealand, and a large proportion of the Antipodean marine fauna is unique, making recognition of some alien species potentially easier. This of course presupposes comprehensive baseline knowledge of the local biota, which is yet to be achieved. Determining the status of native, alien or cryptogenic species can be extremely difficult, not to mention the status of undescribed species without sufficient baseline data. Fourteen to 20% of marine Crustacea established in Australia and New Zealand are presently regarded as cryptogenic. Ongoing taxonomic research is simply a must.

The current state of knowledge of the number and identity of marine crustacean invasions in New Zealand and Australia is still developing, though government initiatives in the last few decades have significantly progressed knowledge and capabilities. Baseline port surveys in both countries provide important data on invasive and native faunas, and targeted research informs development of national response plans. Ongoing research, however, is required, especially in assessing relative risks associated with existing invasion pathways (Minchin et al. 2009); in understanding the parameters that promote greatest propagule pressure (Johnston et al. 2009); and in fundamental taxonomic research that underpins accurate recognition of invasive and native species (Gould and Ahyong 2008).

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# Part IV
# Commercial Exploitation of Invasive Decapods

# The Pacific White Shrimp, *Litopenaeus vannamei*, in Asia: The World's Most Widely Cultured Alien Crustacean

**I Chiu Liao and Yew-Hu Chien**

**Abstract** The Pacific white shrimp, *Litopenaeus vannamei*, is native to the western Pacific coast of Latin America, from Peru to Mexico where water temperatures are normally over 20°C throughout the year. It was introduced into Asia experimentally from 1978 to 1979, but commercially only since 1996 into Taiwan and China and subsequently to several countries in southeast and south Asia. In 2008, 67% of the world production of cultured penaeid shrimp (3,399,105 mt) consisted of *L. vannamei* (2,259,183 mt). Such dominance was attributed to an 18-fold increase of production in Asia, from 93,648 mt in 2001 to 1,823,531 mt in 2008, which accounts for 82% of the total world production of *L. vannamei*. The commercial success of introducing *L. vannamei* into Asia can be attributed to its superior aquaculture traits compared with *Penaeus monodon*, the most popular cultured Asian penaeid. These include higher availability of genetically selected viral-pathogen-free domesticated broodstock, high larval survival, faster growth rate, better tolerance to high stocking density, lower dietary protein requirement, more efficient utilization of plant proteins in formulated diets, stronger adaptability to low salinity, better tolerance to ammonia and nitrite toxicity, and lower susceptibility to serious viral pathogens infecting *P. monodon*. China leads the world cultured *L. vannamei* production from 33% in 2001 to 47% in 2008 (1,062,765 mt), among which 51% (542,632 mt) were produced in inland freshwater ponds. The culture of *L. vannamei* in freshwater is expected to continue increasing in China, Thailand, and other countries in Asia due to higher profits compared to other freshwater aquaculture species, and higher land availability in inland than in coastal areas. Although Taura Syndrome Virus, the most economically significant viral pathogen of *L. vannamei* is not reported to be detrimental to aquaculture production in Asia nor have affected indigenous cultured or wild shrimp populations, precautionary measures have been advocated or enforced by government authorities and executed

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by some private sectors. Potential problems that can affect future Asian production of *L. vannamei* include: decreasing genetic diversity through domestication and selection; increasing trans-boundary movements between continents and within the Far East; and emergence of new and Asian-specific viral and other microbial diseases. These potential problems will require Asian governments to take preventive measures through legislative control as well as scientific and technical measures.

## 1 Distribution and Natural Habitat of *Litopenaeus vannamei*

The classification of the Pacific white shrimp or white leg shrimp, *Litopenaeus vannamei* (Boone, 1931), is: Phylum Arthropoda, Class Crustacea, Order Decapoda, Family Penaeidae, Genus *Litopenaeus* and Species *vannamei* (see Perez Farfante and Kensley 1977). It is native to the western Pacific tropical coast of Latin America, from southern Mexico in the north to northern Peru in the south, between latitude 32°N and 23°S. This penaeid is highly abundant along the coast of Ecuador to Esmeraldas (the border Province of Columbia) where gravid females are available year-round (Huang, pers. Comm. 1984) and is commercially fished in Gulf of California and Gulf of Tehuantepec (ICES/FAO 2005). However, there are few publications on the biology and ecology of *L. vannamei*.

*Litopenaeus vannamei* is extremely euryhaline, capable of inhabiting low salinity waters (1–2 psu), as well as hypersaline waters (40 psu) (Menz and Blake 1980). Fry and juveniles inhabit muddy bottoms in warm (25–32°C), saline (28–34 psu) waters, shallower than 70 cm, where they exhibit a little burying behaviour. Adults prefer higher salinity (34–35 psu) and deeper water (30–50 m). Abundance of juvenile stages presented an inverse correlation with salinity and a positive correlation in a coastal lagoon system in Mexico (Rivera-Velázquez et al. 2008).

## 2 Recent Development of Shrimp Culture in Asia

According to Fishery Statistics presented by the Food and Agriculture Organisation of the United Nations (FAO), world shrimp landings have been stagnant at around 3.20 million mt since 2003. In comparison, aquaculture production exhibits a continuous growth since 1993. Such growth has accelerated after 2000 and in 2007, aquaculture production (3.28 million mt) exceeded fishery production (3.19 million mt) for the first time, with a 50.2:49.8% ratio. In 2008, aquaculture production reached a new record, 3.40 million mt, while shrimp landings fell to 3.03 million mt, resulting in a 52.9:47.1% ratio (Fig. 1). Rapid growth in aquaculture production was attributed to an 18-fold increase in *L. vannamei* farming activities in Asia, from

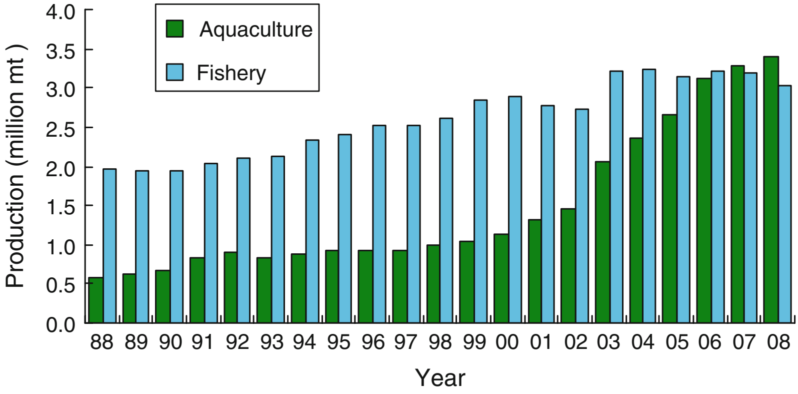

**Fig. 1** World shrimp production, 1988–2008

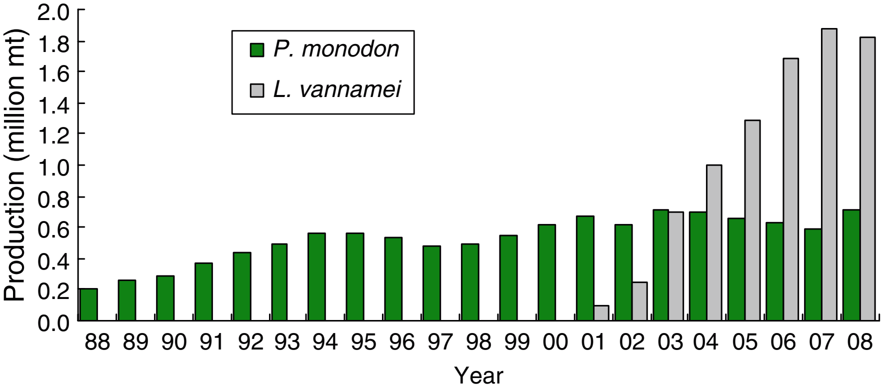

**Fig. 2** Production of *Penaeus monodon* and *Litopenaeus vannamei* in Asia, 1998–2008

0.94 million mt in 2001 to 1.82 million mt in 2008. In contrast, *P. monodon* production continued to decline from its peak of 0.72 million mt in 2003 to 0.58 million mt in 2007, an 18.3% decrease (Fig. 2). In 2008, *P. monodon* production (0.71 million mt) rebounded almost to its peak in 2003 and *L. vannamei* production had its first decrease of 0.06 million mt from the previous year.

*Litopenaeus vannamei* was introduced into Asia experimentally from 1978 to 1979, but commercially into Taiwan and China only since 1996 and 1998 respectively, and subsequently to the Philippines, Indonesia, Vietnam, Thailand, Malaysia and India (SEAFDEC 2005). Among Asian countries, sizable *L. vannamei* productions from aquaculture activities were recorded by the FAO in 2000 for Taiwan (2,300 mt), 2001 for China (87,800 mt), 2002 for Thailand (60,000 mt) and Vietnam (10,000 mt), and 2004 for Indonesia (53,200 mt) (Fig. 3). In 2008, Asia (1.28 million mt) accounted for 75% of the world (1.71 million mt) *L. vannamei* production and shared 45% of the world penaeids (2.85 million mt) aquaculture. China has led the

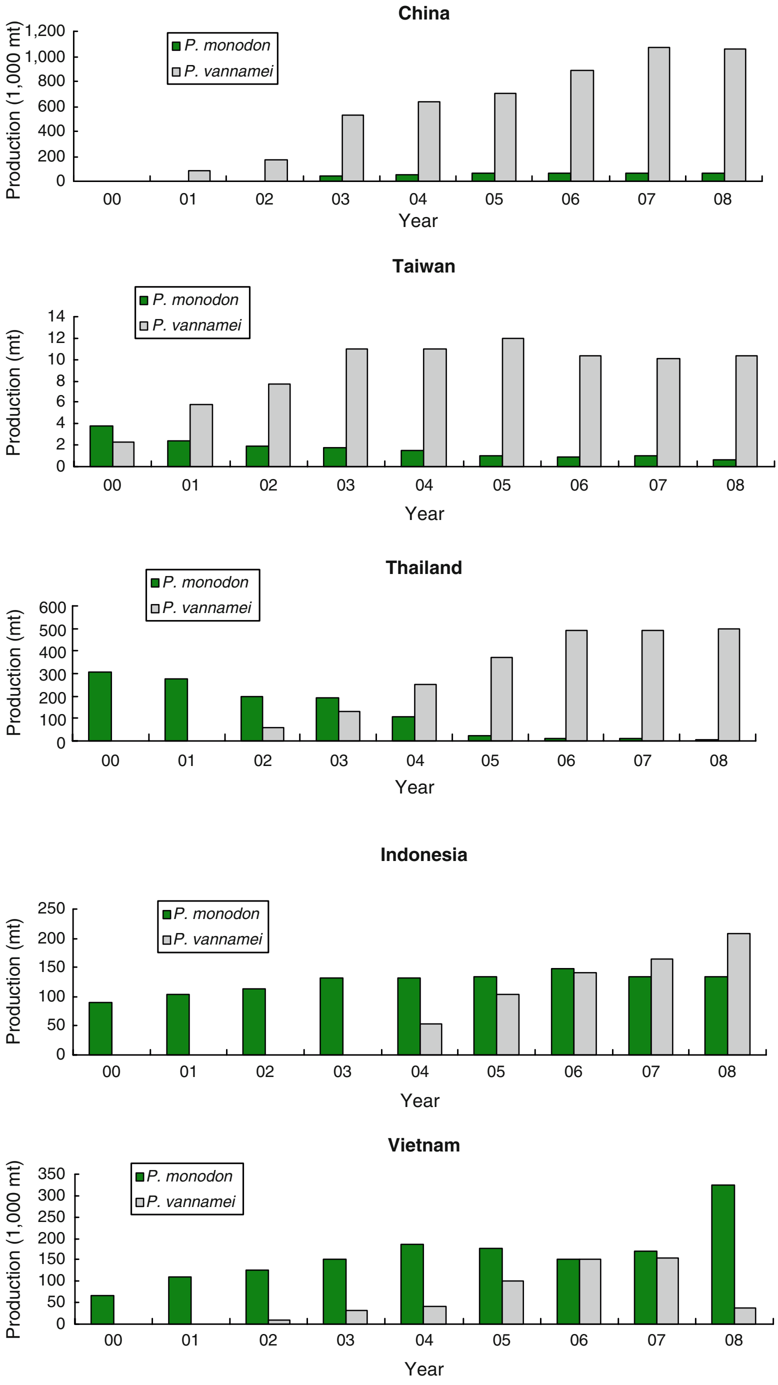

**Fig. 3** Production of *Penaeus monodon* and *Litopenaeus vannamei* in China, Taiwan, Thailand, Indonesia and Vietnam, 2000–2008

world *L. vannamei* production since data were first reported to the FAO in 2003. Its share of world *L. vannamei* production has increased from 33% in 2003 to 46% in 2007 but decreased to 41% in 2008. The inverse relationship between *L. vannamei* and *P. monodon* production is most significant in Thailand. Until 2007, except Taiwan, *L. vannamei* production in China, Thailand, Vietnam and Indonesia continued to increase since its commercial production first started (Fig. 3). From 2007 to 2008, except Indonesia, the production of *L. vannamei* in the other four countries did not significantly increase, in fact production in Vietnam even decreased from 153,000 to 38,600 mt.

The impact of farming *L. vannamei* in China, Taiwan, Thailand, Indonesia and Vietnam is briefly described below.

## 2.1 China

Shrimp culture in China started when Mr. Shan-Chin Wu and his colleagues first bred *Fenneropenaeus chinensis* in 1965 (Wu et al. 1965; Liao et al. 2006). China's shrimp farming industry began mainly in the northern provinces around Bohai Gulf using *F. chinensis* in semi-intensive ponds. The first cultured shrimp production was recorded in 1970, at 79 mt and the first golden era of shrimp culture industry in China was between 1981 and 1988 when production increased from 10,093 to 199,418 mt. By 1987, China had become the world leader in shrimp farming, with annual production of 153,000 mt. This rapid increase was due to an expansion in culture area and increase in productivity. However, deterioration of water quality in Bohai Gulf due to self-pollution by organic discharge from the shrimp farms as well as increasing domestic, agricultural, and industrial pollution resulted in red tide blooms, sporadic disease, and even viral disease epidemic (Rosenberry 1990; INFOFISH 1994). These problems halted production from 1988 to 1992 and later it actually dropped to its lowest level in 1994, at 63,872 mt (Fig. 4). It was not until

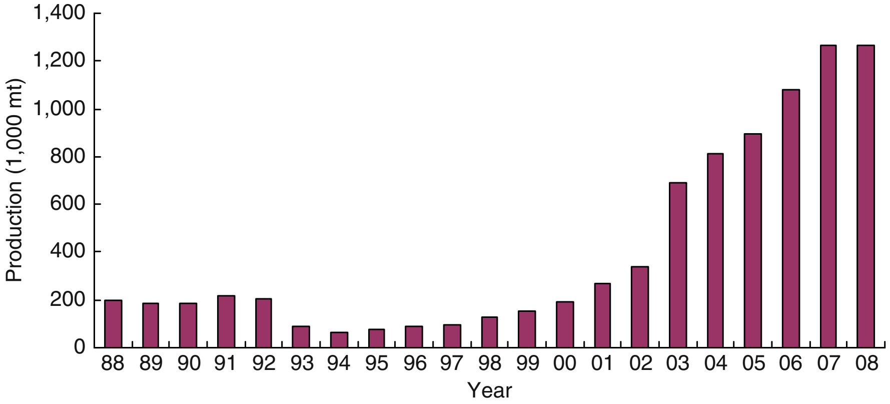

**Fig. 4** Cultured shrimp production in China, 1988–2008

2000 that production (192,339 mt) recovered to almost its previous record of 219,571 mt back in 1991. However, from 2000 onwards shrimp production increased dramatically and was mainly attributed to the rapid expansion of *L. vannamei* culture. This abrupt increase in production was due to the unreported culture of *L. vannamei* in freshwater, which was estimated at 160,000 mt in 2002. In 2003, production was reported according to the four most cultured shrimp species i.e., *L. vannamei*, *F. chinensis*, *P. monodon*, and *Marsupenaeus japonicus*. *Litopenaeus vannamei* production was further separated into fresh and brackish water environments. The composition of cultured shrimp production in 2003 was: *L. vannamei* brackish water 40.63%, *L. vannamei* freshwater 38.97%, *F. chinensis* 8.11%, *P. monodon* 6.72%, and *M. japonicus* 5.58% (Miao 2005). Remarkably, total shrimp production in 2007 and 2008 was 1.2 million ton, almost six times as that in 1988 (Fig. 4). According to Miao (2005), *L. vannamei* was first introduced to China from the United States by the Oceanography Research Institute of the Chinese Academy of Science in 1988. The successful artificial propagation trial of the shrimp in 1992 was followed by production of postlarvae in 1994 and the first culture in brackish water. Following a serious viral disease outbreak in brackish water during 2001, shrimp farmers tried culturing desalinized shrimp fry in freshwater. The freshwater culture expanded rapidly after it proved to be even more successful than brackish water culture conditions. In 2003, *L. vannamei* production reached 526,446 mt, of which 255,979 mt came from freshwater and 270,467 mt from brackish water. In 2004, 2007, and 2008, more *L. vannamei* was being produced in freshwater than in brackish water (Fig. 5). For 2008, *P. monodon* production (60,899 mt) was only 5.7% of *L. vannamei* production (1,062,765 mt) (Fig. 5).

Although the Chinese government has generally encouraged the introduction of exotic species for aquaculture purposes, it is concerned about preventing the spread of new disease pathogens, especially since the serious outbreak of Taura syndrome virus (TSV) associated with *L. vannamei* caused tremendous economic loss in 2001

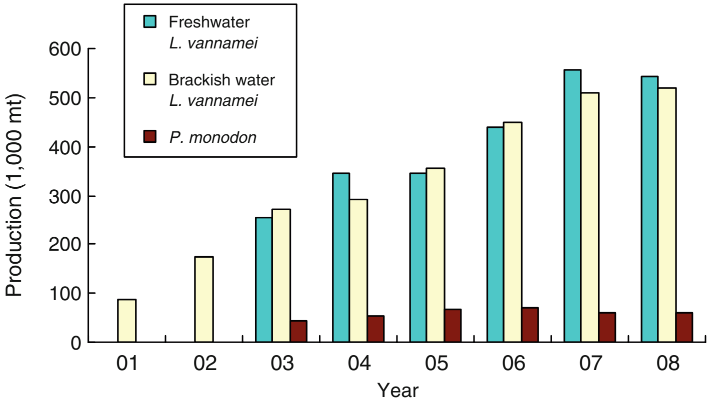

**Fig. 5** Production of *Litopenaeus vannamei* in freshwater and brackish water environment and *Penaeus monodon* in China, 2001–2008

(Miao 2005). However, the main constraint to the expansion of *L. vannamei* farming in China is the supply of a quality broodstock. While the ‘first generation’ specific-pathogen-free (SPF) broodstock imported from Hawaii was an ideal product, its price was 15–20 times higher than the domestic ‘second generation’ broodstock. Repeated use of the expensive broodstock deteriorates fry quality, which can result in slow growth, size variation, and susceptibility to disease. The domestic Chinese broodstock suffers from poor quality control and few batches are SPF certified.

## *2.2 Taiwan*

The penaeid species that have been commercially cultured in Taiwan are mainly *L. vannamei*, *P. monodon*, *M. japonicus*, *Fenneropenaeus penicillatus* and *Metapenaeus ensis*. Their production figures are currently listed in the Taiwan Fishery Statistics. Successful artificial breeding of *P. monodon* in 1968 (Liao et al. 1969), led to the commercial culture of this species in Taiwan. Rapid expansion of *P. monodon* culture was evident by the remarkable production increase from 1,100 mt in 1977 to 78,548 mt in 1987, which made Taiwan the second largest penaeid culture country (next to China) in the world at that time. This success can be attributed to the following factors: mass production of fry, adoption of commercial formulated feed, marketing success in Japan (Chiang and Liao 1985), and fully integrated peripheral and sub-businesses (Liao 1988). However, a plunge of *P. monodon* production to 30,603 mt occurred in 1988. This was mainly attributed to the outbreak of diseases from Monodon Baculovirus (MBV), bacteria, and protozoa, *Epistylis* sp. which resulted from the absence of disease prevention practices, deterioration of pond environment, overstocking and poor quality fry (Liao 1988). The shrimp industry slightly regained its vitality when some *P. monodon* farmers changed to farm *M. japonicus* after the culture crash. The production of *M. japonicus* increased from 4,000 mt in 1988 to 6,600 mt in 1990 and 11,500 mt in 1991 (Liao and Chien 1994). In both years, Taiwan became the largest producer of cultured *M. japonicus* in the world. Since mid-1992, *M. japonicus* was plagued by baculoviral midgut gland necrosis and then all penaeids by white spot syndrome virus (WSSV). Cultured penaeid production declined to a record low of 5,191 mt (Fig. 6), before *L. vannamei* was produced on a large commercial scale.

*Litopenaeus vannamei* was first introduced to Taiwan in 1978 for experiment purposes. It was not cultured commercially because of difficulties in accessing broodstock and insufficient knowledge concerning the exploitation of this alien shrimp. After the shrimp industry was hard hit by viral diseases in the late 1980s and early 1990s, SPF broodstock of *P. vannamei* from Hawaii was introduced to Taiwan in 1996. Trials yielded production of 12 mt/ha of 12–15 g shrimp in 75 days (Wyban 2002). This success stimulated a worldwide search for *L. vannamei* broodstock, and wild specimens were imported from Latin America. The use of wild animals inevitably introduced diseases and the lack of biosecurity measures in producing homegrown broodstock for a low production cost only served to increase

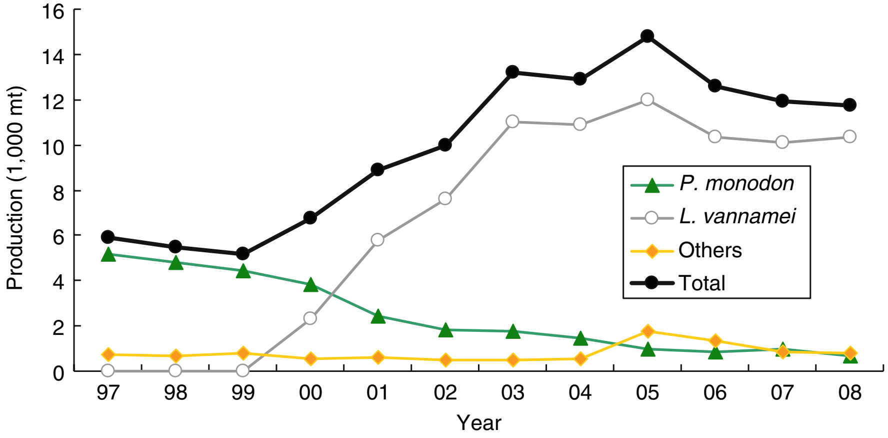

**Fig. 6** Production of all penaeids, *Penaeus monodon*, *Litopenaeus vannamei*, other penaeids (*Marsupenaeus japonicus*, *Fenneropenaeus penicillatus* and *Metapenaeus ensis*) in Taiwan, 1997–2008

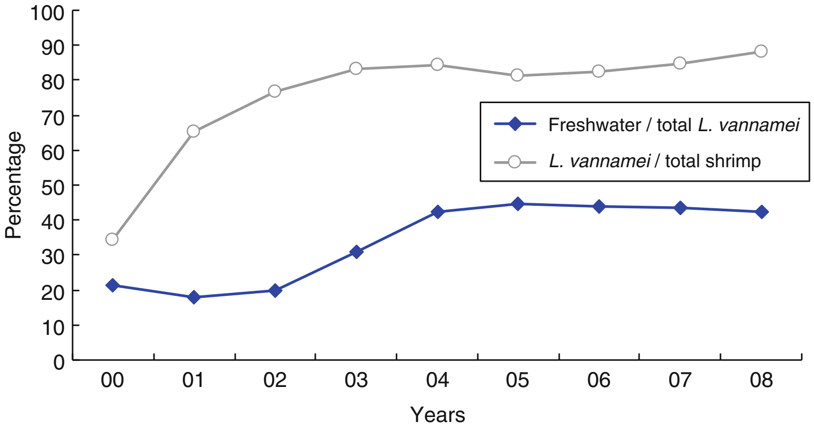

**Fig. 7** Fraction of *Litopenaeus vannamei* production in total penaeid production and fraction of freshwater *L. vannamei* production in total *L. vannamei* production in Taiwan, 2000–2008

the spread of viral diseases into the seed supply system (Wyban 2002). Despite these problems, from 2001 *L. vannamei* has become the leading cultured penaeids in Taiwan (Fig. 6) and since 2003 it has shared more than 80% of the shrimp production (Fig. 7). In 2005, *L. vannamei* production reached 12,012 mt but decreased to 10,347 mt in 2008, possibly due to low prices and competition with imports. When *L. vannamei* production was first recorded in Taiwan Fishery Statistics in 2000, 21% of it already came from freshwater ponds and during 2004–2008, stabilized to 42–45% (Fig. 7). However, even with the many measures taken to solve the problems with *P. monodon* and *M. japonicus* cultures, recovery of the shrimp industry to the previous peak in 1987 has not been matched due to the high production cost resulting from limited natural resources (land, water, biota), human resources (labour), and associated resources (logistics) and strong competition from the neighbouring shrimp producing countries. *Litopenaeus vannamei* culture will be sustained in Taiwan so long as there is no emergence of new viral and other microbial diseases. Its production will still serve the domestic market subject to competition of import frozen products.

## 2.3 Thailand

In Thailand, *L. vanname*i was first introduced in 1999 illegally and soon its successful production was achieved. The Thai Department of Fishery (DOF) launched the regulation for *L. vannamei* broodstock importation in 2002, requiring these to be certified free of WSSV, infectious hypodermal and hematopoietic necrosis virus (IHHNV), TSV, and yellow head virus (YHV). However, an outbreak of TSV and IHHNV disease brought the import regulation to an end in early 2003. Importation of broodstock was allowed again in June 2004 after new regulations required its source to be registered and approval by DOF. *Litopenaeus vannamei* production increased ten-fold from 30,000 mt in 2002 to 300,000 mt in 2004. In the hatchery, postlarvae at stage III-V began acclimation to a low salinity environment. In inland farming areas, brine at salinity over 100 psu was added to fresh pond water reaching 3–4 psu and stocking density were 43–50/m$^2$. In coastal area, salinity was kept over 10 psu and stocking density to 75/m$^2$. DOF's directions for the research and development of *L. vannamei* culture were to develop capability in producing local SPF and specific-pathogen-resistant (SPR) broodstock, and to evaluate and monitor coastal areas on the habitation of *L. vannamei* in natural waters (Tookwinas et al. 2005).

## 2.4 Indonesia

The shrimp industry in Indonesia significantly contributes to foreign exchange earnings. In most years during 1993–2003, more than 60% of shrimp production comes from capture fishery. In that period, slow annual growth (2.80%) in cultured shrimp production was due to disease rated problems caused mainly by viruses such as MBV and WSSV, which started in 2000. In 2000, the Director General of Aquaculture (DGA) issued licenses to the private sector to import broodstock and postlarvae of *L. vannamei* from Hawaii, Florida, and Taiwan. *Litopenaeus vannamei* culture in Indonesia started in East Java. Successful pond grow-out were reported: 7–10 mt/ha yield in 90 days, 15 g final individual weight, 75–90% survival rate and 1.1–1.4 feed conversion ratio (Taw et al. 2002). As *L. vannamei* culture expanded, aquaculture to total shrimp production increased from 37% in 1999 to 41.2% in 2003. During 2001–2004, no WSSV disease was detected and TSV was only found in broodstock at one hatchery. To sustain the development of *L. vannamei* culture, DGA formulated short, middle and long-term strategies focused on the production of reliable and quality broodstock, seed by implementing biosecurity and promoting best management practice in the hatchery system (Budhiman et al. 2005).

### 2.5 Vietnam

According to Tien and Trieu (2005) and www.fistenet.gov.vn, the shrimp species mainly cultured in Vietnam are *P. monodon*, *L. vannamei*, *F. merguiensis* and *M. ensis*. Although Vietnam cultivates *L. vannamei* as elsewhere in Southeast Asia, its production of *P. monodon* has not decreased. In fact production of *P. monodon* has increased continuously from 67,486 mt in 2000 to 185,569 mt in 2004, and in 2008, 324,600 mt. Consequently Vietnam has become the leading *P. monodon* producing country (Fig. 3). *Litopenaeus vannamei* was first imported from Taiwan to Bac Lieu province. Broodstock and postlarvae were also later imported from China and Hawaii. Trials on breeding and grow-out were first assigned to some state-run enterprises. The production of *L. vannamei* increased continuously from 1,766 mt in 2002 to 153,000 mt in 2007. The culture of *L. vannamei* has been under the Government's control for 7 years to ensure that there would be no outbreak of disease due to lack of knowledge in culturing techniques as well as in disease management. According to the guide of Ministry of Agriculture and Rural Development, the government opened the access of *L. vannamei* cultivation to all farmers from the 4 February 2008. There is no record of TSV occurrence in Vietnam. It is not known if during 2007–2008 the abrupt drop of *L. vannamei* production is related to two-fold production increase of *P. monodon*.

## 3 Dominance of *L. vannamei* Culture in Asia

During the past 2 decades, world penaeids production has been through a dramatic change with regard to species cultured (Fig. 8). The share of *F. chinensis* (Osbeck, 1765) has declined from 34.6% in 1988 to 13.2% in 1998 and further down to 1.3% in 2007. The share of *P. monodon* has increased from 34.7% in 1988 to 51.0% in 1998, but declined to 17.8% in 2007. The share of *L. vannamei* has increased from 13.40% in 1988, 19.63% in 1998 to 70.25% in 2007. From 2007 to 2008, there was no change in the share of *F. chinensis*, but *P. monodon* increased to 21.2% and *L. vannamei* decreased to 66.5% (Fig. 8). Such a high share of *L. vannamei* globally is attributed to the dominance of its aquaculture over *P. monodon* in China and Thailand and 100% *L. vannamei* aquaculture in Ecuador, Mexico, and Brazil (Fig. 9).

Shrimp is the most internationally traded aquaproduct. Its export value in 2006 ranked first when compared to the widely popular species such as diadromous fishes (salmonids and eels) and the large pelagic fish (various species of tuna and swordfish)

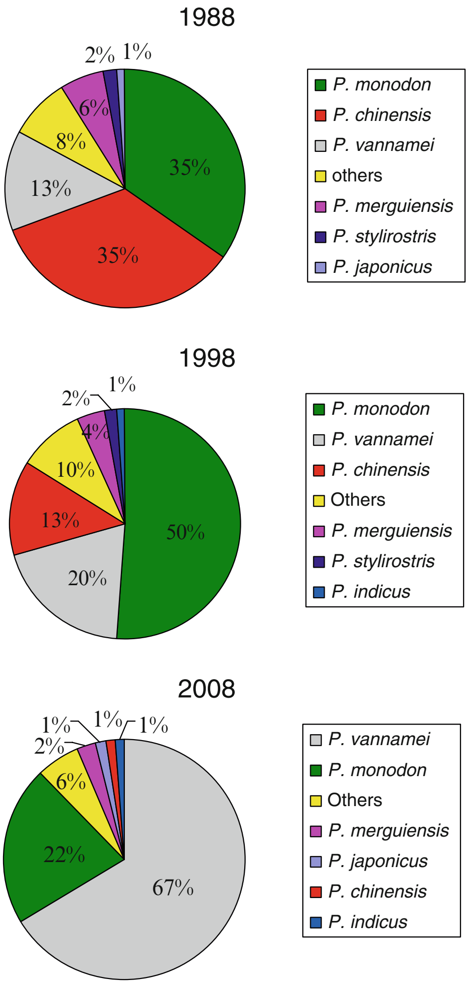

**Fig. 8** Species composition of world cultured shrimp production (*in descending order*) in 1988, 1998, and 2008

(Fig. 10). This large market is mainly composed of processed shrimp. While there is no apparent difference for shell-off market between *L. vannamei* and *P. monodon*, the former is favoured by the processors since it has a higher meat yield of 66–68% compared to *P. monodon* with only 62%. Therefore, once processed *P. monodon* fails to meet the demand i.e., due to production disruption by disease outbreak or higher price, *L. vannamei* can readily fill the market demand. Since *P. monodon* can grow larger than *L. vannamei*, its dominance in jumbo size shrimp market has remained. Moreover, consumers in the U.S., the world's largest shrimp market (Table 1), appear to prefer the taste of *L. vannamei* when compared with *P. monodon* (Rosenberry 2002). Results of a consumer acceptance test by the Food

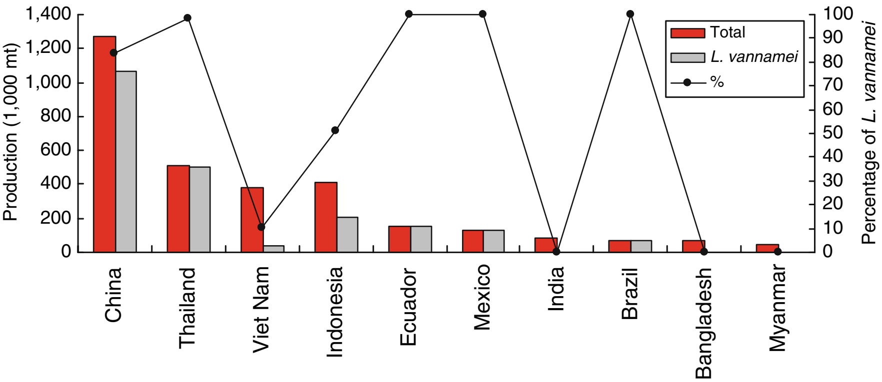

**Fig. 9** Total shrimp production, *Litopenaeus vannamei* production, and percentage of *L. vannamei* production to total shrimp production in top ten shrimp aquaculture countries

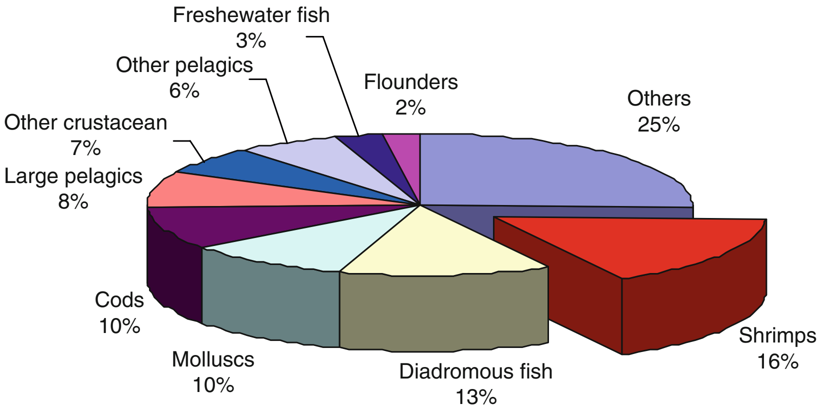

**Fig. 10** World aquaproduct export value by species group in 2006

**Table 1** Top five shrimp import countries and their import quantity (mt) in 2006 and 2007

| | 2006 | | 2007 | |
|---|---|---|---|---|
| 1 | United States of America | 418,332 | United States of America | 415,427 |
| 2 | Japan | 230,708 | Japan | 207,876 |
| 3 | Spain | 175,281 | Spain | 174,607 |
| 4 | Denmark | 112,182 | Denmark | 90,226 |
| 5 | France | 88,047 | France | 85,811 |
| Amount | | 1,024,550 | Amount | 973,947 |
| Total import quantity of the world | | 1,678,336 | Total import quantity of the world | 1,715,613 |

*Source*: FAO, 2009, 2

Science and Human Nutrition Department of the University of Florida showed that U.S. consumers particularly preferred freshwater grown *L. vannamei* over those produced in brackish or salt water or harvested from the sea (UF/IFAS 2003).

With regards to supply, *L. vannamei* has the following production advantages over *P. monodon*: lower production cost, higher productivity, and wider available culture area. These advantages are interrelated and all associated with several superior aquaculture traits compared with *P. monodon*. These include lower fry cost for higher availability of viral-pathogen-free and genetically selected domesticated broodstock, higher larval survival, lower feed cost and dietary protein requirement, more efficient utilization of plant proteins in formulated diets (Cuzon et al. 2004; Shiau 1998), and concomitantly less demand for fishmeal, higher productivity (10–20 mt/ha vs. 4–8 mt/ha for *P. monodon*) for faster growth rate, better tolerance to high stocking density (four to five times higher) and to ammonia and nitrite toxicities (Lin and Chen 2001, 2003), and wider available culture area for their stronger adaptability to low salinity. A side-by-side field experiment by Limhang et al. (2005) in Thailand especially exhibited several production advantages of *L. vannamei* over *P. monodon* in low salinity water. With the same stocking size using 15-day-old postlarvae ($PL_{15}$) under low salinity (4–6 psu), even though *L. vannamei* were stocked at higher density (100 vs. $25/m^2$) the former was harvested after shorter period (140 vs. 156 days), with larger final size (20.9 vs. 15.9 g), higher growth rate (0.17 vs. 0.08 g/day), greater yield (3,075 vs. 460 kg/rai), and more homogeneous size (coefficient of variation: 8 vs. 10%). When cultured inland, *L. vannamei* needs little water change to conserve the minimum salinity or mineral concentration, thus saving not only on pumping cost but also some feed cost. This is because of the nutrients that accumulated could enhance natural productivity of the pond (McIntosh and Fitzsimmons 2003), which can serve as food for shrimp fry and juvenile (Bray et al. 1994; Chien and Liao 1995). Another comparative field study conducted in normal salinity ponds in Indonesia also showed better feed efficiency (conversion ratio) and higher production in *L. vannamei* than *P. monodon*: 1.31 vs. 1.98 and 10,094 vs. 4,184 kg/ha (Taw et al. 2002).

Production stability and farmers' confidence are also the driving forces for the rapid development of *L. vannamei* culture in Asia. The supply of *L. vannamei* broodstock is more stable than that of *P. monodon*. *Litopenaeus vannamei* can mature at a smaller size than *P. monodon* and is able to mature in captivity so that broodstock improvement can be achieved easier, faster and earlier. On the other hand, *P. monodon* production industry still relies mostly on wild broodstock since the supply of domesticated broodstock is not always available or reliable. For the same reason, commercial accessibility to SPF broodstock of *L. vannamei* is better than *P. monodon*. Initially available from private hatcheries in Hawaii and Florida, improved broodstock are now available from public/local sources. By cross breeding strains of *L. vannamei*, Indonesia government researchers have pioneered an improved shrimp breeding stock called "Indu Vannamei Nusantara I", a fast-growing and highly disease-resistant shrimp which are available to farmers at a lower and affordable price. Besides, farmers can now breed their own *L. vannamei* broodstock in ponds, which is much less feasible for *P. monodon*. This alternative source provides abundant supply of homegrown broodstock, however, the quality is less manageable and debatable. This is because negligence on genetic makeup or biosecurity in producing homegrown broodstock may introduce viral diseases and inbreeding disorders into the seed supply system (Wyban 2002). On the contrary, when those considerations are implemented, the broodstock produced can become a reliable seed resource. De Donato et al. (2005) present an analysis of production records for 11 generations (1990–2001) of a Venezuelan strain of *L. vannamei* under mass selection and inbreeding in a closed reproductive cycle. Symptoms of IHHNV disease were reported during the first years of selection. The reproductive stock of the farm was established from three different populations mixed in successive generations (Mexico first generation, Panama second generation, and Colombia third generation). Production related parameters exhibited significant improvements through time, such as increased survival, growth, feed conversion ratio and production and decreased deformities and size variation. No signs of deterioration on the fitness-related traits have been seen in the last generations. The absence of symptoms for IHHNV disease in the last generation, could suggests that this strain may be tolerant, or even resistant to this pathogen.

Since *L. vannamei* is generally regarded as less susceptible to WSSV (Briggs et al. 2004), than *P. monodon* and *F. chinensis*, lower disease risk gives farmers confidence to accept this indigenous shrimp sooner than was expected. It was shown that *L. vannamei*'s infections of TSV and WSSV in Asia are lower than in Latin America where *L. vannamei* originated (Rosenberry 2004). However, the susceptibility of *L. vannamei* to viral pathogens infecting *P. monodon* can be similarly serious. For example, in central Thailand 20 study farms rearing *L. vannamei* infected with YHV disease during 2007 and 2008. According to the Thai Animal Aquaculture Association the estimated economic loss was approximately US$3 million (Senapin et al. 2010).

## 4 Development of Inland *L. vannamei* Culture

According to FAO Fishery and Aquaculture statistics 52% (555,700 mt/1,062,700 mt) and 51% (542,600 mt/1,062,700 mt) of *L. vannamei* were produced in inland freshwater ponds during 2007 and 2008, respectively. When FAO first reported *L. vannamei* production statistics from inland ponds of China, production was already rivaling marine production (Fig. 5). The increase of *L. vannamei* production in China is mainly attributed to the expansion of new culture area inland and not to the replacement of *P. monodon*. Although it can be seen that while the production of *L. vannamei* increased in both inland and coastal ponds, *P. monodon* production did not decrease (Fig. 5).

While *L. vannamei* is cultured in inland ponds, where the ecosystem is much stable than coastal ponds since salinity fluctuation is minimized, its production is concomitantly more predictable. The culture of marine penaeids in brackish water is a common practice among farmers who believe that the growth of shrimp in lower salinity water is better than in seawater (Rosas et al. 2001a; Sowers and Tomasso 2006). Culturing marine shrimp in inland ponds first started in *P. monodon* to prevent the introduction of possible vectors of viral pathogens from seawater ponds. Most of these viral diseases such as WSSV have brought the industry to a near collapse (Lo et al. 1996a; Jory and Dixon 1999; Lightner 1999; Lotz and Soto 2002; Flegel 2006). The economic impact almost reached US$ 10 billion (OIE 2006). As *L. vannamei* is more resistant to WSSV (Briggs et al. 2004), and has strong adaptability to low salinity, pilot grow-out studies were undertaken in 1994–1999 (Wyban 2002). The success in these pilot studies encouraged farmers in Taiwan and China not only to accept *L. vannamei* as aquaculture species, but also explored its culture potential in low-salinity ponds. Furthermore, inland production of shrimp in low-salinity ground water can provide another potential solution to disease and environmental problems, as production is conducted in isolated areas away from other host species (Samocha et al. 2002).

To successfully culture *L. vannamei* in low salinity water, postlarvae must be transferred from high (seawater) salinity larval rearing system to low-salinity grow-out conditions. The optimum range in salinity for hatchery culture of penaeid shrimp is about 26–32 psu. Mature adult and postlaval shrimp are natural found in the ocean, where the salinity is approximately 35 psu (Treece and Fox 1993). When salinity is lower than 22 psu, fertilized eggs of *L. vannamei* are unable to develop normally (Peng et al. 2002). However, the salinity in grow-out at stocking can be as low as 3–5 psu. Before the acclimation process starts in a hatchery, target salinity must be agreed upon between the hatchery and grow-out operators. In China and Taiwan, acclimation generally starts at $PL_{8\text{-}15}$ and ends when salinity is reduced to 10–6 psu. Further acclimation to 2–1 psu is done in the nursery ponds of grow-out farms. However, when nursery ponds are not available, the contracted hatchery or nursery specialized in salinity acclimation handles the whole acclimation process. It is advised that salinity adjustment during acclimation is done twice a day at 2–3 psu per adjustment down to 20 psu, 1–2 psu per adjustment down to 10 psu, and finally <1 psu per adjustment down to the final salinity of 2–1 psu. Despite the fact that $PL_{15\text{-}20}$ can be acclimated to 1 psu with good survival at 48 h (McGraw et al. 2002), hatchery operators in China and Taiwan are quite reserved with such acclimation rate. Through experience, short acclimation period often results in red-leg syndrome during grow-out culture (Song and Chang 2008). Roy et al. (2009c) also attributed the initial mortality (8–12%) occurred immediately following stocking to inadequate acclimation process and poor handling of postlarvae. Ogle et al. (1992) demonstrated that lowering salinity from 32 psu to 16, 8, 4, and 2 psu for 24 h and 120 h resulted in lower survival of $PL_8$ and $PL_{22}$ of *L. vannamei*. Growth after 30 days was not significantly different among the salinities tested. Nonetheless, the best observed growth was at the intermediate salinities of 8 and 4 psu. Esparza-Leal et al. (2010) evaluated the rearing performance of *L. vannamei* postlarvae acclimated from seawater (30 psu) to low-salinity well water (<1 psu) at a constant hourly reduction rate of 40, 60, 80 and 100 h and then reared in tanks at densities of 50, 100, 150 or 200 shrimps/m$^2$ for 12 weeks. They conclude that *L. vannamei* can be successfully grown in low-salinity well water, and that the growth, yield and survival rate are significantly higher when shrimp are acclimated for longer periods. Shrimp yield ranged from 0.32 to 1.14 kg/m$^2$ for density of 50 and 200/m$^2$.

Although thorough feasibility studies on inland freshwater culture of *L. vannamei* were not conducted nor published, full scale commercial culture operations had already expanded into inland China and Thailand. Some recent technical researches related to culture of *L. vannamei* in low salinity environment are outline below.

## *4.1 Technical Advancement*

### 4.1.1 Disease Infection

Apparently *L. vannamei* has less chance to get infected by commonly occurring pathogens when cultured in low salinity. Carbajal-Sanchez et al. (2008) reported more severe WSSV infections of juvenile *L. vannamei* at 15 psu than at 2, 5, 25 and 35 psu, and suggested that salinity may affect the course and outcome of WSSV infections. Sánchez-Barajas et al. (2009) used RT-n PCR to detect YHV, WSSV, and Gill Associated Virus (GAV) during single-culture cycles of *L. vannamei* for 60 days on two freshwater farms in Mexico. They found that samples were negative to WSSV and GAV, but positive to YHV with a prevalence of 13%. The average temperature at the farms was around 29.7°C. The environmental stress due to osmotic condition acting on the farmed shrimp might synergistically interact with temperature, which has been reported to be one of the main agents of stress affecting pathogen dynamics in aquatic systems (Bray et al. 1994; Jimenez et al. 2000). Adaptation to salinity change can affect the resistance of *L. vannamei* against infection. Pan and Jiang (2002) found that upon sudden change of salinity, *L. vannamei* had higher antibacterial and bacteriolytic activities but lower phenoloxidase activity than *F. chinensis*. Low salinity also stimulated the production of radicals for scavenging, and increased superoxide dismutase (SOD) and catalase (CAT) activities for scavenging radicals that insured the healthy status of *L. vannamei* to a certain degree (Li et al. 2008a). Besides, shrimp at 3.0 psu produced more B cells in the hepatopancreatic tubules than at 17.0 psu. Under stressful environments, the health of aquatic animals has been assessed by monitoring the level of SOD and CAT (Angel et al. 1999), which are the two main primary enzymes in antioxidant systems for scavenging radical. In crustaceans, a high level of radicals provokes an increase in SOD and CAT activities (Chien et al. 2003). However, an earlier study of Wang and Chen (2005) showed that *L. vannamei* injected with *Vibrio alginolyticus* and then transferred from 25 psu to 5 and 15 psu had lower immune ability and resistance against infection and higher mortality than transferred to 35 psu. Li et al. (2010) further demonstrated that the innate immunity was weakened in *L. vannamei* that received combined stresses of *V. alginolyticus* injection, and low-salinity transfer.

### 4.1.2 Metabolism and Culture

*Litopenaeus vannamei* exhibits hyper-osmotic regulation at low salinity and hypo-osmotic regulation at high salinity, with an iso-osmotic point of 718 mOsm/kg (equivalent to 25 psu) (Castille and Lawrence 1981; Bray et al. 1994). Optimal salinity for *L. vannamei* culture varies with the stock or strain, culture system, stocking density, dietary nutrition, mineral and nutrients in water, and temperature. It is believed by some shrimp farmers in the Western Hemisphere that the Ecuadorian strain of *L. vannamei* grows better at low salinity, while the Mexican strain fairs better at higher salinity (Bray et al. 1994). Using Ecuadorian strain, Bray et al. (1994) demonstrated that the growth of juvenile *L. vannamei* at 5 and 15 psu was superior to growth at 25, 35, and 49 psu. However, based on the lowest stress that *L. vannamei* juveniles were exposed to, Diaz et al. (2001) proposed the optimal salinity for culturing the Mexican strain to be 25–27 psu, which is close to the iso-osmotic point. All using Mexican strain, Ponce-Palafox et al. (1997) demonstrated a high coincidence between the experimentally determined optimum conditions (28–30°C and 33–40 psu) for survival, growth and concomitantly the overall production of postlarval *L. vannamei*, and the prevailing conditions in the coastal environment from which the animals originated. In an indoor semi-closed recirculating tank system, *L. vannamei* was successfully cultured with good growth and survival at 2–8 psu salinity and stocking density of 28 juveniles/m$^2$ (Samocha et al. 1998b). In raceways under reduced water discharge, Samocha et al. (2002) reared 1-mg size *L. vannamei* postlarvae in municipal freshwater salinity adjusted to 15 psu at 1000–2020 PL/m$^2$ for 35–48 days and obtained survival rates mostly above 80%. In the study of Wang et al. (2006), specific growth rate, food consumption, food efficiency and absorption efficiency were highest at 20 psu, highest survival rate was at 35 psu, while lowest specific growth rate, food consumption and absorption efficiency were observed at 0.5 psu. Li et al. (2007) demonstrated that *L. vannamei* juvenile could adapt to a wide range of salinity, but spend more energy to compensate the cost for osmoregulation at low salinity. Therefore, shrimp weight gain and survival at 17 psu was highest and significantly different than those at 3 psu. Zang et al. (2003) showed that the optimal salinity for growth of *L. vannamei* was 7.5–24.6 psu, which was in agreement with the study of Huang et al. (2004). *Litopenaeus vannamei* reared at 0.6 psu for 21 days obtained a weight gain >600% and survival rate close to 90% (Zang et al. 2003). Green (2008) demonstrated that *L. vannamei* can be grown successfully in freshwater supplemented with major ions to a final salinity of 0.7 psu. *Litopenaeus vannamei* juvenile stocked at low density (14/m$^2$) in outdoor tanks and reared for 35 days, its growth greater than 2 g/week was observed at 5 and 15 psu (Bray et al. 1994). Araneda et al. (2008) reported successful culture of this species at 0 psu freshwater under intensive stocking densities. At the lowest stocking density tested (90 shrimp/m$^2$), shrimp with growth rate of 0.38 g/week, final individual weight of 11.7 g, survival rate of 76.1% and yield of 801 g/m$^2$ after 210 days of culture under 25°C were obtained. At the highest stocking density 180 shrimp/m$^2$, although growth rate, final individual weight and survival rate were lower at 0.33 g/week, 9.9 g and 65.9%, respectively, the yield was 1174 g/m$^2$. Using low-salinity (1.8–2.6 psu) ground water, Samocha et al. (2004) produced 2.22 kg/m$^2$ in a 5-week nursery study with stocking density about 20,000 postlarvae/m$^2$. In the grow-out trial, a yield of 4.39 kg/m$^2$ of shrimp with a mean weight of 14.7 g was achieved in a 107 days rearing. These trials indicate that *L. vannamei* can be raised at high densities using low-salinity ground water.

The variation in *L. vannamei* production in low salinity waters can be attributed to the suitability of waters with various ionic compositions for culture. Saoud et al. (2003) found that survival of *L. vannamei* in salinities between 24 and 2 psu appeared to be positively correlated with ions such as potassium ($K^+$), manganese ($Mn^{2+}$) and sulfate, and negatively correlated with high concentration of iron ($Fe^{2+}$). In $K^+$ deficient saline ground waters with salinity of 15 psu, normal growth of *L. vannamei* could be attained by adding $K^+$ salt and reducing the sodium ($Na^+$)/$K^+$ ratio to at least 76 (Zhu et al. 2005). However, Araneda et al. (2008) suggested that individual $K^+$ and $Na^+$ concentrations may not be as relevant as the ratio between them. Roy et al. (2007a) suggested that higher energy cost in *L. vannamei* was associated with depressed aqueous magnesium ($Mg^{2+}$) concentrations that are common in low salinity environments. Liu et al. (2007a) showed that the highest growth rate and activities of enzymes in the shrimp occurred at calcium ($Ca^{2+}$) concentration of 320 mg/L with, $Ca^{2+}$/$Mg^{2+}$ ratio of 1:2.5. A field investigation and associated laboratory experiments suggested that pond-to-pond variations in ionic profiles could be a contributing factor but were not likely the major reasons for variability in survival (Roy et al. 2009c). Sowers and Tomasso (2006) cultured 0.79–0.97 g *L. vannamei* at 100 animals/m$^2$ in environments containing 1 g/L sea salt + 1 g/L mixed salts (688 mg/L NaCl, 21 mg/L KCl, 138 mg/L $CaCl_2$, 151 mg/L $MgCl_2$) for 53 days had a production similar to those of shrimp in 2 g/L sea salt. Further, the production harvest weight (in kg/m$^2$) of both treatments was 79% of the harvest weight in the 20 g/L treatment. It appears that culturing *L. vannamei* in low salinities and partially substituting mixed salts for sea salt may be a useful option for inland shrimp farmers during the early part of the grow-out period.

Despite the practice of culturing *L. vannamei* in inland freshwater ponds where environmental conditions deviated much from the optimum, the acceptable survival, growth, and production may be linked to acclimation process and culture practices. As a euryhaline species, *L. vannamei* can tolerate and adapt to a wide range of salinity, depending on its life stages. During postlarval stage, the resistance of marine shrimp, including *L. vannamei*, to salinity shocks is often used as a representative criterion of their quality (Samocha et al. 1998a). Lotz et al. (2005) found that chronically TSV-infected shrimp were not able to tolerate a salinity drop as strongly as uninfected shrimp. Le Moullac and Damez (1991) reported a positive correlation on survival of *L. vannamei* postlarvae with regard to salinity shocks and increase in size. Age appears to influence postlarvae tolerance to salinity end-point. McGraw et al. (2002) reported that $PL_{10}$ of *L. vannamei* can be successfully acclimated to 4 psu, while $PL_{15}$ and $PL_{20}$ can be acclimated to 1 psu. At juvenile stage, *L. vannamei* is well adapted to tolerate sudden salinity changes during acclimation to low salinity (Rosas et al. 2001b). Within optimum range of temperature (25–28°C), *L. vannamei* postlarvae and juvenile exhibits better growth and survival in low salinity (<20 psu) and, when acclimated, can survive and grow in freshwater (McGraw et al. 2002; Saoud et al. 2003; Huang et al. 2004; McGraw and Scarpa 2004). However, at a relatively low temperature (20°C), *L. vannamei* juveniles have limited capacity to tolerate salinities lower than 10 psu. The survival rate at 5 psu was significantly lower than that higher than 10 psu, either during salinity drop from 35 psu or 30-day's rearing after acclimation (Zhang et al. 2009).

Tolerance of *L. vannamei* to toxicity is also affected during salinity change. Salinity decrease from 35 to 15 psu decreased the tolerance of *L. vannamei* juveniles to ammonia and nitrite toxicity (Lin and Chen 2001, 2003). Li et al. (2007) further demonstrated that *L. vannamei* juveniles at 3 psu was most susceptible to ambient ammonia-N ($_{96\ h}LC_{50}$-9.33 mg/l), which was significantly lower than the results of Lin and Chen (2001) which reported that the $LC_{50}$ of ammonia to *L. vannamei* at 15, 25, and 35 psu were 24.39, 35.40 and 39.54 mg/L, respectively. Gross et al. (2004) estimated a safe concentration for shrimp production in ponds to be less than 0.45 mg/L $NO_2$-N at salinity of 2 psu, which was much lower than the results of Lin and Chen (2003) which reported that the $LC_{50}$ of nitrite to *L. vannamei* at 15, 25, and 35 psu were 6.1, 15.2 and 25.7 mg/L, respectively. Li et al. (2008b) also found that *L. vannamei* at 20 psu salinity is less sensitive to the ambient boron toxicity than at 3 psu. $LC_{50}$ value of boron at 96 h was 25.05 mg/L to the shrimp at 3 psu as compared to 80.06 mg/L at 20 psu. Acute toxicity of several heavy metals to *L. vannamei* postlarvae was studied by Frías-Espericueta et al. (2001, 2003), but the effects of salinity on these toxicity has not yet been tackled.

### 4.1.3 Dietary Adjustment for Low Salinity Culture

It is presumed that shrimp under hypo- and hypersaline environments may require some specific nutrients (mineral, lipid, and protein), which may differ from those in the marine habitat. The results of Perez-Velazquez et al. (2007) are in agreement with reports on superior and inferior growth of *L. vannamei* juvenile reared in hyposaline (2 psu) and hypersaline (50 psu) environments, respectively.

When culturing *L. vannamei* in inland low salinity waters, which are often deficient in key ions essential for normal physiological function, aquaculturists amend this limitation through improved diet, e.g., supplementation of $K^+$ and $Mg^{2+}$. Cheng et al. (2005) determined the dietary $Mg^{2+}$ requirement for optimal growth of juvenile *L. vannamei* at water salinity of 2 psu to be at 2.60–3.46 g/kg. They further recommended at the same salinity that dietary $Ca^{2+}$ should be reduced to minimize dietary phosphate supplementation (Cheng et al. 2006). Roy et al. (2007b) showed that dietary supplementation of $K^+$-amino acid complex could help improve growth of *L. vannamei* cultured in low salinity waters. However, in later experiment, they used magnesium chelates as dietary supplements at levels higher than what is required, to enhance survival, growth, and osmoregulatory capacity of *L. vannamei* reared in low salinity well waters, the results appeared to have limited practical use

(Roy et al. 2009a). They therefore recommended that until effective specialized diet formulations are produced, farmers should continue to supplement pond waters with fertilizers containing $K^+$ and $Mg^{2+}$.

Dietary supplementation of highly unsaturated fatty acid (HUFA) was found beneficial for survival of *L. vannamei* during a salinity stress test (Palacios et al. 2004). The working hypothesis behind this finding is that HUFA enrichment improves the fatty acid composition of cellular membranes in gills, which can modify permeability and modulate the activity of $Na^+/K^+$-ATPase, and concomitantly enhances osmoregulatory capacity to low salinities in shrimp. Moreover, Hurtado et al. (2006) found no beneficial effect of acclimation to low salinities from dietary HUFA-enrichment on *L. vannamei*. In a follow up study Hurtado et al. (2007) found that neither osmotic pressure, $Na^+/K^+$-ATPase activity, nor free amino acid was affected by HUFA supplementation. The osmoregulatory capacity of shrimp to low and high salinities was achieved within 15 h of acclimation and did not depend on HUFA supplementation in the diet. A recent study confirmed that supplementation of docosahexaenoic acid and arachidonic acid from algal meal was effective in promoting growth and survival of juvenile *L. vannamei* cultured in 4 psu, but did not elucidate how the n-3 and n-6 fatty acid balance in the diet was related to shrimp growth or osmoregulation (González-Félix et al. 2009).

Enhancement of hemolymph protein through dietary protein supplement has been considered to improve osmoregulation. The study of Rosas et al. (2001a) suggested that hemolymph of *L. vannamei* was able to store proteins after salinity acclimation from 30 to 15 psu. Depending on the salinity, the hemolymph proteins could be used as a source of osmotic effectors or as metabolic energy. Robertson et al. (1993) demonstrated that nutritional requirements for subadult *L. vannamei* vary with culture salinity and at each protein level (25, 35, and 45%) shrimp growth at 12 psu was greater than at 46 psu. Yu et al. (2002) suggested that 37% of dietary protein was adequate for *L. vannamei* juvenile reared in an indoor super-intensive recirculation culture system at 26–28°C, salinity of 20–25 psu, and stocking density of 250 shrimp/$m^2$. Culturing *L. vannamei* in low salinity water require less protein than in normal salinity water as demonstrated by Huang et al. (2003). In their study, optimum dietary protein level for *L. vannamei* juveniles was about 26.7% at 2 psu and about 33% at 28 psu. Roy et al. (2009b) suggested that a variety of ingredients such as poultry meal, pea meal and distiller's dried grain with solubles can serve as alternatives to fish meal as a protein source for *L. vannamei* reared in low salinity environments.

Aside from minerals, fatty acids, and protein, other nutrients have been tested for growth improvement of *L. vannamei* cultured in low salinity. Saoud and Davis (2005) demonstrated that betaine supplementation to practical diets formulated for *L. vannamei* did not improve production at extremely low or high salinities. Roy et al. (2006) found dietary supplementation of cholesterol and phospholipids in excess of the requirement was not warranted for *L. vannamei* reared in low salinity waters. On the other hand, vitamin E might play a potentially useful role as an effective antioxidant in regulating osmotic balance and resistance to salinity changes in *L. vannamei* (Liu et al. 2007b).

## *4.2 Socioeconomic Advantages*

Culturing *L. vannamei* in low salinity water is not only technically viable but also offers some socioeconomic advantages that encourage farmers to invest in low-salinity inland culture for the following reasons.

### 4.2.1 Market, Price, and Profit

In China, live and fresh ‘seafood’ is the preferred food items by urban population, which consider them as gourmet food items. They are served in popular restaurants of big urban cities like Beijing, Xi’an, Wuhan, Chengdu, and Chongqing. Producing a marine shrimp inland provides a competitive edge and easy access to local market with significant savings on live-transportation cost compared to coastal marine culture.

Freshwater crabs or shrimps usually command higher prices than freshwater fin fishes in China, not to mention the marine shrimp which are regarded as luxury seafood. The production cost for inland freshwater culture of *L. vannamei* is not much different from that for freshwater prawn *Macrobrachium rosenbergii* culture, except for the higher shipping cost of *L. vannamei* postlarvae from coastal hatcheries, as well as brine and mineral fertilizer inputs. Consequently, higher profits can be expected from freshwater culture of *L. vannamei* than other freshwater species.

### 4.2.2 Room for Culture Expansion

Inland has more area that can be allocated for *L. vannamei* culture than the coastal areas. Inland freshwater culture ponds are readily convertible to *L. vannamei* culture if the climate is suitable. It is a common practice in Taiwan to culture *L. vannamei* in ponds used for freshwater prawn culture. Moreover, inland areas are subject to less users’ competition, pollution, and ecological and legislation constraints compared to coastal areas.

# 5 Impact of Inland *L. vannamei* Culture

There are numerous introductions of non-native freshwater aquatic organisms throughout the world and their consequences were evaluated in various points of view (Gozlan 2008, 2009; Simõs Vitule et al. 2009). However, the instances of euryhaline marine organisms being cultured in inland freshwater are rare and their impacts never evaluated, e.g., milkfish (*Chanos chanos*) and grey mullet (*Mugil cephalus*) culture in Taiwan. In the case of introduced *L. vannamei*, which is now widely cultured in Asia, its impacts as a new aquaculture species with regard to disease infection (Briggs et al. 2005), and on shrimp fishing activities (Gillet 2008) have been extensively reviewed. However, the impacts of inland *L. vannamei* culture have not yet examined.

## 5.1 Ecological Impact

The reduced use of fish meal in *L. vannamei* culture compared to *P. monodon* will result in the reduction of pressure on marine sources, so is the impact of fish meal industry on marine ecosystem (Deutsch et al. 2007). Feedback from farmers suggest better feed efficiency when *L. vananmei* are cultured in freshwater, which may also reflect the higher natural productivity of freshwater ponds compared to brackish water ponds and better feed utilization in low-salinity ponds (Bray et al. 1994). The shift of farming species from *P. monodon* to *L. vannamei* and from *L. vannamei* coast mariculture to inland freshwater culture actually has higher efficiency of natural resource use and saving.

In inland low-salinity shrimp farming, farmers often practice near zero-water-exchange to conserve the salinity acquired from seawater, brine supplementation or mineral fertilization. This is especially important for smooth acclimation during early grow-out stage. Water replacement during later grow-out further dilutes salinity in the neighbourhood. However, the seepage, overflow, or discharge at the end of a crop of this higher-than-normal mineral concentration into the neighbouring environments is inevitable. As to what extent the impact of this salinity pollution may cause to the freshwater ecosystem, including soil salinization, remains to be assessed. This is despite the low salt concentration and continues dilution by rainfall or surface water flow. However, an investigation on the effluent from an inland, low-salinity shrimp farm showed a potential benefit of this rich nutrient effluent in irrigation of field crops (McIntosh and Fitzsimmons 2003).

Escapes of cultured *L. vannamei* into the wild may also have some ecological effects. Whether they will become predator, prey, or pathogen carrier also remains to be studied. WSSV, which was first reported on *P. monodon* (Chou et al. 1995), has a broad host range within decapod crustaceans including freshwater crayfish (Lo et al. 1996b; Wang et al. 1998). The virus, which comes from *L. vannamei* may also infect freshwater prawn.

Among the more than 20 shrimp species introduced for aquaculture, three species have established population in alien habitats. *Penaeus monodon* (from Asia Pacific) has been found from trawler catches in Nigeria (Chemonics 2002). *Litopenaeus vannamei* (native to west coast of the Americas) had been caught in the Gulf of Mexico (Briggs et al. 2005), while *Fenneropenaeus merguiensis* (from southeast and south Asia and Indian Ocean) have established its population in Fiji (Gundermann and Popper 1975; Pérez Farfante and Kensley 1997) and in Mediterranean sea (Özcan et al. 2006). The chances of *L. vannamei* establishing a population in inland ecosystem is regarded as small, since its spermatophore has lower weight and higher abnormal rate at 5 psu (Yuan and Cai 2006), and its fertilized eggs cannot develop normally when the salinity is below 22 psu (Peng et al. 2002).

The expansion of *L. vannamei* culture into inland areas may lessen new development of penaeid mariculture in coastal regions. This may concomitantly alleviate the pressure on coastal resources and the adverse impacts on sensitive ecosystems caused by penaeid mariculture. *Litopenaeus vannamei* culture in inland area should have less ecological impacts than in coastal area, since the former is practiced in a more isolated and semi-enclosed environment.

## *5.2 Socio-Economic Impact*

The massive and rapidly increasing production of *L. vannamei* has had the expected impact of a reduction in commercial prices on the international and domestic markets (Fig. 11). The reciprocal relationship between production and price is evident up to 2003. However, since 2003, price has remained relatively constant despite the continuous increase in production, which almost doubled in 2007. The increase of imports to U.S. reduced prices during 2000 (USD6.30/kg) and 2003 (USD3.96/kg). However, imposed antidumping duty discouraged importation and pushed prices down further during 2003 and 2005 (USD3.94/kg). It appeared that the import volume and market price have reached a balance for now (Fig. 11).

The price may also have reached its tolerable minimum because farmers and suppliers are now working on the narrowest profit margin. They compensate for this by augmenting the volume shrimp produced. Production increase may not be good news for producers, but it is certainly for consumers.

Further production growth will be ultimately be balanced by lowering profit margin in the producer sectors including hatcheries, farmers, feed millers, and processors. Expansion of domestic market (e.g., consumers in China) will also contribute

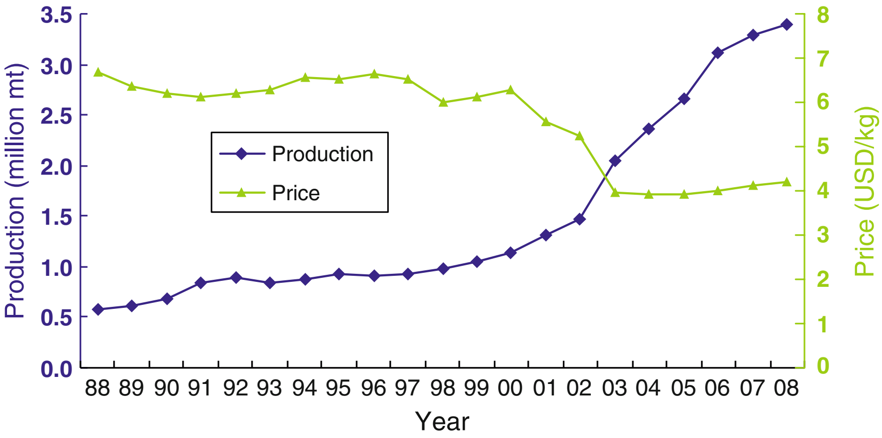

**Fig. 11** Production and price of world cultured shrimp, 1988–2008

to the market balance. The imposition of anti-dumping tariff may not be able to help U.S. Gulf of Mexico shrimp fishermen to compete with their foreign rivals, especially with the tremendous increase of fuel costs during the last 3 years.

## 6 Prospects and Outlook

The farming of *L. vannamei* has been of economic benefit to the producing countries (SEAFDEC 2005). While more and more Asian countries allow the introduction and culture of *L. vannamei*, the production of *P. monodon* will further decrease (Merican 2009). The reason is, once farmers experienced successful harvest of and higher profit from *L. vannamei*, they more likely will not return to culture *P. monodon*. While production increase in *P. monodon* is bleak, it's potential for use in organic culture to produce jumbo-sized prawns for a niche market similar to lobster market is still high (Shinoj et al. 2008). In this niche market, price is high, cost is of less concern, and most importantly, species origin is restricted. Another alternative is to culture 'super monodon' which would have even better culture traits than *L. vannamei*. *Penaeus monodon* has a much wider geographical distribution than *L. vannamei*, so is its expected higher genetic diversity. Therefore, the probability of obtaining a 'high health monodon' can be no lower than a 'high health vannamei', especially now that modern genomic technology exists. This is achievable, and it is just a matter of time and effort for visionary scientists and investors to make this a reality.

The growth of *L. vannamei* culture in freshwater is expected to continue in China, Thailand, and other Asian countries due to higher profits compared to other freshwater aquaculture species. This may happen in countries where other *peneaoid* are traditionally cultured, such as India and Thailand, because a higher price and wider international market is available for *L. vannamei*. However, the impacts on the ecosystem by the extensive use of freshwater resource during salinity acclimation processes in coastal hatcheries and nurseries should be properly assessed and regulated.

WSSV-infected wild shrimp was found in coastal water of South Carolina, in the northern Atlantic Ocean (Chapman et al. 2004), and in coastal and offshore waters in the southern Atlantic Ocean (Cavalli et al. 2010). Other virus infections of wild animals were captured in coastal waters of Taiwan (Lo et al. 1996b), of the southeastern (Uma et al. 2005), and eastern-coasts of India (Vaseeharan et al. 2003), and also in coastal water of Panama (Nunan et al. 2001). Although TSV, the most economically significant viral pathogen of *L. vannamei* (Funge-Smith et al. 2003), is not reported to be detrimental to aquaculture production in Asia nor has affected indigenous cultured or wild shrimp populations (Briggs et al. 2005), precautionary measures have been advocated or enforced by government authorities and executed by some private sectors (SEAFDEC 2005). This is through the introduction and sole use of SPF and even SPR broodstock, mostly coming from the USA or USA-based aquaculture ventures in Asia. Furthermore, the advantage in producing broodstock within the culture ponds allows domestication and genetic selection for favourable traits, besides being SPR.

Aquaculture of *L. vannamei* in Asia is expected to be further sustained and to continuously expand in the years to come. Potential problems that can affect future Asian production of *L. vannamei* include: decreasing genetic diversity through domestication and selection; increasing trans-boundary movements between continents and within the Far East; and emergence of new and Asian-specific viral and other microbial diseases. These potential problems will require Asian governments to take preventive measures through legislative control as well as scientific and technical measures.

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# The Invasive History, Impact and Management of the Red King Crab *Paralithodes camtschaticus* off the Coast of Norway

**Lis Lindal Jørgensen and Einar M. Nilssen**

**Abstract** The red king crab, *Paralithodes camtschaticus*, was intentionally transferred from Russian territorial waters in the Northern Pacific Ocean and introduced into the Barents Sea between 1961 and 1969 in order to create a new commercial fishery. A decade later a reproducing population was found to be well established in the latter region. The red king crab has since dispersed southwards along the coast of Northern Norway. Its ecological impacts on the native fauna have been investigated. From 2002 till 2007 the management of the commercial fishery has been undertaken jointly by Norway and Russia. Since then, management has continued within the countries respective fishery zones in the Barents Sea. In 2004 Norway was given free rein to apply all necessary management methods to limit the spread of the crab westwards of 26°E longitude.

## 1 Introduction

The red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Lithodidae Samouelle, 1819) (Fig. 1) is among the world's largest arthropods, reaching ~220 mm carapace length (CL), a weight over 10 kg (Powell and Nickerson 1965a, Powell and Nickerson 1965b), and living up to 20 years (Kurata 1961).

It is native to the Northern Pacific Ocean (Fig. 2) with reported range from the Korea and Japan, Kamchatka, the Aleutian Island chain, Alaska, and southeast to Vancouver Island, Canada (Rodin 1990).

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**Fig. 1** Dorsal view of *Paralithodes camtschaticus* (photographer: Lis Lindal Jørgensen, Institute of Marine Research)

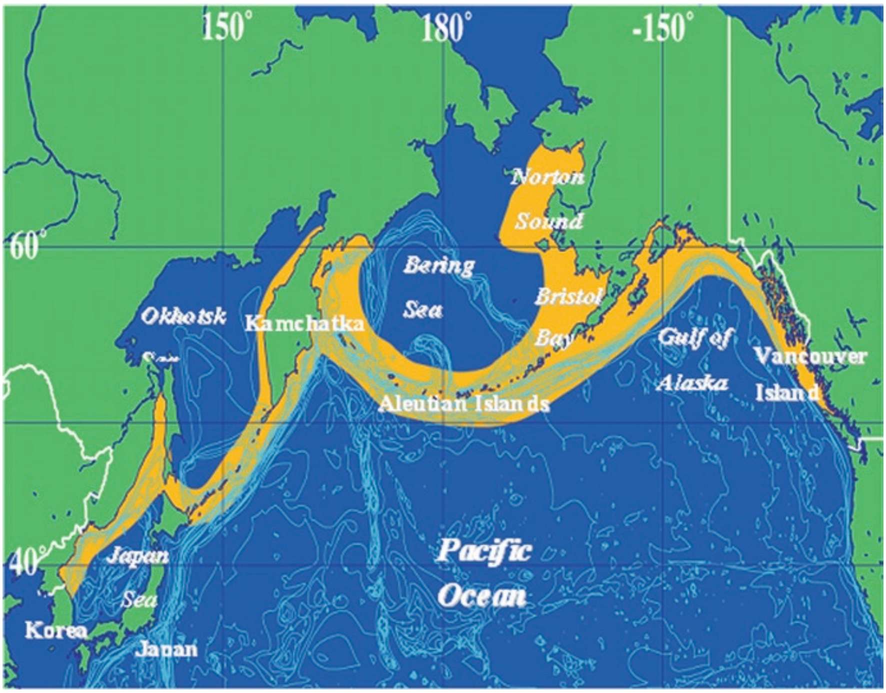

**Fig. 2** The native distribution of the red king crab (*yellow colour*) along the coasts of Korea, Japan, Russia, Alaska, and Canada

The red king crab was collected by Russian scientists during the 1960s and 1970s from Peter the Great Bay, Okhotsk Sea, and introduced into the Barents Sea (Orlov and Karpevich 1965; Orlov and Ivanov 1978) (Fig. 3). Between 1961 and 1969, 1.5 million first stage zoeae, 10,000 1–3 year old juveniles (50% females and 50% males) and 2,609 5–15 year old adult (1,655 females and 954 males) crabs from West Kamchatka, were intentionally released into the Kolafjord, east Barents Sea, Russia, in order to create a commercial fishery (Orlov and Karpevich 1965; Orlov and Ivanov 1978). In the Russian part of the Barents Sea the highest densities were observed on both sides of the Rybachi Island (Fig. 4) during late 1980s and early 1990s. Later in the 1990s, the red king crabs became abundant along the eastern part of the Kola Peninsula and were reported from Cape Kanin and the entrance of the White Sea during 2002. Further northwards the crab was found on the Kanin Bank and at the Goose Bank (Zelina et al. 2008).

**Fig. 3** Red king crab dispersal in the Barents Sea. Embedded map showing the translocation of crabs from West Kamchatka, North Pacific Ocean westwards into Kolafjord (see fig. 4), east Barents Sea

**Fig. 4** The spreading of the red king crab along the northern coast of Norway

In 1992 the red king crab became abundant in Norwegian waters, initially reported from southern Varangerfjord (Fig. 4). By 1994 *P. camtschaticus* spread to the northern side of the fjord. The crab has increased fourfold in Varangerfjorden within 12 years (Table 1). In 1995 it was recorded in Tanafjord and the population has been relatively stable in the period 1999–2007 (Table 1). Further range extensions were noted in Laksefjord and Porsangerfjord during 2000, and by 2001 several adult crabs were caught west of Sørøya and west of the North Cape. In 2002 the crab were captured close to Hammerfest and three specimens were recorded about 120 nautical miles west off the North Cape (Hjelset et al. 2003; Sundet 2008).

The crab population along the northern coast of Norway was estimated to number 2.9 million individuals in 2001 and 3.5 million in 2003 (Hjelset et al. 2003). In 2007 the population in Norwegian waters was estimated at 4–5 million individuals (Sundet 2008). That number is an underestimate as only individuals with a carapace longer than 70 mm and at water deeper than 100 m are included.

**Table 1** Average catch per unit of effort (CPUE) (number of crabs per trawl hour) with 95% CI (confidence interval) of the red king crab from the scientific cruises in the period 1995–2007 (From Hjelset et al. 2009)

| Year | Varangerfjorden CPUE ± CI | Tanafjorden CPUE ± CI | Laksefjorden CPUE ± CI |
|---|---|---|---|
| 1994 | [a] | | |
| 1995 | 10.5 ± 3.6 | | |
| 1996 | 19.1 ± 7.0 | | |
| 1997 | 21.0 ± 7.7 | | |
| 1998 | 13.7 ± 2.9 | | |
| 1999 | 17.4 ± 4.5 | 18.3 ± 9.7 | |
| 2000 | 25.0 ± 13.3 | 5.2 ± 2.7 | |
| 2001 | 20.5 ± 10.0 | 6.0 ± 2.8 | |
| 2002 | 15.6 ± 5.8 | 18.9 ± 9.7 | 2.5 ± 4.9 |
| 2003 | 19.7 ± 7.5 | 38.8 ± 18.9 | 37.9 ± 71.7 |
| 2004 | 30.4 ± 17.2 | 25.8 ± 8.2 | 25.4 ± 39.1 |
| 2005 | 33.3 ± 21.9 | 23.5 ± 9.6 | 13.0 ± 16.0 |
| 2006 | 41.5 ± 25.4 | 31.0 ± 14.2 | 25.0 ± 31.0 |
| 2007 | 45.8 ± 25.7 | 24.8 ± 9.2 | 25.9 ± 19.1 |

[a] Not available

## 2 Spreading, Settling, Podding and Migration

The larvae of the red king crab develop in the coastal zone. In the 2 months after hatching, the pelagic larval stages can be transported by currents considerable distances (Pedersen et al. 2006). This period must be synchronised with the spring phyto- and zooplankton peaks in the upper 15 m of the water column (Shirley and Shirley 1989). The larvae settle in shallow waters (<20 m) on sponges, bryozoans and macroalgae (Marukawa 1933). Successful recruitment depends on a well-developed sessile community with extensive areas of dense concentrations of hydroids, bryozoans, and sponges needed to support a massive settlement of larvae.

Red king crabs smaller than 20 mm carapax length (CL) lives a cryptic and solitary life, sheltering beneath rocks and stones and in crevices. In the second year podding behaviour (Fig. 5) appears (Dew 1990). Podding is when the crabs congregate in large, tightly packed groups (Powell 1974). The smallest and largest crabs found in any pod are 24 and 69 mm CL, respectively. Pods therefore form during the latter part of the second year, exist throughout the third year, and continue a short time into the fourth (Powell and Nickerson 1965a, Powell and Nickerson 1965b). When the density of the crab approaches 6,000 individuals, pod structures transforms into elongate piles and dome shaped piles do not commonly occur until the fourth year when crabs are 60–97 mm CL (Powel and Nickerson 1965a). The pods are held during the daytime, but disperse into a nightly foraging aggregation. This was explained by changes in water temperature, crab weight, and time of

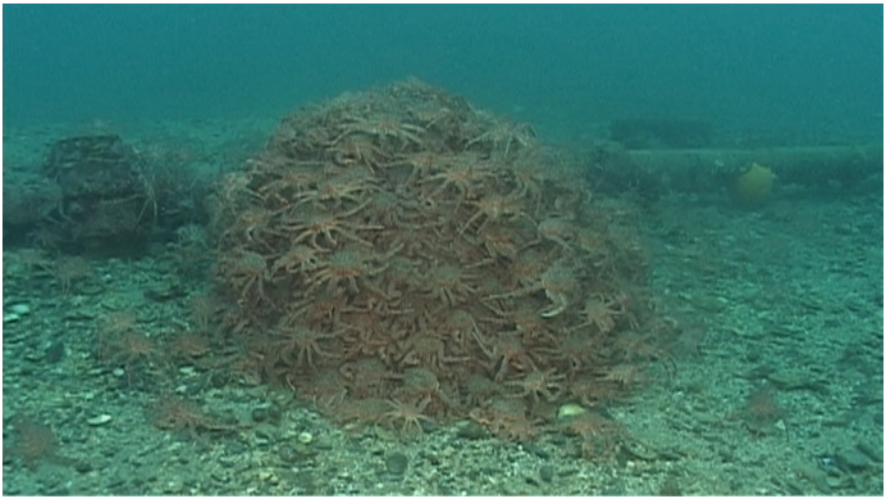

**Fig. 5** Podding of juvenile red king crab (*Paralithodes camtschaticus*) in Norwegian fjord (Photographer: Geir Randby, Lillehammer Film)

sunset by Dew (1990). A trend of increased foraging time and movement to deeper, cooler water was apparent after mid-April, as water temperatures reached 4°C and began a sustained summer increase (Dew 1990).

Immature crabs (CL<120 mm), generally remain along the coast at 20–50 m depth (Wallace et al. 1949), and are seldom associated with adults in deep water.

Adults occur on sand and mud bottoms (Vinogradov 1969; Fukuhara 1985) and aggregate according to size, life history group or sex. The adult crab undergoes two migrations, a mating-moulting migration and a feeding migration (Fig. 6). The patterns of behaviour are similar off the coasts of Japan, Russia, and Alaska (Marukawa 1933; Powell and Reynolds 1965; Vinogradov 1969). The shoreward migration to shallow waters (10–30 m) takes place in late winter and early spring when the crabs mate, breed (Marukawa 1933; Wallace et al. 1949; Powell and Nickerson 1965a, b) and hatch their eggs (Stone et al. 1992). Extensive aggregations of both sexes occur during the spring spawning season. These spawning aggregations may also be found also in shallow water where kelp occurs (Powell and Nickerson 1965a, b). The kelp may provide shelter for the females following moulting ecdysis, and during mating (Jewett and Onuf 1988). Spawning is followed by migratory feeding movements, of both sexes, towards progressively deeper water (300 m). After this period, the sexes form separate aggregations for the remainder of the year (Fukuhara 1985), and are not found together until the following mating season (Cunningham 1969).

In Russian waters the crab occurs both along the coast and offshore, while in Norwegian waters, the crab is distributed solely along the coastline (Fig. 3). Since along the Russian coast the bottom slopes gradually, whereas in the Norwegian

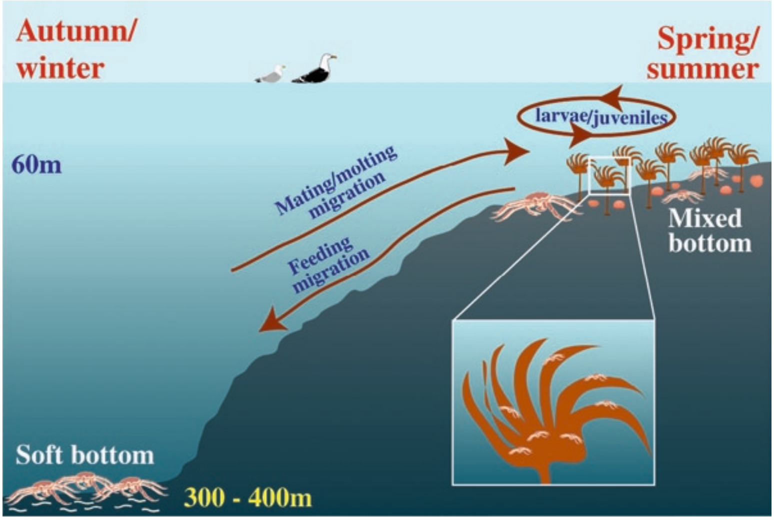

**Fig. 6** Seasonal migration of *Paralithodes camtschaticus*: the mating-moulting migration in the spring/summer period to various substrates with benthic communities principally composed of calcified prey organisms, and a subsequent feeding migration in winter/autumn to soft substrate where annelids occur (*inset*: juvenile red king crabs associated with kelp)

fjords the bottom descends abruptly to deep water (300 m), it is proposed that the pattern of distribution is dependent on the coastal topography. This gently sloping coastal topography is also found in the north Pacific habitats, where the crab migrates far from the coast to reach deep water. The steeper topography may keep the Norwegian population close to the coast or inside the fjords year round.

## 3 Temperature Tolerance

The red king crab tolerates temperatures from −1.7 to at least +15°C (Rodin 1990), these tolerance limits vary at different stages of its life history. Temperature preferences of immature crabs (50–100 mm CL) are at <3°C as determined in laboratory studies (Hansen 2002). In the Barents Sea and the northern Norwegian Sea the temperature at 100 m depth in winter varies from 0°C to ~+6°C. Recently, it has been experimentally demonstrated that larval survival is affected by the water temperature in which the egg carrying females had been kept (Sparboe pers. comm.). Females acclimated to 14°C produced larvae with higher survival rates at high temperature compared with larvae from females acclimated to 4°C and 8°C. Survival was high (almost no mortality) for all crabs exposed to challenge temperatures from −1.7°C to 15°C independent of acclimation temperatures (4°C , 8°C and 14°C)

(Sparboe pers. comm.). This result may indicate that the red king crab may successfully invade also more southern habitats along the Norwegian coast (Larsen 1996; Sparboe pers. comm.).

The population of West Kamchatka overwinters on the continental slope where the warmer Pacific Ocean water mixes with the colder waters of the shallow shelf. The migration from the over wintering area to shallow water depends on bottom water temperatures, as well as the physiological conditioning prior to spawning and moulting (Rodin 1990). Large numbers of adult crabs assemble in shallow waters (10–15 m) in May–June when temperatures are approximately 2°C. Following reproduction in June and July, adults forage at around 50 m depth where the water is 2°C. Once temperatures decrease, the crabs disperse to deeper water for overwintering (Rodin 1990).

Amazingly, a single red king crab male was recorded in the comparatively "warm" Mediterranean Sea, though no explanation is given of its mode of introduction and survival so far south (Faccia et al. 2009).

## 4 Food and Feeding

The crab's food preference varies with age and stage. The pelagic larvae feed on both phytoplankton and zooplankton (Bright 1967). Once settled, the juveniles feed on hydroids, the dominant component of the epifauna on the Kamchatka shelf (Tsalkina 1969). Dew (1990) reported that young crabs (CL > 20 mm) feed on sea stars, kelp, *Ulva* spp., red king crab exuviate, bivalves of the genera *Protothaca* and *Mytilus*, nudibranch egg masses, and barnacles. Occasionally, crabs were observed dragging around large sea stars during the nocturnal foraging period. These stars were sometimes left near the base of the pod in the morning, and taken up again upon pod break-up. Adults are opportunistic, omnivorous feeders (Cunningham 1969). They feed on the most abundant benthic organisms, though usually one food group/species dominate their diet and this varies regionally (Kun and Mikulich 1954; Kulichkova 1955; Jewett et al. 1989). Most common food items are echinoderms (*Ophiura* spp., *Strongylocentrotus* spp.) and molluscs (*Nuculana* spp., *Clinocardium* spp., buccinid and trochid snails) (Cunningham 1969). Calcareous-shelled food items are more frequent in the diet of post-moult crabs (Herrick 1909; Fenyuk 1945; Logvinovich 1945). Kulichkova (1955) suggested that crabs need to replace calcium carbonate lost during moulting and that the young clams and barnacles in shallow waters fulfill this need. At times of moulting, growth and reproduction, the food intake declines but such pauses do not normally last more than 2–3 weeks (Kulichkova 1955) and thereafter the crabs feed avidly (Takeuchi 1967). The crabs feed on bivalves and echinoderms during spring and summer months when in shallow areas, and polychaetes in autumn and winter where they migrate to deeper water (Gerasimova 1997). Crabs contain significantly more food in their guts during spring-early summer (Takeuchi 1967; Jewett et al. 1989) when compared with the late summer-autumn-winter (Jewett and Feder 1982).

Adult crabs feed either by grasping and tearing apart larger invertebrates or by scooping sediment by the lesser chela and sieving it through the third maxillipeds. Scooping sand was often observed by Cunningham (1969) during periods when no larger food was immediately available. Logvinovich (1945) referred to the frequent presence of sediment in the stomachs and intestines of crabs. Foraminifera, minute molluscs and amphipods found in stomach contents probably result from feeding by sieving, as these either burrow in or occur on sediments. Logvinovich (1945) suggested this as an alternative method of feeding when larger prey is unavailable. Observations on the degree of gut fullness would indicate that crabs browse on food as it is encountered (Cunningham 1969). Calculations indicate that a young adult crab consumes 6 g, and juvenile crab 1.7 g within 25 h at 3°C, and 16 g and 3.5 g respectively at 6°C (Jørgensen et al. 2004). Laboratory studies indicate a daily ingestion rate of more than 70 g (squid) for young adult crabs at 5–9.4°C (Zhou et al. 1998). Pavlova et al. (2007) showed that juveniles consume a mixture of polychaetes, bivalves, ophiuroids, echinoids, asteroids weighing 0.7–26 g daily, based on soft tissues. However, identification of prey items and calculation of their weight from gut contents is inaccurate because decapods rarely swallow prey whole, rather they tear it apart. These fragments are shredded further in the gastric mill and are mostly unidentifiable. If to the weight of consumed soft tissue are added the undigested shells (*Chlamys islandica*, *Strongylocentrotus droebachiensis*, *Modiolus modiolus*, *Astarte* sp., *Buccinum undatum*, *Asterias* sp. or *Henricia* sp.) mature and immature crab show a daily foraging rate (killing or mortally damaging) between 150 and 300 g at 5–6°C (Jørgensen 2005; Jørgensen and Primicerio 2007), 17–408 g when feeding solely on scallops within 24 h (Anisimova et al. 2005; Jørgensen and Primicerio 2007), and 1–101 g per 24 h when feeding on sea urchins (Gudimov et al. 2003; Jørgensen and Primicerio 2007).

The above results might indicate a range from "low" (high abundance of prey, high species richness, prey of low foraging preferences, or not foraged benthic species) to a "strong" (low abundances of prey, species richness is low, highly preferred and flat-bodied prey species) impact on native local communities depending on the abundance of prey and the number of red king crabs. Because food appears to be the sole factor that could limit the increase in red king crabs numbers within the Southern Barents Sea (Gerasimova 1997), it is most likely that the invasive species, particularly in high abundances, will have a measurable effect on native prey populations.

## 5 Ecological Impact

There is a growing recognition that aliens may interact negatively with the native species in the recipient communities (e.g., Elton 1958; Lodge 1993; Carlton 1996; Ruiz et al. 1997; Walton et al. 2002; Ross et al. 2003). Due to the body size, long life span, predaceous behaviour, large population size and rapid dispersal of the red king crab, questions have been raised as to its impact on the native benthic community.

Since the establishment of the crab in the Barents Sea, studies on its predatory effect have been undertaken (Sundet et al. 2000; Haugan 2004). The crab feeds on a range of molluscs, sea urchins (*Strongylocentrotus droebachiensis*) and other echinoderms, crabs, polychaetes, sipunculids and fish (Sundet et al. 2000). Indeed, it was shown that some benthic taxa decreased considerably in abundance since its introduction, and that changes have occurred in the benthic community structure in the investigated fjords (Anisimova et al. 2005). It was calculated that the crab preys upon 15% of the total coastal population of *Strongylocentrotus* urchins (Gudimov et al. 2003; Pavlova 2009). Experiments of the potential impact of the invading crab on the beds of the native scallop, *Chlamys islandica*, showed that the scallop had no size refuge. The scallop's flat shell is easily handled by both small and large crabs (Jørgensen 2005; Jørgensen and Primicerio 2007), though small crabs seem to prefer smaller scallops (Gudimov et al. 2003). Larger prey items with dome shaped bodies, sponges, sea cucumbers and sea anemones were not preyed upon (personal laboratory observations made by the author). Scallop beds with a rich associated fauna are less vulnerable to predation than beds with few associated species, had several possible prey items to forage in the rich species associated scallop bed compared to the scallop bed with few other species than the scallop (Anisimova et al. 2005; Jørgensen 2005; Jørgensen and Primicerio 2007).

Anisimova et al. (2005) calculated that the crab population consumes 37 tonnes of capelin (*Mallotus villosus* Cuvier, 1829) eggs in a Barents Sea fjord during 3 months, and extrapolated this value to the whole Barents Sea crab population. The study concluded that the crab may impact 0.03% of the egg mass laid by the capelin.

In order to forecast possible impact in new or in already invaded areas, a study of the quantitative values of the prey (killed or mortally damaged specimens) is needed, and possible recipient areas need to be surveyed ahead of the crabs' arrival. The baseline surveys should include epifauna and infauna as the crab preys on components of both.

## 6 Economic Impacts

The development of the crab fishery in Norway is illustrated in Table 2. The data indicate that from 1994 to 2007 the total allowable catch (TAC) and effort increased dramatically. The overall increase in number and size of fishing vessels indicate the development of the economic importance of the crab. After 2001 the overall harvest rate increased along with the growth of the stock.

The increase in crab stocks in recent years has resulted in severe by-catch issues, particularly in the cod gillnet fishery. However some available size distribution data for crabs caught by the gillnet fishery show that few juvenile specimens are caught. Most crabs seem to be larger than CL 120 mm. More than 60% of the crabs caught in the gillnet fishery in Varangerfjord were females, while large males dominate the by-catch in the lumpsucker gillnet fishery during early summer. The by-catch of crabs increased from 1997 to 1999, but declined in 2000–2002, and the estimated number

**Table 2** The number of vessels, fishing effort in traps allowed per boat, TAC, and size of the vessels participating in the research- and commercial fishery of the red king crab in Norwegian waters from 1994 to 2007 (From Hjelset et al. 2009)

| Year | Number of vessels | Fishing effort traps per boat | TAC (legal males) | Harvest rate (%) | Overall vessel length(m) |
|---|---|---|---|---|---|
| *Research fishery* | | | | | |
| 1994 | 4 | 20 | 11,000 | 41 | 7–15 |
| 1995 | 4 | 20 | 11,000 | 11 | 7–15 |
| 1996 | 6 | 20 | 15,000 | 17 | 7–15 |
| 1997 | 6 | 20 | 15,000 | 14 | 7–15 |
| 1998 | 15 | 20 | 25,000 | 17 | 7–15 |
| 1999 | 24 | 20 | 38,000 | [a] | 7–15 |
| 2000 | 33 | 20 | 38,000 | 6 | 7–15 |
| 2001 | 116 | 20 | 100,000 | 22 | 7–15 |
| *Commercial fishery* | | | | | |
| 2002 | 127 | 30 | 100,000 | 13 | 7–15 |
| 2003 | 197 | 30 | 200,000 | 15 | 7–15 |
| 2004 | 260 | 30 | 280,000 | 21 | 6–21 |
| 2005 | 273 | 30 | 280,000 | 34 | 6–21 |
| 2006 | 264 | 30 | 300,000 | 29 | 6–21 |
| 2007 | 253 | 30 | 300,000 | 31 | 6–21 |

[a] Not available

in 2002 was a third as large as in 1999 (Sundet and Hjelset 2002; Hjelset et al. 2003). This is probably due to the decline in the cod gillnet fishery. Low abundance of cod has forced the fishermen to move further west along the coastline in search of fish, thereby reducing the by-catch of the crab. The crab impacts the longline fishery by removing the bait off the hooks, thereby reducing catches of target fish.

In order to compensate the fishermen for the loss of the traditional fishery and equipment (i.e., gillnets, long-lines) caused by the invasion of the crab, the criteria for participation in the annual fishery are set in favour of the local fishermen. This is generally acknowledged by fishermen from other parts of Norway, since the presence of the crab directly impacts the local fishermen (Jørgensen et al. 2004).

## 7 Management and Future Challenges

From 1994 to 2001, the newly introduced red king crab stock was exploited through a research fishery limited by TAC numbers (Table 2) in the territorial waters of Russia and Norway. The harvest rate of the crab was relatively low (Sundet and Hjelset 2002). Thereafter the management regime and the following harvest pattern ensured that the largest males were removed from the population (Nilssen and Sundet 2006).

In 2002, the fishery had become commercial, and the Norwegian quota was set at 100,000 crabs (Nilssen and Sundet 2006), and increased to 300,000 crabs in 2006 (Table 2). The management of the fishery was based on annual joint agreements between Russia and Norway through the Mixed Russian-Norwegian Fishery Commission. During 2004, Norway and Russia agreed to limit the spread of the crab westwards by establishing a border at 26°E in the Norwegian zone (Fig. 3 North Cape). West of this longitude Norway was given free rein to apply all necessary management methods with a view to limit the spread of the crab. The joint Norwegian and Russian management ended in 2007. Since then management has been continued by each country within their respective fishery zones in the Barents Sea.

At present two management regimes are implemented in Norwegian waters and located to two different geographical areas/regions. One commercial eastern area from the Russian border at 31°E to North Cape at 26°E which are controlled by the governmental management plan for a king crab fishery where the population of king crabs are managed in order to give the best possible biological and economical output. The second area is the western area, south and west of 26° E, with a free fishing of the red king crab in order to reduce the rate of spreading south along the Norwegian coastline (St. meld. 40 2006; Øseth 2008).

The commercial stock in the eastern area is managed according to the '3-S' regime (sex, size and season) and only males with a CL > 137 mm may be landed (Nilssen and Sundet 2006). This strategy is similar to the Alaskan management model (Otto 1986; Kruse 1993). In the western "free fishing area" all crabs are landed without regard to size and sex.

It was not legal to land females CL > 137 mm in the eastern commercial management area before 2008, but now allowed. This regime with an eastern commercial managed area and a western free fishing area is still under evaluation and king crab assessment and management in relation to harvest strategies, by-catch problems, changes in gear technology, targeting ground fish and reducing the spread of this invasive species is still under consideration (Jørgensen et al. 2007).

Both extended periods of heavy fishing pressure (Pollock 1995; Jørgensen et al. 2007) and lack of food can affect the life history traits of crustaceans. There will always be a trade off between food available and the investment in growth, size/age at maturation and reproductive output (Stearns 1992). Reduction in reproductive output could be effected by lack of food which will be a consequence of the increased biomass of crab. It is therefore necessary to investigate the variation in size at sexual maturity and reproductive output in the population along the Norwegian coast in order to establish a baseline for future management and monitoring (Hjelset et al. 2009). Therefore, registration of size at sexual maturity, fecundity and moulting frequencies of the crab has been collected since 1992 and will be published in nearest future.

Precise scientific predictions cannot be given concerning the future impacts of the red king crab in the Southern Barents Sea. All indications suggest that this invasive species will spread further north in the Barents Sea, as well as southwards along the coast of Norway. The possibility of transporting larvae in ballast water to other regions is an alarming reality, especially as the traffic of oil and gas vessels around the Barents Sea and northern Norway is likely to increase in the near future.

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# The Commercial Exploitation of the Chinese Mitten Crab *Eriocheir sinensis* in the River Thames, London: Damned if We Don't and Damned if We Do

**Paul F. Clark**

**Abstract** The invasive Chinese mitten crab *Eriocheir sinensis* is now well established in the River Thames, London. This crab is considered to be a delicacy in many SE Asian countries and their expatriates when its gonads are ripening and fully developed prior to mating. Sexual maturity is attained during the autumn months as mitten crabs migrate in large numbers from freshwater streams to the higher salinity brackish waters of estuaries where mating occurs. Up to US$ 40 can be paid for a single mature female mitten crab in the right condition at high-class restaurants in China, Japan and Singapore. Consequently, commercial exploitation of mitten crabs may be a viable method of reducing the population size in the Thames catchment. A recent pilot study concluded that Thames mitten crabs were fit for human consumption and that the population is large enough to be exploited. There are, however, still major issues that need to be discussed, including whether we really want to start a mitten crab fishery in the Thames. Basically, we are damned if we do and damned if we don't.

Mitten crabs appear to have few natural enemies in the River Thames that are capable of considerably reducing their numbers. If exploitation of mitten crabs does not go ahead therefore, evidence suggests that the population will continue to increase in numbers and expand its distribution westwards in the Thames catchment. The density of mitten crab burrows already recorded in unprotected river banks will probably proliferate, causing more erosion. Furthermore, larval densities will continue to rise in the estuarine plankton, increasing the risk of uptake into ballast water for subsequent risk of dispersed into new watersheds nationally by local coastal shipping and to other continents via trans-oceanic vessels.

If commercial exploitation is regarded as a suitable method by which to reduce numbers of Thames mitten crabs, then another set of potential environmental impacts of this activity needs to be addressed. For example, the European Commission has initiated an Eel Recovery Plan (Council Regulation 2007b, No 1100/2007) to

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try to return the European eel stock to more sustainable levels of adult abundance and glass eel recruitment. However, during a pilot fisheries study using fyke nets, the eel proved to be a significant part of the Thames mitten crab by-catch. Consequently, commercial exploitation of mitten crabs could be to the detriment of the Thames eel population as fisherman are unlikely to return such a valuable catch back to the river. Moreover, if the Thames mitten crab fishery were to be a financial success, there is a real concern that this contentious immigrant could be intentionally dispersed throughout other UK watersheds, as has been the case, for example, of the invasive freshwater crayfish, *Pacifastacus leniusculus*. Furthermore, a mitten crab fishery would require strict controls with respect to fishing equipment, fishermen, traders and restaurants including the possible restriction of live imports of *Eriocheir sinensis* into the UK.

# 1 Introduction

## *1.1 River Thames Mitten Crab Records*

The first River Thames Chinese mitten crab record was a single specimen captured at Lots Road Power Station, Chelsea in 1935 (Harold 1935). Over 40 years on, Ingle and Andrews (1976) recorded the capture of three crabs at West Thurrock Power Station and further sporadic sightings of the crab from the Thames were noted later by Ingle (1986). Clark and Rainbow (1997) and Clark et al. (1998) provided evidence that the mitten crab population in the Thames appeared to have increased during the early 1990s and was continuing to rise. They used Environment Agency mitten crab records collected from the filter screens at West Thurrock (1976–1993 when it closed) and Tilbury (1993–1996) Power Stations. From a relatively constant background baseline the mitten crab captures at West Thurrock suddenly increased in 1992 (see Clark et al. 1998: Fig. 3), and for the first 3 months of 1993 before the power station closed on 31 March of that year (see Clark et al. 1998: Fig. 4). Large numbers of crabs were collected from Tilbury Power Station in 1994 and 1995, and when collecting ceased during the first half of 1996, just as many crabs were caught (over 500) as for the whole of the previous year. The West Thurrock data show an increase in crab numbers during 1992 that had been further enhanced and maintained at Tilbury from 1993 to 1996. Clark et al. (1998: Fig. 5) presents data in terms of the numbers of crabs collected in separate 4 h counting period at Tilbury from 1994 to 1996. Data for more than one collection in a given month have been averaged to provide objectively comparable data. These data confirm the increase in crab numbers continued in 1996. The seasonal occurrence of crabs at Tilbury corroborates the view that crabs are migrating through the estuary and peak numbers appear at this power station in May. The first juvenile was found in 1992 (Attrill and Thomas 1996a), while Robbins et al. (2000) reported that high numbers of juveniles were found in the river, indicating that *E. sinensis* had become established and was successfully breeding.

## 1.2 Early Records of Ovigerous Crabs

Andrews et al. (1981: Table 1) appear to have recorded the first berried mitten crab (see Fig. 1) for the Thames taken from West Thurrock Power Station in January 1979, which incidentally was returned live to the river, and later in December of the same year. Ingle (1986) too recorded an ovigerous mitten crab from the Thames stating only, "During 1979 a female mitten crab bearing eggs was caught at Southend-on-Sea". Attrill and Thomas (1996a) listed all records of *Eriocheir sinensis* from 1986 to 1993 in the Thames including notes on ovigerous crabs. Table 1 summaries the collection of berried crabs from the Thames Estuary between 1990 and 1992. The earliest capture of an ovigerous specimen in the year reported by Attrill and Thomas was August (20.9.1990) and their latest December (12.12.1991). Attrill and Thomas (1996a) suggested that the pattern of mitten crabs collected at West Thurrock Power

**Table 1** Ovigerous crabs recorded in the Thames by Attrill and Thomas 1996a

| Date | Site | Notes |
|---|---|---|
| 20.09.1990 | West Thurrock Power Station | 1 ovigerous crab |
| 28.11.1991 | West Thurrock Power Station | 1 ovigerous crab |
| 10.12.1991 | West Thurrock Power Station | 1 ovigerous crab |
| 12.12.1991 | Crossness | 1 ovigerous crab |
| 13.11.1992 | West Thurrock Power Station | 17 ovigerous crabs |

**Fig. 1** An ovigerous mitten crab. November 2005. According to Hoestlandt (1959) a female can spawn up to 1 million eggs. Phil Hurst NHM Photo unit

Station had changed during 1991–1992 with adults appearing more regularly until 30 individuals were captured on 13 November 1992. According to them, this figure of 30 crabs was more than the total number of mitten crabs caught in the previous 7 years at the power station and suggested that downstream migration (first evidence in the Thames) was occurring because all the females were ovigerous.

## *1.3 River Thames Distribution*

Clark and Rainbow (1997) and Clark et al. (1998) also updated the distribution data in the Thames catchment. In 1996 they made an appeal to the general public for mitten crab sightings, and from 27 August to 15 November 162 mitten crab reports were received. The updated distribution of the mitten crab in the Thames catchment is shown in Clark et al. (1998); compare their Figs. 1 and 2. At that time *Eriocheir sinensis* was known from as far west as the River Colne at Staines and in the east, the crab was found in the Cray, Darent, Quaggy, Pool and Ravensbourne. In the north-east, sightings were really common in the River Lee with the most northerly report of *E. sinensis* being in this watershed at Enfield, some 15 km from the River Thames. The survey also recorded *E. sinensis* in almost every tributary from Chelsea upstream to Chertsey including Beverley Brook and the Rivers Wandle, Brent, Duke of Northumberland, Crane, Hogsmill, Longford, Ember, Mole and Ash.

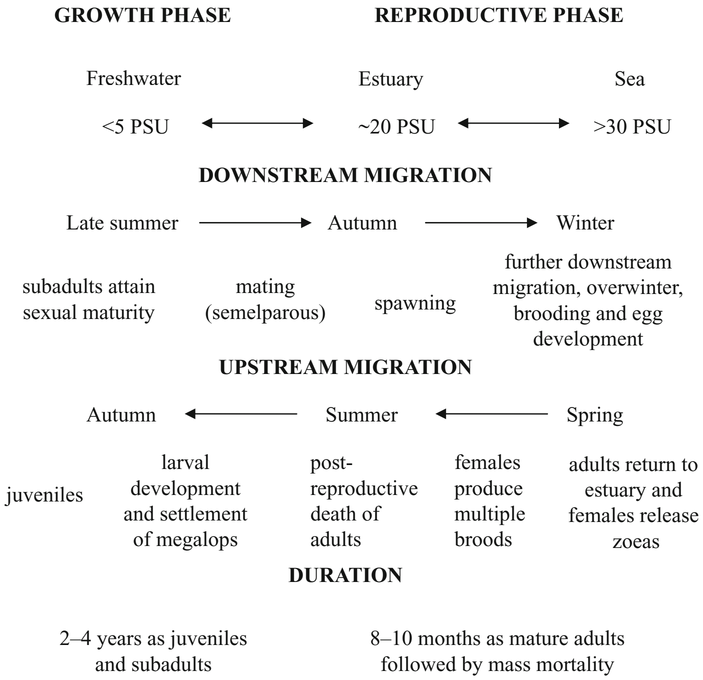

**Fig. 2** A schematic representation of the catadromous and semelparous mitten crab life cycle

## 1.4 Life History

Mitten crabs are catadromous; they live most of their life in fresh water but must return to higher salinity waters to mate, spawn and hatch first stage zoeas. *Eriocheir sinensis* is semelparous, in that it reproduces only once during its lifetime, after which it dies. For a schematic mitten crab life cycle illustration see Fig. 2. During the reproduction phase mitten crabs migrate downstream becoming sexually mature. Mass migration downstream in the Thames commences in late summer and continues through the autumnal mouths. Mating and spawning takes place in salinities of ca. 20 psu in the vicinity of the Dartford crossing. After mating and spawning the crabs move further downstream to overwinter in the lower reaches on the estuary. During early spring the crabs move back upstream to the more brackish water of the Dartford crossing and there until mid-summer the eggs release zoeas, after which, adults of both sexes die. The downstream/upstream crab migration in the Thames can be illustrated by re-interpretating the old Tilbury data of Clark et al. (1998: Fig. 5). The numbers of specimens captured and illustrated in red are the previous year's migrating crabs returning upstream to the estuary and are migrating upstream past Tilbury Power Station. The ovigerous females will hatch off zoeas and both sexes eventually die. These mass deaths of the previous year's migration are completed by July and early August at the latest. The new downstream migration of sexually mature specimens is represented in blue and crabs start to pass Tilbury Power Station too, and eventually overwinter from about early October (see Fig. 3).

This scenario is supported by crab capture data from the site of the old West Thurrock Power Station upstream of the electric generating plant at Tilbury (Fig. 4). Again the numbers of specimens captured and illustrated in red are the previous year's migrating crabs returning upstream to the estuary and the new downstream migration is shown in blue. These crabs appeared to be lethargic compared to the crabs captured at a site further upstream at the River Lee during the same month. Crabs at the River Lee appeared much more aggressive and are considered to be starting their downstream migration (Fig. 5). The crabs at West Thurrock are now believed to be in the process of post-reproductive dying off and this is finished by the end of July or early August.

Further evidence of this overwintering and movement of mitten crabs back into the Thames estuary is presented by the capture of male and female (Fig. 6) mitten crabs with barnacle settlement on their carapaces. Two species of barnacle have settled: *Balanus improvisus*, a native species only found in estuaries and *Elminius modestus*, which can be found both within and outside estuaries and is an invasive species from Australasia. In the Thames (also in Germany, Gollasch pers. comm.), even the invasive species have settlements of invasive species! All the spat represent new fouling from 2006; in fact the carapace had barnacle cypris larvae settling on its dorsal surface.

The hatched zoeas pass through five or six stages (Anger 1991) before the metamorphosis to megalopa and first crab stage. Juvenile crabs then move back upstream (Fig. 7) to commence a 3–4 year period in freshwater before migrating downstream to breed.

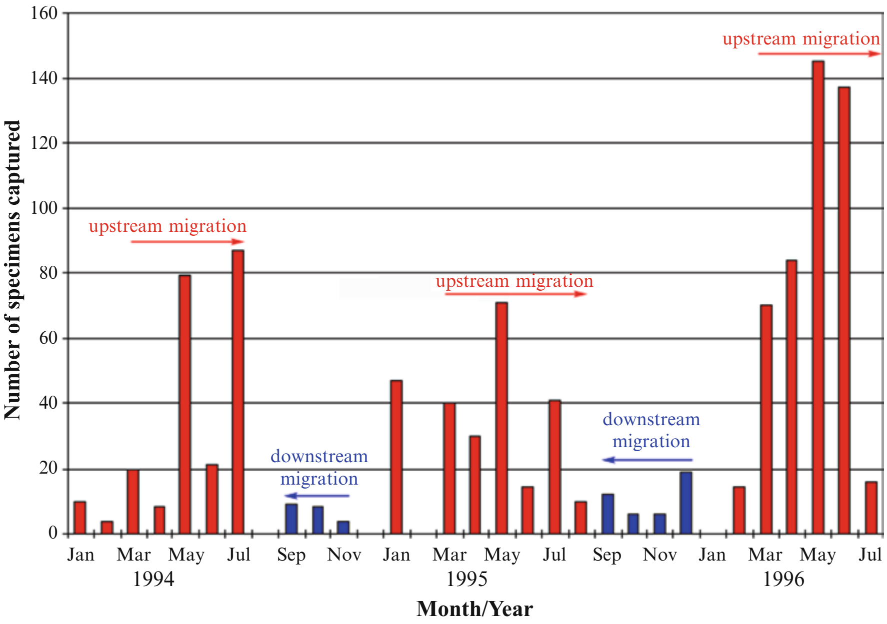

**Fig. 3** Monthly captures of *Eriocheir sinensis* from the intake screens at Tilbury Power Station (average number in 4 h collections at 2 week intervals) from January 1994 to July 1996. *Red columns* represent mitten crabs including ovigerous females returning into the estuary and migrating upstream past Tilbury Power Station from east to west. *Blue columns* are mitten crabs migrating downstream past Tilbury Power Station from west to east

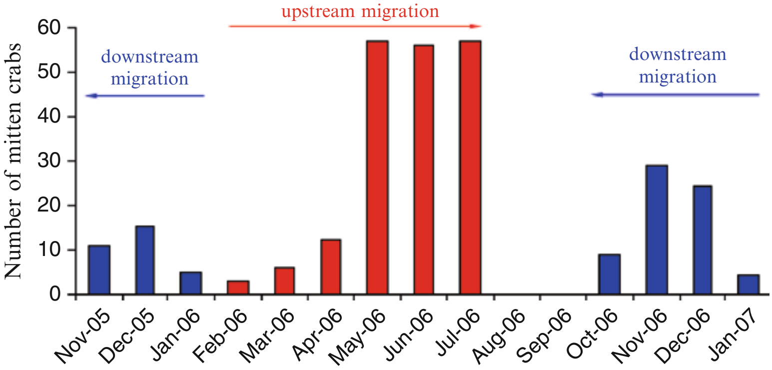

**Fig. 4** Mitten crabs captured in fyke nets at the site of old West Thurrock Power Station. *Red columns/line* represents mitten crabs including ovigerous crabs returning into the estuary and migrating upstream beyond Tilbury Power Station from east to west. *Blue columns/line* represents mitten crabs migrating downstream towards Tilbury Power Station from upstream, west to east

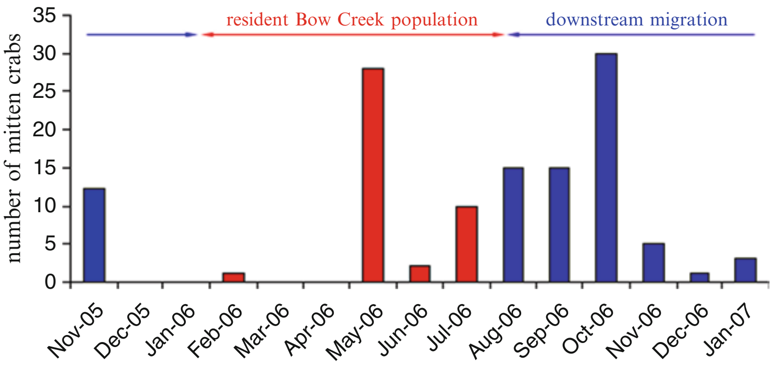

**Fig. 5** Mitten crabs captured in fyke nets at the River Lee. *Red columns/line* represents resident Bow Creek population of mitten crabs. *Blue columns/line* represents mitten crabs migrating downstream towards, West Thurrock and Tilbury Power Stations, from upstream, west to east

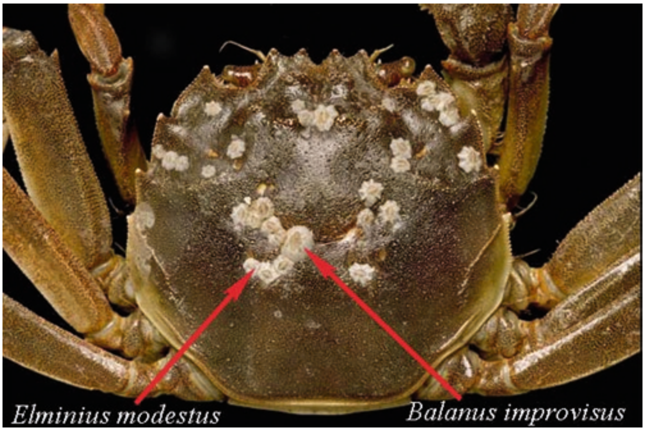

**Fig. 6** A female mitten crab captured on 27 July 2006 at 51°27.626′N 000°18.062′E, from the south bank of the Thames approximately opposite site 1, with barnacles on the dorsal surface of the carapace. Harry Taylor, NHM photo unit

## 1.5 Economic Impacts

Increasing numbers of *E. sinensis* could have an unforeseen economic impact on the Thames. Ingle (1986) noted that mitten crab burrowing behaviour (Panning 1939; Adema 1991), may be an issue in some areas where banks are unprotected; Panning (1939) and Adema (1991) commented on the problems of estuarine fishing, capture of large numbers of mitten crabs and damage to gear in Germany and Holland; Gollasch (2006) estimated that the damage to German rivers since the unintentional introduction of *E. sinensis* in 1912 has been €80 million and White et al. (2000) consider that millions of dollars a year have been spent preventing entrainment of Californian Chinese mitten crabs during water abstraction.

**Fig. 7** Juvenile mitten crab collected on the lock wall at Richmond, 7 November 2005. © Joelle Lai, National University of Singapore

The European eel, *Anguilla anguilla,* is now considered an endangered species (ICES 2006) and the European Commission has initiated an Eel Recovery Plan (Council Regulation 2007b, No 1100/2007) to try to return the European eel stock to more sustainable levels. Consequently restrictions on eel fishing may become necessary in order to conserve the Thames population. Therefore, commercial exploitation of the mitten crab could provide Thames eel fishermen with an alternative fishery, while reducing their impact on eels. This would be a positive economic impact by providing Thames eel fishermen with an alternative fishery of possible value.

## *1.6 Control of the Thames Mitten Crab Population*

Although the population in Thames had remained low from 1976 to the late 1980s, evidence suggests that mitten crab numbers have since increased and continue to do so (Attrill and Thomas 1996a, b; Clark and Rainbow 1997; Clark et al. 1998). Furthermore, the migration pattern of *E. sinensis* is well established and documented within the Thames watershed. This sudden proliferation may have potential environmental and economic implications. To date there has been no attempt to control this invasive pest with a view to reducing its population size. One potential method of control may be the commercial exploitation of this species as it is considered to be a delicacy by the South East Asian community. A pilot project was therefore proposed to investigate the population structure and density of the species in the River Thames, to determine whether commercial exploitation of the mitten crab population is feasible, and also to assess the suitability of the crab for human consumption with respect to trace metals and organic chemical contaminants (see Clark et al. 2009; Rose et al. 2009). Mitten crab fishing in the

Thames was undertaken for this project between November 2005 and January 2007 (see Clark et al. 2008). The results of this project and implications for a commercial Thames mitten crab fishery are discussed.

## 2 S.E. Asian Delicacy

### *2.1 Human Consumption*

During their downstream migration mitten crab gonads develop prior to mating. It is the developing ovaries and testes that are considered to be the delicacy in South East Asia; although the hepatopancreas (the brown meat) and the white meat in the walking legs, sternum and claws are also consumed but these are of secondary importance. The ripening ovary is particularly sought after and large females in perfect condition command a high price (up to US$ 40) in restaurants. Consequently, mitten crabs are only eaten during the migration period in the autumn. Females appear to be popular at the beginning of the season whereas males are favoured later towards the end of the season. Female crabs are steamed for 4–5 min and males between 10 and 15 min until the gonads are soft. Once the females have spawned their eggs they are no longer of commercial value.

### *2.2 China*

Eating mitten crabs has been part of Chinese culture for many centuries, so much so that this whole process of migration and consumption is depicted in beautiful paintings (Fig. 8). Furthermore, in the Ming Dynasty (1368–1644), craftsmen made a set of utensils for eating a crab that included a mallet, scissors, a shell cracker, a round salver, scoop, spoon, a long fork and combined scraper and pricker. This is referred to in modern China as the Eight-Piece Set and these can be made of copper or silver. There is also etiquette to eating mitten crabs. First the crab is placed on the round salver and the chelae and the pereiopods are removed. The carapace is then hit with the mallet to split the shell. Using the spoon, the crab spawn cream (ovary), as well as meat are removed and then eat with seasonings spoon. The white meat in the claws, walking legs and sternum are removed using the scraper and picker. After the meal, well-mannered people piece the remaining shell back together in the shape of a crab.

However there are six taboos to eating mitten crabs: (1) do not eat dead crabs; (2) do not eat raw crabs (possible reference to lung fluke); (3) do not eat cooked crabs which have been preserved for too long; (4) do not eat every part of the crab, remember to remove the stomach, intestines, heart and gill; (5) do not eat too much at one time; (6) do not eat the crab with persimmons!

See website:-
http://www.cultural-china.com/chinaWH/html/en/Kaleidoscope2789bye8009.html

**Fig. 8** Chinese art depicting *Eriocheir sinensis* being prepared for eating. By Meishuaihaozhe Zhiyou, Courtesy Jiangsu Fine Arts Publishing House

According to Hymanson et al. (1999), wild Asian populations are on the decline due to over-exploitation, river pollution and irrigation schemes that have disrupted the natural migration patterns of this species. However, local and international demand for *E. sinensis* has been met by an intensive aquaculture programme set-up along the Yangtze valley, China (Jin et al. 2001; Wang et al. 2006). This attempt to supply markets with live crabs all the year around is estimated to be worth ca. $1.25 billon annually.

## *2.3 Germany and the Netherlands*

Mitten crab fishing is already in progress on the continental mainland of Europe being undertaken in Germany and Holland. For crab fishing in Germany see:-

1. http://www.zdf.de/ZDFde/inhalt/22/0,1872,7003926,00.html Go to the middle of the page – you see a fisherman in his boat. The paragraph below says that he catches more crabs than eels in the Laacher Lake (NW Germany).

2. http://www.faz.net/s/RubCD175863466D41BB9A6A93D460B81174/Doc~E5E3A24E7E3DB4B6EB371A20CF41BC5A9~ATpl~Ecommon~Scontent.html Go to second last paragraph – it says that several tonnes of crabs are marketed.
3. http://www.welt.de/hamburg/article1078121/Elbfischer_versorgt_chinesische_Gourmets.html Fisherman in Elbe near Hamburg catches crabs.

On 27 May 2005, Fishing News (2005) carried a story on the Dutch mitten crab fisheries. This article finished by stating that 22 tonnes were supplied to the market at an average price of €3.80 per kg.

### 2.4 London

See Woo Chinese supermarket at Charlton, London now imports Dutch mitten crabs under the name of "big gate crabs"; the minimum size appears to be around 60 mm in carapace width. But grading of crabs is probable, with larger crabs especially females commanding a higher price tag. Mitten crabs at See Woo were selling for £5.50 per lb or £14 per kilo on 17 October 2006. It seems that there is the potential for a specialised market for Thames mitten crabs.

## 3 Trapping Thames Mitten Crabs: A Feasibility Study

### 3.1 Trapping

Trawling and dredging in the Thames on a commercial scale are not permitted upstream of Lower Hope, at Cliffe, as such practices damage the ecosystem and may be hazardous to shipping navigating in the relatively narrow deep-water channel. Furthermore, the use of such fishing gear would also damage the product as only specimens with both claws and a full set of walking legs are acceptable for the restaurant market. Traditional crab and lobster fishing methods in the UK involve baited pots. However, Thames eel fishermen had already reported that they collect large numbers of mitten crabs in their fyke nets. Therefore the Thames feasibility project trialled the trapping efficiency of baited pots versus fyke nets. Both types of traps carried Environment Agency (EA) tags for legal identification purposes, they were set as close to the bank as possible but always remained covered at low water, when set they were electronically marked using a Global Positioning System so they were effectively hidden from view as would not have been the case if traditional fishing buoys were used and all set traps were lifted within 48 h being retrieved by use of a grapple. Four sites along the Thames were selected as permanent sampling stations (Fig. 9). The traps were deployed on the Thames for a period of 15 months from November 2005 to January 2007.

One fleet of fyke nets comprised four double nets ca. 30 m long with ca. 9 m of rope at each end to attach anchors. The nets stood approximately 55 cm above the river-bed and were positioned in areas that were least likely to impact on navigation.

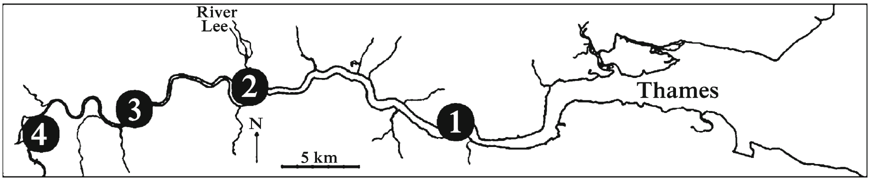

**Fig. 9** Four sites along the Thames were selected as permanent sampling stations: site 1. West Thurrock Power Station water intake jetty: 51°27.886′N, 000° 17.230′E. West Thurrock Power Station; site 2. River Lee, 51°30.422′N, 000° 00.474′E; site 3. Lots Road Power Station, north bank, 51°28.519′N, 000° 10.754′W; south bank, 51°28.519′N, 000° 10.633′W; site 4. Richmond Lock. Downstream Twickenham Road Bridge, west buttress; 51°27.638′N, 000° 18.898′W

The EA requested that otter guards were tied into the fyke nets set at site 3, so as not to trap any large freshwater fish. Moreover, the EA would not allow fyke nets to be set at site 4 due to the possible problems associated with freshwater fish capture and consequent mortalities.

The pots were supplied by the EA and comprised four to a fleet. At sites 1 and 2 these were always attached to one end of the fyke nets. Initially flounder was used as bait, but this was later changed to herring because it was considered that its oil may attract the mitten crabs.

At each site the following set of data was collected. Captured crabs were measured (carapace width), sexed, weighed, ovigerous crabs noted and missing limbs identified; all fish were identified and measured, except eels which were only counted; and physical measurements taken including water temperature, salinity, pH, dissolved O2; air temperature will be taken using a YSI 556–01 Multiparameter Instrument.

A typical sampling programme was as follows. First week of each month; Monday, set traps at site 3 and 4, take physical measurements only. Wednesday, retrieve traps at site 3 and 4, record physical measurements, fish and crab data. Set traps at sites 2 and 1 and record physical measurements only. Friday, retrieve traps at site 1 and 2, record physical measurements, fish and crab data.

## 3.2 Results

A total of 539 crabs was caught, weighed, measured and sexed including noting of females in an ovigerous condition (Fig. 1). This figure may be considered low but fishing with nets at site 4, Twickenham Road Bridge, was not permitted. 226 females, of which 57 were ovigerous, were trapped compared to 333 males. All captured crabs were bagged for the contaminant analysis and taken to the NHM for deep freezing.

Fyke nets proved overwhelmingly to be the most efficient method of catching mitten crabs with the pots trapping just 44 crabs in total (Fig. 10). Changing the bait from flounder to herring and increasing the size of the entry to the pots did not improve catching efficiency. Furthermore the pots were considered to be fishing because at site 1 in November 2005 38 *Carcinus maenas* (Linnaeus, 1758) were

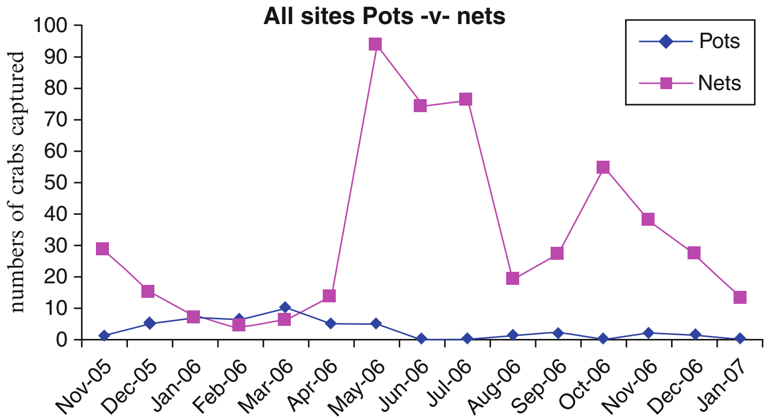

**Fig. 10** Pots versus nets, total number of mitten crab caught

collected. Another factor that may have reduced the efficiency of the pots was the loss of bait at some sites. Eels were considered to be responsible for bait removal.

### *3.3 Net Captures*

At site 1, 288 crabs were caught, including all 57 ovigerous crabs. This was the largest number collected for the project at any one site with 170 crabs being trapped between May and August 2006. At site 2, 122 crabs were caught, with no ovigerous crabs. Most crabs were caught during May 2006 (28) and 57 between August and October 2006. At site 3, 85 crabs were caught, with no ovigerous specimens. Most crabs were caught between May and July 2006 (33) and September and October 2006 (28).

### *3.4 Size of Thames Mitten Crabs*

In Singapore, the author met with Mr Low of Allswell Marketing, Singapore an importer of live seafood including the razor shell, *Ensis siliqua* (Linnaeus, 1758) from Scotland. Mr Low imports 300 kg of live *Eriocheir sinensis* from Yang Cheng Lake, China @ US$ 37–39 per kg including cost and freight. Crabs can sell in restaurants for US$ 40 per crab. Sold by weight, a high price is fetched for females between 175 and 220 g and males 250 and 350 g. According to Mr Low there could be an alternative market where the gonads are used as an ingredient in other food products. Additional cost data was provided by a display (21 November 2007) of mitten crabs in a Singapore Restaurant/market indicated the following size ranges and prices. Male hairy crab 250 g plus 65SGD (£22) reduced to 33.50 SGD (£11 each), and 200–250 g 45 SGD (£19) reduced to 22.50 SGD (£9.50).

From November 2005 to January 2007 a total of 539 crabs was caught during this limited feasibility study and weighed. Weights of crabs will vary from the initial wet weight to drying as water drains from the gill chambers and evaporates from exoskeleton for example. Using the Singapore Restaurant as a guide, the total number of Thames mitten crabs captured were divided into weight classes, <50, >50, >100, >150 and >200 g. Figure 11 shows the distribution of weight classes for all mitten crabs collected from November 2005 to January 2007. A total of 23 crabs was caught with weights greater than 100 g, including 2 crabs greater than 150 g and 1 at 200 g. Of the total number, 339 male crabs caught (Fig. 12), 13 had a weight greater than 100 g including two crabs greater than 150 and 200 g. Ovigerous crabs have no commercial value, therefore only the non-ovigerous crabs (149 in total) were placed into an appropriate weight class (Fig. 13). Five non-ovigerous crabs were collected with a weight greater that 100 g, none was greater than 150 g.

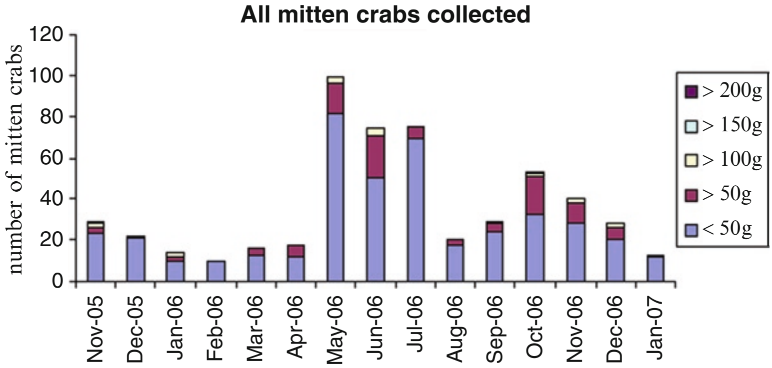

**Fig. 11** Distribution of weight classes for all mitten crabs collected from November 2005 to January 2007

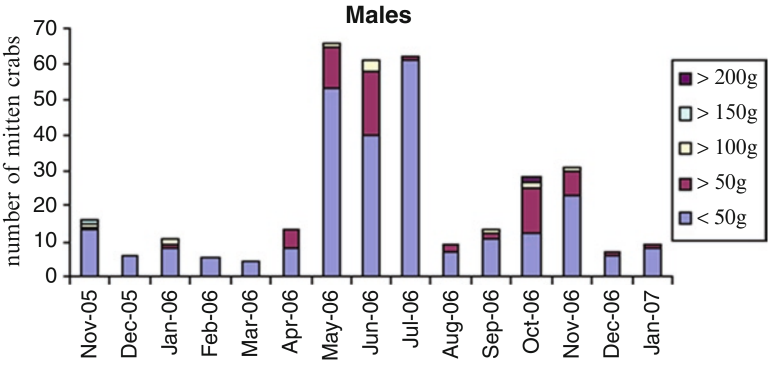

**Fig. 12** Distribution of weight classes for all male mitten crabs collected from November 2005 to January 2007

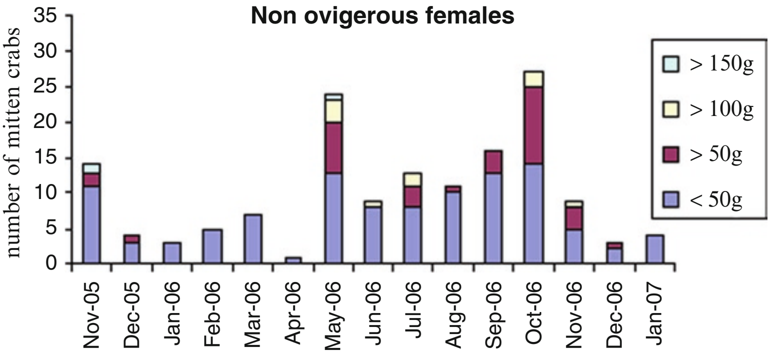

**Fig. 13** Distribution of weight classes for all non-ovigerous mitten crabs collected from November 2005 to January 2007. Ovigerous mitten crabs have no commercial value

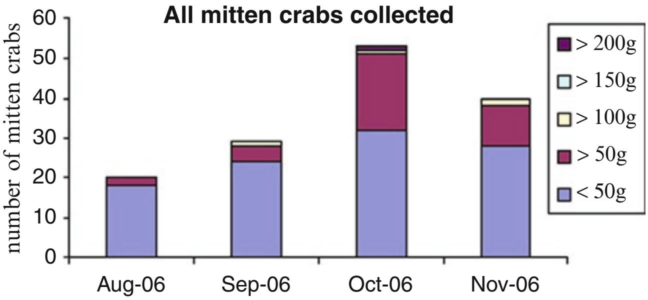

**Fig. 14** Distribution of weight classes for all mitten crabs collected during the proposed fishing period from August to end of November the same year

This study suggests that the fishing season for mature and non-ovigerous mitten crabs could be permitted from the beginning of August to the end of November. A total of 144 mitten crabs was caught during the proposed fishing period (Fig. 14). Five males had a weight greater than 100 g with only one greater than 200 g (Fig. 15) and three non-ovigerous females with a weight greater than 100 g with none greater than 150 g (Fig. 16).

During this study 539 crabs were caught and measured across the carapace width. Using the See Woo Chinese supermarket at Charlton as a guide, the total number of Thames mitten crabs captured were divided into width classes, <60, >60 and >70 mm. Figure 17 shows the distribution of width classes for all mitten crabs collected from November 2005 to January 2007. A total of 18 crabs was caught with a width greater than 60 mm, including two crabs greater than 70 mm. Of the total number of 339 male crabs caught, ten having a carapace width greater than 60 mm (Fig. 18). Only 149 non-ovigerous crabs were captured (Fig. 19). Five non-ovigerous crabs were collected with a carapace width size of greater than 60 mm.

A total of 144 mitten crabs was caught during the proposed fishing period (Fig. 20). Four males had a width greater than 60 mm with only one greater than 70 mm (Fig. 21), and three non-ovigerous females were caught with a carapace width greater than 60 mm (Fig. 22).

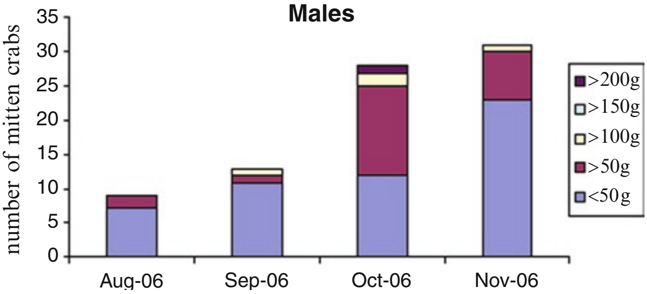

**Fig. 15** Distribution of weight classes for all male mitten crabs collected during the proposed fishing period from August to end of November the same year

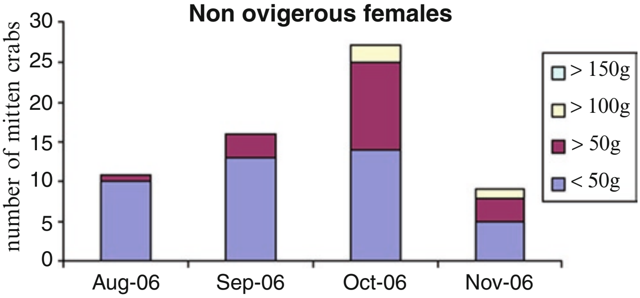

**Fig. 16** Distribution of weight classes for all non-ovigerous male mitten crabs collected during the proposed fishing period from August to end of November the same year. Ovigerous mitten crabs have no commercial value

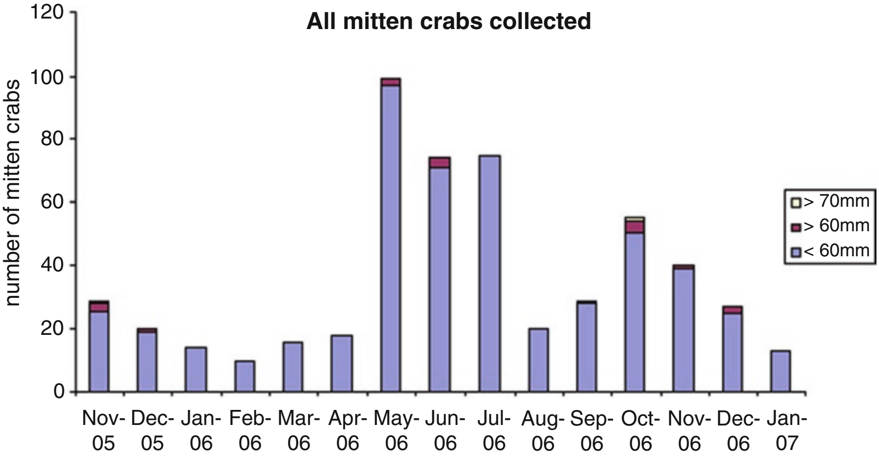

**Fig. 17** Distribution of width classes for all mitten crabs collected from November 2005 to January 2007

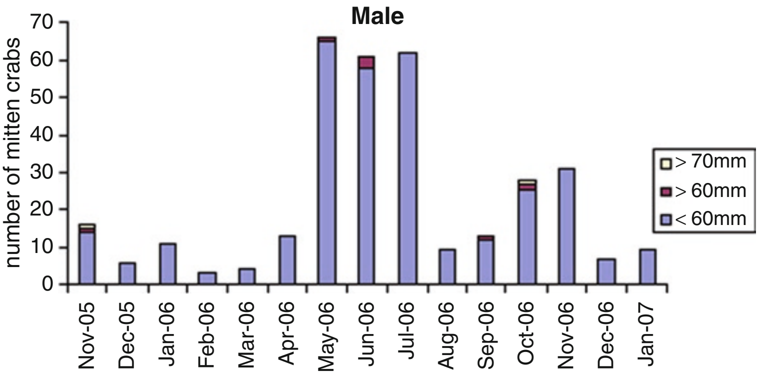

**Fig. 18** Distribution of width classes for all male mitten crabs collected from November 2005 to January 2007

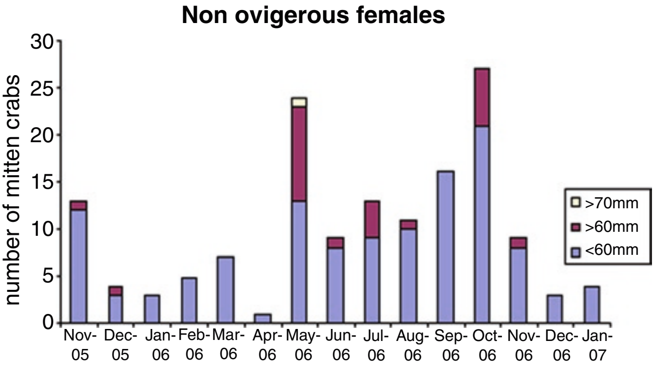

**Fig. 19** Distribution of width classes for all non-ovigerous mitten crabs collected from November 2005 to January 2007. Ovigerous mitten crabs have no commercial value

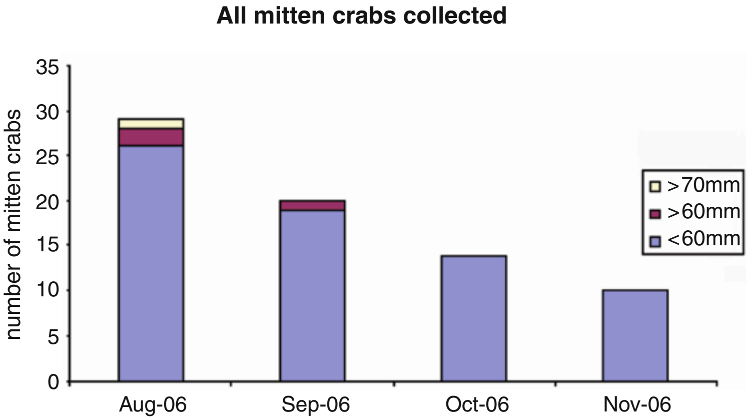

**Fig. 20** Distribution of width classes for all mitten crabs collected during the proposed fishing period from August to end of November the same year

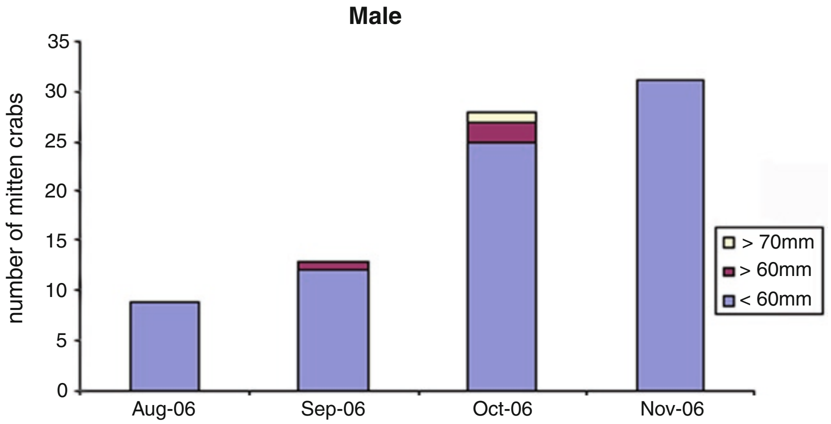

**Fig. 21** Distribution of width classes for all male mitten crabs collected during the proposed fishing period from August to end of November the same year

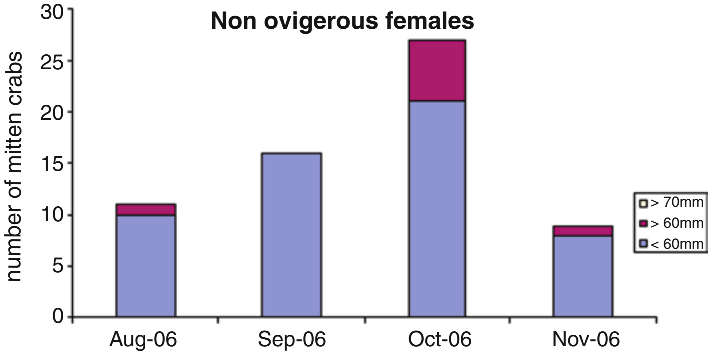

**Fig. 22** Distribution of width classes for all non-ovigerous male mitten crabs collected during the proposed fishing period from August to end of November the same year. Ovigerous mitten crabs have no commercial value

# 4 Time and Place to Fish

## *4.1 A Place to Fish*

Port of London Authority by-laws do not allow commercial fishing upstream of Tower Bridge, therefore trapping of migrating mitten crabs can only be undertaken downstream of this landmark. From net capture data, mitten crab numbers started to increase from July at Bow Creek. As the River Lee is known to be particularly infested (see Clark et al. 1998: Fig. 2) with mitten crabs, commercial fishing could start downstream of Trinity Buoy Wharf (Fig. 23) at the beginning of September each year. However, although fishing could start during August (Fig. 24) at site 2 (River Lee), there is a perceived problem around the Dartford Crossing and downstream thereof. Early fishing at site 1 (August) in this area could still capture the remnants of the previous year's migrating population that is in the process of dying off (Fig. 25). This population is not a commercially viable product as such crabs would not be suitable for sale as the gonads are spent and these specimens have a limited survival time. Sale of such crabs would not be productive for this fledgling industry. However, the crab fishing season could start in August between the River Lee outlet and say the Barking Power Station water outlet point at 51°30.818′N, 000°08.011′E. Then during September, when the "dying off" of the previous year's population is finished, mitten crab fishing could move downstream to include the Dartford crossing area, further east to Tilbury Power Station and possibly beyond.

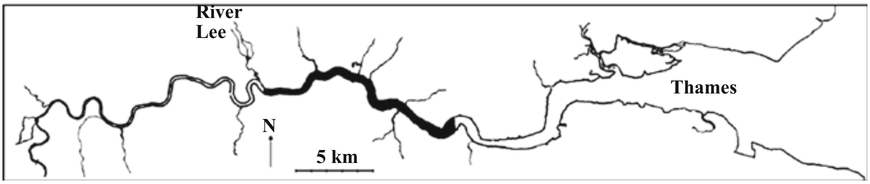

**Fig. 23** Proposed site for fishing Thames mitten crabs from the River Lee downstream to the Dartford Crossing, August to November

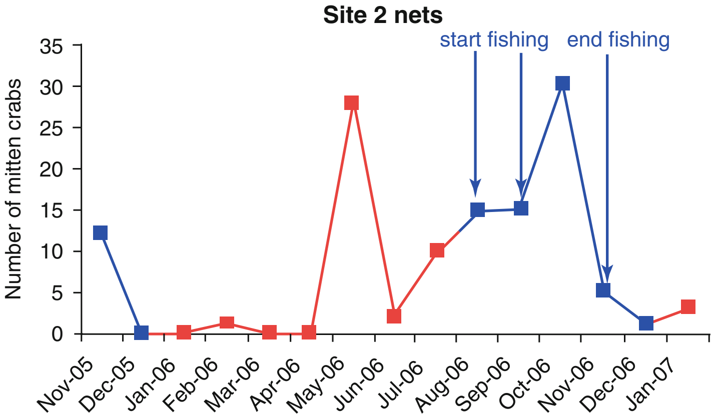

**Fig. 24** Proposed mitten crab fishing period at site 2, River Lee area. *Red lines* represent resident Bow Creek population of mitten crabs (no ovigerous crabs present). *Blue lines* represent mitten crabs migrating downstream towards site 1, West Thurrock Power Station, from upstream, west to east

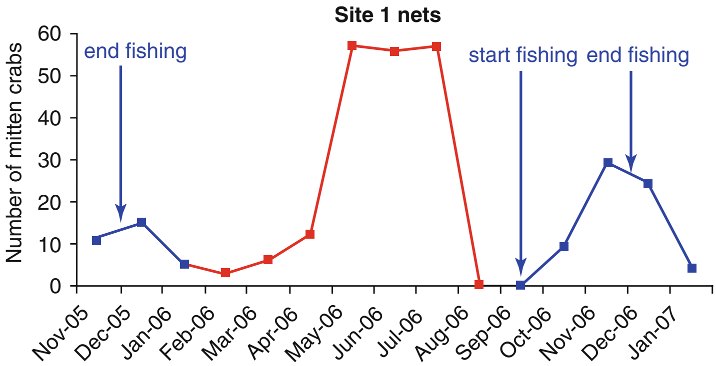

**Fig. 25** Proposed mitten crab fishing period at site 1, West Thurrock Power Station area. *Red lines* represent mitten crabs including ovigerous crabs returning into the estuary and migrating upstream beyond Tilbury Power Station from east to west. *Blue lines* represent mitten crabs migrating downstream towards Tilbury Power Station from upstream west to east

## 5 Are Thames Mitten Crabs Fit for Human Consumption?

### *5.1 London Port Health Authority*

London Port Health Authority (LPHA), City of London Corporation, is responsible for enforcing public health related legislation within a district, which extends for 150 km from Teddington Lock to the outer limits of the Thames Estuary. It is the health authority for the tidal Thames. The Authority, the largest in the UK, has been in existence since 1872 and is part of the City of London's Department of Environmental Services. The LPHA monitors the harvesting of the cockles, oysters, mussels and other bivalve molluscs, to ensure that they meet the appropriate standards for processing in order to prevent illness to consumers. Consequently, before the mitten crab population can be commercially exploited in the Thames, the LPHA must be satisfied that the product is suitable for human consumption and meets similar health standards as those set down for shellfish. LPHA required the Thames mitten crab population to be analysed with respect to the lung fluke, *Paragonimus westermani*, microbiology (with specific reference to *Vibrio parahaemolyticus*), trace metals and organochlorines.

### *5.2 Lung Fluke, Paragonimus westermani*

LPHA has taken a proactive interest in the possibility of commercially exploiting the Thames mitten crab population. For certain, a mitten crab population infested with the lung fluke parasite would present a potential health hazard to humans. Therefore LPHA commissioned a project to perform a seasonal parasitological and histopathological survey to address the potential for *Eriocheir sinensis* from the Thames Estuary to be infected by metacercaria larvae of the human lung fluke, *Paragonimus westermani*. The results of this project were reported to the LPHA by Stentiford (2005). The report concluded that *Paragonimus westermani* cysts were not detected in any of the crabs sampled (over 1,000 crabs) for the 17 months of the study using traditional parasitology and histopathological methods. By using this dual approach Stentiford was confident that this parasite (lung fluke) was not present in the Chinese mitten crabs from the Thames estuary and therefore, the infection risk for those consuming the raw product is negligible.

## *5.3 Microbiology of Mitten Crabs*

Susanne Surman-Lee reported that it has been established that the River Thames (Health Protection Agency report for the London Port Health Authority 2007) is frequently contaminated with sewage especially during periods of high rainfall, and human pathogens (disease causing micro-organisms) such as Salmonellae and campylobacters are frequently isolated from the river water. Foods harvested which have contact with the river water are therefore at risk of being contaminated with bacteria derived from sewage.

In food microbiology, indicator bacteria are commonly used to detect the potential for the presence of pathogens because they are present in much larger numbers compared to the relatively low numbers of disease causing bacteria and their presence therefore, is easier to detect. The main indicator organisms used to predict the likelihood of foodborne pathogens being present belong to the family Enterobacteriaceae, which are found in large numbers in the intestine of man and animals and are usually harmless. Enterobacteriaceae also include the species *Escherichia coli*, and whilst most *E. coli* are harmless, there are a number of strains, which can cause serious illness such as *E. coli* 0157. Other food poisoning bacteria such as Salmonellae and *Campylobacter* that may cause illness in man also belong to this family.

*Escherichia coli* is only found in the intestines of warm-blooded animals including man so is used as a specific indicator of faecal contamination of human or animal origin. This may originate from various sources such as faeces; bird droppings, sewage or farm effluent; faecally contaminated water, etc. Enterobacteriaceae including *E. coli* are, therefore, microbiological indicators of the quality of a food product and are useful in the assessment of the safety of a foodstuff.

*Vibrio* species including *Vibrio parahaemolyticus* are a group of bacteria which are a recognised source of food poisoning associated with the consumption of seafood *V. parahaemolyticus* is widely distributed in inshore marine waters throughout the world (ICMSF 1996). When ingested, *V. parahaemolyticus* causes watery diarrhoea often with abdominal cramping, nausea, vomiting fever and chills usually within 24 h of ingestion. Illness is usually self-limited and lasts 3 days. Severe disease is rare and occurs more commonly in persons with weakened immune systems.

There is a risk of *V. parahaemolyticus* infection to harvesters if they have open wounds when collecting the mitten crabs. Salmonellae and campylobacters are recognised human pathogens and were included because of the known prevalence of salmonella and *Campylobacter* spp. in the Thames.

It is understood that mitten crabs or parts of them may be eaten raw and as such are considered a delicacy by some ethnic groups, as such they are then considered as a ready to eat food i.e., consumed after harvesting without further processing such as cooking; smoking etc. If it is assumed that these crabs are eaten raw then microbiological quality guidelines such as the PHLS Ready to Eat Guidelines can be applied. Of the 23 samples examined, 17/23 contained high levels of Enterobacteriaceae and of these three contained unsatisfactory levels (>100 cfu/L) of *E. coli.* Of greater concern; 12 contained >1,000 colony forming units (CFU)/gram (g) of *Vibrio parahaemolyticus* which if the mitten crabs were to be eaten raw would constitute a significant risk of diarrhoeal disease. These levels are likely to be an underestimate of those at the time of harvesting as freezing is likely to have significantly reduced the levels by about 1–2 $\log_{10}$ (ICMSF 1996). There is no observable seasonal effect in the levels of bacteria detected. No samples contained *Salmonellae* or *Campylobacter* spp.

*Vibrio* species are susceptible to heat and normal cooking procedures at >60°C with appropriate hygiene measures would be effective at ensuring the microbiological safety.

## 5.4 Vibrio parahaemolyticus Detection in Mitten Crabs

Wagley et al. (2009) reported that *Vibrio parahaemolyticus* is an autochthonous, halophilic, non-sucrose fermenting bacterium that can be commonly isolated from temperate estuarine and marine environments. It can be associated with gastroenteritis following consumption of raw or undercooked seafoods characterised by watery or bloody diarrhoea, vomiting, abdominal cramps, headaches, fever and nausea (Joseph et al. 1982) and occasionally with wound infection following exposure to contaminated seawater (Johnson et al. 1984). Traditionally infections have been restricted to subtropical regions of USA and Southeast Asia where ambient seawater temperatures are in excess of 20°C and where it is reported to be the primary cause of seafood-associated gastroenteritis (Joseph et al. 1982; Nishibuchi and Kaper 1995). Pathogenicity is associated with thermostable direct haemolysin (TDH) and the thermostable-direct related haemolysin (TRH), encoded by the *tdh* and *trh* genes respectively. Up to 99% of clinical strains posses either the *tdh* and/or *trh* gene. However studies carried out largely in the Gulf Coast States of the United States indicate that detection of these genes in strains isolated from environmental sources is rare (1–5%) (Nishibuchi and Kaper 1995).

All Thames samples of mitten crabs and water tested throughout the year were positive for *V. parahaemolyticus*. Levels of *V. parahaemolyticus* in crabmeat peaked during the summer months, in August 2006 with total counts exceeded a median of $10^9$ cfu/g. The FDA level of concern for *V. parahaemolyticus* is reported to be >$10^4$ TDH/TRH positive MPN/g (FDA 2001; Cook et al. 2002). Genes encoding for the production of TDH/TRH isolates were not identified in any of the crab or water isolates tested. The prevalence and distribution of TDH/TRH positive strains as a proportion of total recoveries in the UK environment is not known, but the high levels of total *V. parahaemolyticus* cells found in this small study indicate that subpopulations of clinically significant strains may be present purely by stochastic variation. Thus consumption of the product particularly raw or lightly cooked may therefore pose a public health risk (see Wagley et al. 2009 for full details).

### 5.5 Trace Metals and Organochlorines

The pollution of the Thames in the recent past is well documented (i.e., Harrison and Grant 1976), therefore this present fishing project under the guidance of LPHA needed to investigate trace metals and organochlorines present in the Thames mitten crab population. The European Union Commission Regulation (EC) No 1881/2006 of 19 December 2006 sets maximum levels for certain contaminants in foodstuffs, clarifying the situation from original regulation (EC) No 466/2001 as amended by several further regulations (Consleg 2006). This report sets the mandatory regulations with regard to contaminants in crustaceans.

As described by Clark et al. (2009), crab tissues were analysed for polyaromatic hydrocarbons (PAH), for dioxins and dibenzofurans, and for dioxin-like chlorobiphenyl congeners (CB) by high resolution gas chromatography; high resolution mass spectrometry (HRGC-HRMS). Analysis for PAH used SAL Organic SOP12, for dioxins and dibenzofurans SAL Organic SOP1, and for CB SAL Organic SOP11, with isotopically labelled congeners and deuterated PAH added to test samples as appropriate as standards. The trace metals were determined by atomic absorption spectroscopy (Hg) and inductively coupled plasma mass spectrometry (ICP-MS) (Cd and Pb). For Hg analysis, the sample was ashed and Hg vapour trapped on a gold amalgam, before purging and analysis. For Cd and Pb the sample was digested with a mixture of hydrochloric and nitric acids before ICP-MS. All methodology used was accredited by the UK Accreditation Service (UKAS) to the ISO/IEC 17025:2005 Standard.

In summary, the concentrations of toxic organochlorines in the ‘brown meat’ were at times well above EC recommended limits (no. 1881: 2006) particularly when the crabs were lipid-rich, while lead and benzo[*a*]pyrene concentrations also strayed occasionally above recommended limits. Should Thames Chinese mitten crabs therefore be harvested for human consumption, thereby providing a possible control mechanism to restrict mitten crab numbers? Crucial points here are the likely intake of toxic contaminants from a meal and the frequency of meals of mitten crab brown meat in the diet of the consumer. From the fishing study (Clark et al. 2009), a harvestable crab of 100 g total wet weight contained about 8 g brown meat and 11 g white meat. A typical meal might consist of two steamed crabs, providing 16 g of brown meat and 22 g of white meat. As a result of the low fat content of the white meat, the levels of the highly lipophilic dioxins, dibenzofurans and PCBs was insignificant in comparison to the levels in brown meat and can therefore be ignored.

The estimated daily intake of dioxins and dioxin-like PCBs in the typical British diet of a 60 kg adult is 0.9 pg/kg body weight, in comparison with a tolerable daily intake (TDI) of 2 pg/kg body weight (Fernandes et al. 2004). However, it should be noted that the TDI has been established to protect the most sensitive target, the developing foetus. Therefore, in the case of males and females past child-bearing age, a higher TDI might be acceptable. In fact, the Committee on Toxicity of Food, Consumer Products and Environment (COT) has estimated that the TDI for the latter groups might be as high as 8 pg WHO-TEQ/kg body weight (Scientific Advisory Committee on Nutrition etc. 2004). Based on average data, an adult consuming a single 16 g portion of mitten crab brown meat per week would have an averaged daily intake of dioxins and dioxin-like PCBs at around the TDI. On the other hand, based on the higher TDI, a male or female past child-bearing age could consume several portions per week. Furthermore, it should be borne in mind that the adverse effects of exposure to dioxins and PCBs are chronic, not acute, and that mitten crabs are ripe for harvest only for a limited period of the year; the autumn. Consumption is therefore likely to be restricted to a period of 3–4 months annually. With a caveat over excessive partaking of mitten crab brown meat, particularly in the case of children and women of child-bearing age, it does appear that the harvesting of mitten crabs from the Thames for culinary use need not be discouraged. Such harvesting would represent a commercially viable method of population control of this alien invader capable of causing ecological and structural damage to British freshwater habitats (see Clark et al. 2009; Rose et al. 2009 for full details).

The London Port Health Authority, with advice from the Food Standards Agency, considers that Thames mitten crabs are, within certain limits, fit for human consumption (Clark et al. 2009).

## 6 Thames Mitten Crab Fishery?

A letter from the European Wildlife Division, Department for Environment, Food and Rural Affairs (DEFRA) written to the author and date 21 April 2005 read:-

> Advice from English Nature suggests the Chinese mitten crabs are now well established within the Thames and as a result would be considered to be an “ordinary resident” under the provisions of section 14(1)(a) of the Wildlife and Countryside Act 1981. Furthermore, Chinese mitten crabs are not listed on Schedule 9 of the 1981 Act.

*Eriocheir sinensis* is one of only two brachyuran crabs on the International Union for Conservation of Nature and Natural Resources’ (IUCN) list of the World’s worst 100 invasive alien species (see Lowe et al. 2000). Furthermore, the Chinese mitten crab is listed in The Handbook of Alien Species in Europe (DAISIE 2009). Therefore *E. sinensis* is not regarded by the international community as an ordinary resident and the Chinese mitten crab should be listed on Schedule 9, of the Wildlife and Countryside Act 1981 (note that *E. sinensis* was added to Schedule 9 as of 6 April 2010, Mackown, Non-native species policy, Defra, pers. comm.).

In summary, the Thames mitten crab population would probably support a commercial fishery and the product appears suitable for human consumption.

This could be a method of controlling *E. sinensis*. The question remains however, do we really want to start a Thames mitten crab fishery? Basically we are damned if we don't and damned if we do!

## 7 Damned if We Don't!

Large freshwater decapods have few natural documented enemies although there are some sparse records of London birds feeding on crayfish and mitten crabs. Figure 26 captures a gull consuming an *Astacus leptodactylus* Eschscholtz, 1823 (the Turkish crayfish) from the Serpentine Lake in Hyde Park, London and Fig. 27

**Fig. 26** Lesser black-backed gull with crayfish by Serpentine Lake, London. Photo by © Elinor Wiltshire

**Fig. 27** Great crested grebe – London Wetland Centre. Photo by © Laurence Arnold

a grebe attempting to feed on a mitten crab. In addition, a gull was seen feeding on a mitten crab at Erith Marshes by Dave Pearce (pers. comm.). However, the Thames avian fauna is unlikely to have a dramatic impact upon the reduction of the mitten crab population.

### *7.1 Increasing Numbers*

Thames mitten crabs continue to move upstream. The furthest upstream record cited by Clark and Rainbow (1997) and Clark et al. (1998) was at Staines ~65 km from Tilbury. But on 13 October 2007 David Heller, whilst fishing at Boveney Lock (just upstream of Windsor), caught a mitten crab. Although this is now considered to be the most westerly Thames mitten crab record to date, this exotic species is likely to inhabit more localities to the west of this point. Furthermore, Gilbey et al. (2007: Fig. 1) recently sampled seven sites from Teddington Weir to Greenwich. They found juvenile crabs at all sites and their high numbers suggested a significant increase in the population size since previous studies (Attrill and Thomas 1996a, b; Clark and Rainbow 1997; Clark et al. 1998).

### *7.2 Burrows*

There appears to be evidence of mitten crab burrows along some unprotected river banks of the Thames especially on Chiswick Eyot (Fig. 28) and along the banks of Syon Park, Middlesex (Fig. 29 and Dutton and Conroy 1998). The *Phragmites* sp. bed on Chiswick Eyot has been particularly eroded away in recent years by the probable burrowing behaviour of crabs. According to Chris Dutton, (ex. Environment Agency, pers. comm.) the bank at Chiswick Eyot has receded ca. 6 m. The burrows along the banks of Syon Park were studied by Zucco (1999).

### *7.3 Abstraction of Drinking Water*

There are nine raw water intakes along the tidal Thames from Teddington to Windsor, with a licensed abstraction limit of approximately 7,000 ml per day. Thames Water holds the largest single licence (1,818 ml/day) for abstraction to supply the Lower Thames Reservoirs (Environment Agency 2004). During the annual downstream migration from the beginning of August to the end of November 2008, two employees of the Thames Water treatment works at Walton-on-Thames, Surrey, removed 873 mitten crabs from the intake screens over a 13.5 week period (Stanton-Murch 2009). This was the 4th year in succession that Thames Water had experienced this entrainment of mitten crabs and for each successive year the numbers

**Fig. 28** The *Phragmites* sp. bed on the southern bank of Chiswick Eyot is peppered with probable mitten crab burrows. The remnants of the collapsing bank can be seen on the beach in the foreground. November 2005. Phil Hurst, NHM photo unit

**Fig. 29** Mitten crab burrows in the unprotected river bank of Syon Park flood meadow. November 2005. Phil Hurst, NHM photo unit

appear to be increasing. This recording scheme is to be continued for autumn 2009 in collaboration with Thames Water, Royal Holloway University of London and the Natural History Museum.

## 7.4 Eel Fishing

About six fishermen are currently exploiting the eel population in the Thames estuary. They trap *Anguilla anguilla* using fyke nets and according to Dave Pearce (pers. comm.), a Thames fisherman for 15 years, mitten crab numbers caught in fyke nets have been steadily increasing from about over 8 years ago. The increase in crab numbers does have an economic added cost to eel fishing in that when the nets are now hauled they invariably contain mitten crabs as part of the by-catch. These must be sorted and removed from the nets. This takes time! Furthermore the nets must be repaired as catches of large numbers of crabs can damage the netting.

## 7.5 Recent Citations of Ovigerous Crabs

During the 15 month trial fishing period, 57 egg-bearing females (Fig. 1) were collected from site 1 only (see Fig. 9). The present data show (Table 2) that crabs are carrying eggs between December 1 year and the following June. Incidentally, most females (11 out 12) caught at site 1 during December were ovigerous. Field experience has suggested that some females become ovigerous in early October although Attrill and Thomas (1996a) record a specimen from August (Table 1). According to Dave Pearce (pers. comm.), all female mitten crabs he found in the Thames Estuary during December 2005 were ovigerous. Most of the data corroborates previous studies except that for the present project ovigerous female were recorded in the Thames from January to June 2006. Of interest is that some females captured at site 1 during

**Table 2** Ovigerous mitten crabs were only collected at site 1, West Thurrock Power Station

| Ovigerous crabs | | |
|---|---|---|
| Months | Pots | Nets |
| Nov-05 | 0 | 0 |
| Dec-05 | 0 | 11 |
| Jan-06 | 0 | 5 |
| Feb-06 | 0 | 2 |
| Mar-06 | 1 | 4 |
| Apr-06 | 2 | 2 |
| May-06 | 2 | 7 |
| Jun-06 | 0 | 4 |
| Jul-06 | 0 | 0 |
| Aug-06 | 0 | 0 |
| Sep-06 | 0 | 0 |
| Oct-06 | 0 | 0 |
| Nov-06 | 0 | 0 |
| Dec-06 | 0 | 17 |
| Jan-07 | 0 | 0 |
| **Total** | **5** | **52** |

June carried a significantly reduced numbers of eggs under the abdomen, to the point that these were scored as ½ in the ovigerous column of the field data sheets. This suggested that these were still in the process of hatching or that *Eriocheir sinensis* may hatch off zoeas in batches and not all at once or that mitten crabs can spawn eggs a number of times during the breeding season (see Peters 1933; Panning 1939 for *E. sinensis*; Kobayashi 2001 for *E. japonicus*). According to Panning (1939) females can carry between 100,000 and a million eggs.

Hatching takes place around the Dartford crossing/site of the old West Thurrock Power Station (site 1, Fig. 9) and eastwards sometime in early spring through to June the same year. Consequently, during this lengthy period *E. sinensis* larvae must now constitute a significant component of plankton along this part of the Thames estuary. This has serious consequences for the uptake of ballast water by shipping using Tilbury Docks and the proposed London Gateway, which is to be the UK's first twenty-first century major deep-sea container port and Europe's largest logistics park. It will be situated on the north bank of the River Thames near Thurrock in Essex, London. Gateway will provide unrivalled shipping access for the world's leading businesses to an integrated road, rail and sea network. *Eriocheir sinensis* larvae from the Thames must be being transported to other UK destinations by coastal shipping and exported wider a field to other continental ports (Herborg et al. 2003, 2005).

## *7.6 Drought and Water Abstraction*

A slowing in the flow rate of the River Thames due to drought conditions or water abstraction by the Three Valleys Water and Thames Water may have influenced the mitten crab population.

Andrews et al. (1981) commented "Seawater intrusion during the 1976 drought accounted for the occasional records of the velvet swimming crab *Macropipus* (now *Necora*) *puber* at West Thurrock together with a few specimens of a spider crab *Macropodia longirostris* … normally restricted to zones VII (middle Sea Reach) and VIII (Outer Estuary)".

Ingle (1986) wrote, "It is not clear why mitten crabs have failed to colonise British rivers … many would appear to provide the tidal salinity gradients necessary for development of larval and young mitten crabs. However compared with the lowland rivers of central Europe, British and Scandinavian rivers are faster flowing (Haahtela 1963), a factor which may preclude successful upriver migration essential to the crab's development".

Attrill and Thomas (1996a, b) suggested that the increase in population size of mitten crabs is related to the change in flow regime of the Thames due to the drought years of 1989–1991. According to their results, between 1989 and 1991, few adult *Eriocheir* were recorded from the estuary, but the number and particularly the frequency of occurrence, of crabs at West Thurrock Power Station increased during 1992. This apparently culminated in 30 adults (including 17 ovigerous crabs) being caught on 13 November 1992. From 1989, the London area endured several periods of drought, resulting in extended periods of low flow during the summer as more water was abstracted from the freshwater water river Thames to maintain the dwindling reservoir supply. Further, in addition to the drought periods during the summers of 1989 and 1990, the large peaks of flow characteristic of winter were not evident in 1991 and 1992. Attrill and Thomas (1996a, b) considered that this resulted in a decrease in the total amount of water entering the estuary as highlighted by the decline in mean annual flow. Accordingly this decrease in freshwater flow resulted in a general encroachment of sea water up the estuary including West Thurrock. They concluded that the rise in mitten crab numbers in the Thames estuary coincided with the drought period since 1989 therefore allowing the establishment of juvenile crabs during 1989. These crabs matured and formed the downstream migration witnessed at the end of 1992.

Hanson and Sytsma (2008) have also taken an interest in seawater intrusions into estuaries. According to them, the large mitten crab population in San Francisco Bay would place at risk all watersheds around the north western Pacific. They suggest that large stable estuaries with long flushing times are necessary to sustain mitten crab populations. However most Pacific estuaries in the northwest have limited saline intrusion with short flushing times and therefore have a reduced risk of mitten crab populations becoming established. According to Attrill and Thomas (1996b) it would be interesting to record whether the mitten crab population would maintain itself if Thames water flows returned to normal.

Thames Water holds a licence to abstract water from the Lower Thames (i.e., upstream of Teddington Weir). This abstraction is managed under the Lower Thames Operating Agreement and links abstraction rates to flows over the Teddington Weir. Three Valleys Water also holds a licence to abstract surface water from the Thames but this is situated upstream of the Thames Water licence. Thames Water also holds licences to abstract water from the surface water system both in the Upper Lee and Lower Lee (www.environment-agency.gov.uk/cams). However changes in rainfall patterns and land management practices may also be influencing factors in slowing Thames flow rates as drought conditions and abstraction rights can also act in combination as well as separately. The slowing of the River Lee flow rate might explain why this catchment in particular is so heavily invested with mitten crabs (see Clark et al. 1998: Fig. 2).

## 7.7 *Damned if We Don't Summary*

The Thames mitten crabs have few natural predators and this coupled with the current flow rate of the river means that the crab population continues to expand westward and increase in numbers. They are not on the decline! Consequently mitten crabs are beginning to have an economic impact with respect to burrowing, entrainment onto water intake filters and estuarine fishing. Moreover, the percentage of mitten crab larvae in the Thames estuary plankton must now be considered a major issue with respect to ballast water up-take. With mitten crabs hatching zoeas from early spring to June their larvae are being transported locally by coastal shipping and exported abroad by transoceanic vessels. Therefore doing nothing about Thames mitten crabs may not be a suitable option.

## 8 Damned if We Do!

There appears to be a limited mitten crab market in London, but there could also be an export opportunity to include trade with South Korea, Singapore and possibly China. But starting a Thames mitten crab fishery does pose a number of problems for the environment.

### *8.1 The By-Catch*

During the 15 month feasibility study into Thames mitten crabs, 20 species of fish were identified from the by-catch of mitten crab fishing (Table 3). A total of 2,013 fish (Table 3) was trapped as by-catch while fishing for mitten crabs in the Thames from 9 November 2005 to 5 January 2007. Of the total number, only five fish were caught in pots including two *Platichthys flesus*, two *Perca fluviatilis* and one *Ciliata mustela*.

**Table 3** A total of 2,013 fish was trapped as by-catch while fishing for mitten crabs in the Thames from 9 November 2005 to 5 January 2007

| Fish Species | Number |
|---|---|
| Flounder, *Platichthys flesus* Linnaeus, 1758 | 400 |
| Common eel, *Anguilla anguilla* (Linnaeus, 1758) | 1,397 |
| Soles, *Solea solea* (Linnaeus, 1758) | 49 |
| Whiting, *Merlangius merlangus* (Linnaeus, 1758) | 20 |
| Bass, *Dicentrarchus labax* (Linnaeus, 1758) | 64 |
| Sprat, *Sprattus sprattus* (Linnaeus, 1758) | 5 |
| Five-bearded rockling, *Ciliata mustela* (Linnaeus, 1758) | 5 |
| Smelt, *Osmerus eperlanus* (Linnaeus, 1758) | 14 |
| Herring, *Clupea harengus* Linnaeus, 1758 | 3 |
| Perch, *Perca fluviatilis* Linnaeus, 1758 | 6 |
| Red gurnard, *Aspitrigla cuculus* (Linnaeus, 1758) | 2 |
| Sand-smelt, *Atherina presbyter* Cuvier, 1829 | 1 |
| Bib (pouting), *Trisopterus luscus* (Linnaeus, 1758) | 2 |
| Transparent goby, *Aphia minuta* (Risso, 1810) | 1 |
| Cod, *Gadus morhua* (Linnaeus, 1758) | 28 |
| Pogge (Hooknose), *Agonus cataphractus* (Linnaeus, 1758) | 1 |
| Tadpole-fish, *Raniceps raninus* (Linnaeus, 1758) | 2 |
| Roach, *Rutilus rutilus* (Linnaeus, 1758) | 10 |
| Common or freckled goby *Pomatoschistus minutus* (Pallas, 1770) | 2 |
| Dab, *Limanda limanda* (Linnaeus, 1758) | 1 |

**Table 4** The five most common fish species caught in fyke nets from November 2005 to January 2007

| Month | Eel | Flounder | Bass | Sole | Whiting |
|---|---|---|---|---|---|
| Nov-05 | 124 | 41 | 1 | 2 | 4 |
| Dec-05 | 18 | 42 | 4 | 1 | 0 |
| Jan-06 | 8 | 37 | 5 | 0 | 2 |
| Feb-06 | 3 | 17 | 12 | 0 | 0 |
| Mar-06 | 2 | 32 | 6 | 1 | 0 |
| Apr-06 | 30 | 19 | 6 | 2 | 0 |
| May-06 | 141 | 28 | 2 | 4 | 0 |
| Jun-06 | 219 | 41 | 0 | 4 | 0 |
| Jul-06 | 239 | 13 | 4 | 21 | 0 |
| Aug-06 | 96 | 10 | 5 | 8 | 0 |
| Sep-06 | 107 | 18 | 8 | 5 | 0 |
| Oct-06 | 329 | 11 | 2 | 1 | 0 |
| Nov-06 | 27 | 16 | 0 | 0 | 2 |
| Dec-06 | 44 | 57 | 6 | 0 | 4 |
| Jan-07 | 10 | 16 | 3 | 0 | 8 |
| **Total** | **1,397** | **398** | **64** | **49** | **20** |

In comparison the fyke nets efficiently captured over 2000 fish during the same period, with the five most common caught fish being *Anguilla anguilla*, *Platichthys flesus*, *Dicentrarchus labax*, *Solea solea* and *Merlangius merlangus* (Table 4).

## *8.2 Anguilla anguilla*

During the 15-month fishing period 1,397 common eels were netted. Catches were low from December to March because winter temperatures, below 6–7°C, induce torpor and reduce eel activity to a minimum. Eel fishing in the Thames is not permitted upstream of Tower Bridge but starts downstream as temperatures rise in mid-later spring and finishes towards the end of autumn (Fig. 30).

According to Aprahamian and Firth (2004), the trend of glass eel numbers entering European rivers since 1980 is downward, with lowest level of recruitment recorded in 2001. They state that a number of factors have been suggested for this decline including change in ocean climate, habitat loss, predation, turbine mortality, over-exploitation, parasites and pollution. The pollution in the Thames and its subsequent recovery has been well documented (i.e., Harrison and Grant 1976). Dave Pearce (pers. comm.) comes from a family of commercial fishermen. His great grandfather fished eels out the Thames from 1830 to 1850 and had four to five boats working out of Erith. In 1920 his family stopped fishing eels in the Thames due to the pollution in the river. Eel fishing started again around 1980 and Dave commenced fishing full time in 1990. Today there are about six fishermen commercially exploiting eels in the Thames estuary.

There is a new threat to the eels in the Thames. It comes in the form of a swim bladder parasite, *Anguillicola crassus*, and this is cause for concern (Aprahamian

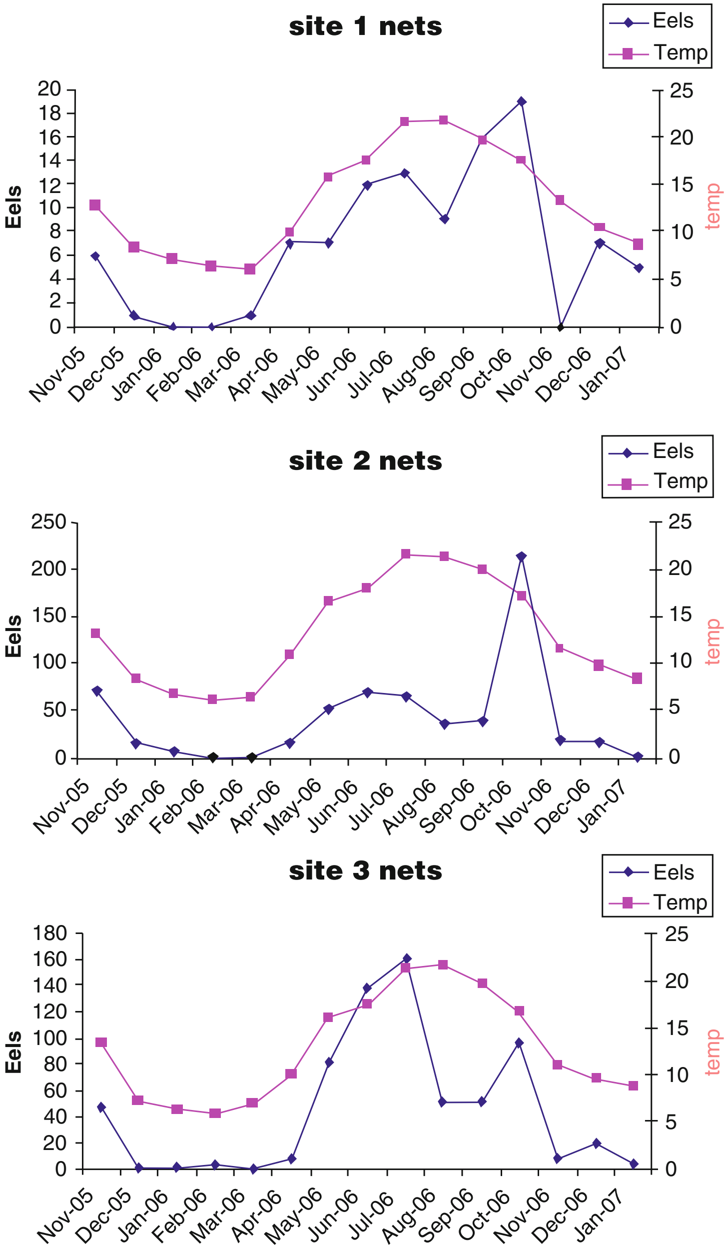

**Fig. 30** Net captures at sites 1–3 of the common eel, *Anguilla anguilla* plotted against Thames water temperature

and Firth 2004). This parasite causes mortalities in farmed and wild population in the presence of other stress factors (Kirk 2003). It is a nematode originating from Asia. Norton et al. (2005) examined eels from the River Thames between 2000 and 2003 for this infection. Their data suggest that prevalence of infection in the Thames estuary was higher during 2000–2003 than for the period 1987–1992 (mean 48% vs. 10% respectively). In June and July 2006, Dave Pearce (pers. comm.) started to get some eel mortalities in his Thames storage facility as river temperatures rose and $O_2$ levels fell. He put this down to a combination of stress and possible swim bladder infections by nematodes. He set up a freshwater storage tank at home using aerated tap water and mortalities ceased immediately. He has used the storage facility during the 2007 eel season and considers this to be a better way to hold his eels. He has not had any eel mortality using this system to date.

## *8.3 Capture of Eels*

There is no point in setting up a mitten crab fishing industry if this activity is going to deplete the Thames eel (*Anguilla anguilla*) population downstream below the River Lee. Consequently consideration must be given to the numbers of eels trapped during the proposed mitten crab fishing period at sites 1 and 2 (see Figs. 31 and 32 respectively). At site 1 from September to November 2005, 35 eels were caught and at site 2 from August to November 2005 the number was 273. Therefore the total number of eels trapped by fyke nets set only seven times for approximately a 48 h period was 308.

To allow the eels to escape, “crab fyke nets” could be made from a 40 mm square mesh size or have a 40 mm brass eye sown into the trap. Incidentally, the Environment Agency, the organisation responsible for eel fishing licences, issued notice in 2009 that all fyke must use an otter guard in the mouth of the net. Perhaps the EA should go one step further and follow the lead as in the Dutch eel fishery and insist that a ca. 20 mm brass ring is sewn into the fyke net to allow the escape of under-size eels. This may help with regard to conservation of eel stocks in the Thames.

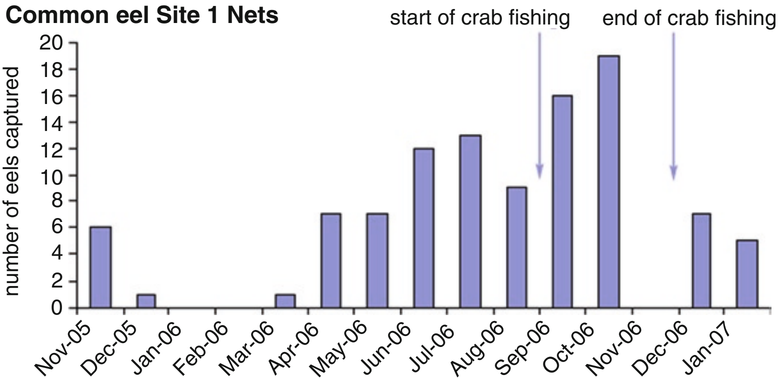

**Fig. 31** Number of common eels captured at site 1, West Thurrock Power Station

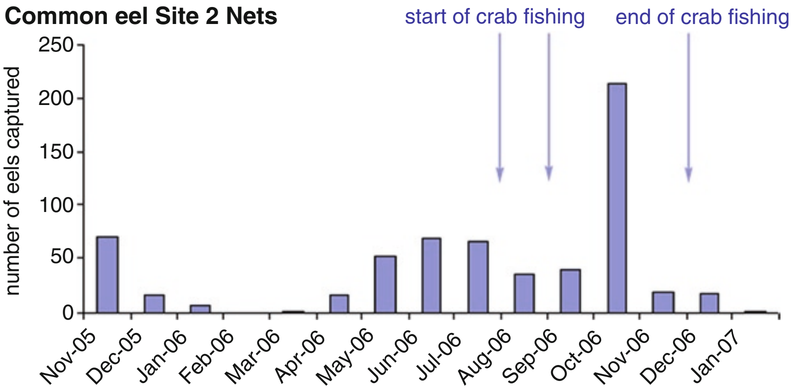

**Fig. 32** Number of common eels captured at site 2, River Lee

## 8.4 Invasive Crayfish

The UK history of invasive crayfish (see Holdich 2000), is poignant reminder to the problems associated with farming and commercial exploitation of an exotic species. This sad episode resulted in an environmental 'own goal' threatening our only native crayfish *Austropotamobius pallipes* (Lereboullet, 1858) and the liberal distribution of three foreign crayfish in watersheds across England and parts of Scotland. The introduced species included the Turkish crayfish, *Astacus leptodactylus* Eschscholtz, 1823 from mainland Europe, and the other two, the signal crayfish *Pacifastacus leniusculus* (Dana, 1852) and the red swamp crayfish *Procambarus clarkii* (Girard, 1852), from North America. The establishment of these crayfish has been a direct result of human introductions by accident (such as escapees from farming) and intentional intervention by deliberately releasing these species into the wild. This environmental vandalism has been committed in the name of expensive cuisine food for high class restaurants and the greed of entrepreneurs wanting to make a perceived fast buck. An example of this is the seeding of Serpentine Lake, Hyde Park, London with *Astacus leptodactylus* as recently reported by Wiltshire and Reynolds (2006). These Turkish crayfish were once harvested and sold on to a restaurant adjacent to the lake. Recently a fourth invasive crayfish, *Orconectes virilis* (Hagen, 1870), was reported from the River Lee, a tributary of the Thames, at Enfield, North London (see Ahern et al. 2008). This latest crayfish invader too has its origins in North America.

If commercial exploitation of Thames mitten crab is acceptable, then the above situation for crayfish will almost certainly apply to *Eriocheir*. In fact it may have already started with the appearance of *E. sinensis* in the Duddon Estuary and Ouse Washes (see Fig. 33). Both citings may be the result of intentional introduction. The Duddon Estuary, part of the Lake District catchment area, is remote from other mitten crab populations, but a number of ovigerous mitten crabs have in recent years been reported from locality. However, just how many ovigerous crabs

**Fig. 33** Mitten crab distribution records for England, Wales and Scotland. Map derived from draft data collated by DASSH for the Defra/JNCC MB102 Contract. © Crown Copyright – Defra – MB0102

are required to "seed" a catchment is debatable. Another explanation is that the crabs came for the hulls of ships being scraped at a shipyard on the river, which incidentally is no longer in operation. Some of the vessels beginning scrapped were reportedly moved from the Mersey, Liverpool, and mitten crabs have been reported in this river.

The origin of the crabs recorded from the Ouse Washes is unknown and is of concern, but these too could be intentional. Natural England recently commissioned the first stage of a two-stage project (see Walker et al. 2010) which aimed to assess the current status and distribution of *E. sinensis* in the drainage ditches associated with the Nene Washes and Ouse Washes Sites of Special Scientific Interest and Special Areas of Conservation (SAC). Their particular interest was the potential physical damage caused by the mitten crab and the threat it posed to spined loach (*Cobitis taenia*) populations in Morton's Leam (Nene Washes SAC feature) and Old Bedford/River Delph (Ouse Washes SAC feature).

There is some circumstantial evidence that trading in English mitten crab (not from the Thames) has already started. This is of concern too because mitten crabs are not frozen but sold live and they are great escape artists, being able to survive out of water on land for long periods. In the wild, mitten crabs are capable of crossing from one watershed to another. Consequently as in the case of the alien crayfish, there are a number of vulnerable points at which mitten crabs can escape into the environment. These include the initial holding area of the fisherman immediately after capture, the premises of the middle man after purchase from fishermen and prior to onward sale for consumption, and the restaurant with the intentional release of females after they become ovigerous and become worthless as an edible commodity.

### *8.5 Damned if We Do Summary*

There are two main concerns with regard to Thames mitten crab fishing; these are the common eel and the intentional/unintentional distribution of mitten crabs to new catchments in the UK for the sake of perceived profit. *Anguilla anguilla* is under threat and now considered to be an endangered species. Unless further research is untaken with regard to use of fyke nets and escape of eels, starting a mitten crab fishery would be counter productive. The deliberate dispersal of mitten crabs is a major environmental issue especially in the wake of the problems associated with invasive crayfish. For certain a Thames mitten crab fishery would have to be strictly managed.

## 9 Management of a Thames Mitten Crab Fishery

The overall reason for a mitten crab fishery in the Thames is to deplete the population size. Management does not refer to a conservation strategy where the population is maintained. What management does concern is fishermen/traders, restaurants/retail outlets and live imports; all of which may require legislation.

### *9.1 Fishermen/Traders*

Traditionally mitten crabs are tied as per Fig. 34, so that they do not loose legs fighting and weight by moving around. Such traditional restraints would also prevent the crabs from escaping after capture and thereby preventing unintentional release back into the wild. However this may be commercially cheap to do in SE Asia but may be involve an expensive labour cost in UK. Furthermore after capture and prior to onward sale, crabs should be placed in clean water for around 2 days to clear mud from the gills and exoskeleton.

### *9.2 Restaurants/Retail Outlets*

Another issue is the intentional release of mitten crabs into our environment from female mitten crabs held in ethnic restaurants or stores that become ovigerous (Fig. 1). Once the females are ovigerous they are no longer of commercial value,

**Fig. 34** A male mitten crab purchased from a local Hong Kong Market, October 2002 and now deposited in the collections of the Natural History Museum registration number 2003.315. Phil Crabb, NHM photo unit

but pose a threat if deliberately released into the environment instead of being killed. These crabs should not be released back into the environment alive with their eggs; they should be destroyed and suitably disposed off. This is an area that may require further legislation and control.

## *9.3 Live Imports*

A number of Government Policies and attitudes require revisiting with a view to amendment.

The decision that because *Eriocheir sinensis* is now well established in the Thames it should be considered to be an ‘ordinary resident’ is difficult to justify. It is not an ordinary resident, it is an extremely aggressive invader, and this report would suggest that any Invasive Species Policy within the UK is not joined up.

There is no mechanism in current UK legislation or willingness to ban the live import of animal products for human consumption. But this may require new EU legislation, (if not cover by Council Regulation (EC) 2007a, No 708/2007) too because at present it may be impossible to ban live imports of mitten crab fished for legitimately in Holland for example. Furthermore, Dutch mitten crabs may not be suitable for human consumption anyway (see Clark et al. 2009). The USA banned all live imports of *Eriocheir sinensis* in 1989 (Horwath 1989), the UK authorities might have acted likewise. In fact legislation should be introduced into the UK banning the live importation of contentious species; this action should now be strongly considered. For certain the conservation agencies of Ireland and Scotland should urgently consider a complete import ban of live mitten crabs as the former has only a few records (Minchin 2006) while the latter has no reports of this invasive species to date (Clark et al. 2002). Just banning the sale of mitten crabs in these two countries, the only course of action available at present, may not be enough to prevent the introduction.

If the many authorities involved give consent to Thames mitten crab fishing commencing, there is a major issue with the intentional human spread of this crab to other catchments in order to provide a fishery in other regions of the UK. This is perceived to be a real problem as the spread of non-native crayfish provides a prime example of such environmental vandalism. The intention of Thames mitten crab fishing is to reduce the population therein and not give the go ahead to set up similar activities in river without this pest. Consequently an active educational programme may have to be launched to coincide with any Thames fishing.

There is a perceived problem with mitten crab escapees infesting new areas of the UK. This problem will also need to be addressed.

Currently, the import trade of live mitten crabs is extremely secretive and records of this are either not available or non-existent. Consequently there is no accountability with regard to the scale of this problem.

## *9.4 Mitten Crab Farming*

During March 2010 the author of this chapter received the following email. The name of the University has been deliberately withheld.

> "I am writing to you to request further information on your mitten crab study. I and several other ****** University students are currently involved in an entrepreneurial campaign, of which our ideology focuses on the sustainability of farming mitten crabs within the UK. We are currently struggling to find some integral information and were hoping to could utilise your expertise around the subject.
>
> Firstly, we noted in your paper the current issues surrounding their over population in the Thames – we therefore would like to know whether it is a viable concept to fish these crabs from this source and then relocate them to one of our own specialised farms? If so could you enlighten us with any of the costs associated with a project of this magnitude? The scale of our farm is relatively small as we are only just starting out and exploring this concept.
>
> Lastly, as our whole business ethos resides around their sustainability we were wondering if any governmental help/aid could become available. If any knowledge around the actual farming process could be passed on that would be greatly appreciated.
>
> Thank you very much for your time, we realise we have asked a whole range of questions – any help would be greatly appreciated".

What a nightmare!

Can current government legislation prevent mitten crab farming in the UK? Allowing such aquaculture in the UK would be an environmental disaster and should not be given the go ahead under any circumstances. Mitten crabs are great escapers as they can live for a long time out of water and across from one watershed into another. There are enough problems with this invasion species in a number of catchment areas as it is and farming will just compound the current issues. Rearing mitten crabs would just be repeating the great crayfish mistake (see Holdich 2000), of the past.

## 10 Conclusions

The Thames mitten crab population is well established and continues to increase in numbers. The Food Standards Agency has advised the London Port Health Authority that within limits the product is safe for human consumption and this may be a means of controlling this invasive pest as in SE Asia this crab is a delicacy. However the question that should be asked is "do we really want to start a mitten crab fishery?" If the Thames population is not controlled, there will be economic consequences including blocked water inlets, destruction of unprotected river banks and damage to estuarine fishing gear. Moreover, London will export this problem to other catchments inside the UK and other continents via the ballast water of shipping. If commercial exploitation of mitten crabs is accepted then this decision has implications for the increasing threatened Thames eel population and the possible intentional dispersal of crabs to other UK watersheds as per the invasive American crayfish for example solely for financial gain. Furthermore such a fishery would need to be strictly regulated with regard to fishermen/traders, restaurants/retail outlets and the possible banning of all live mitten crab imports into the UK. And sanctioning UK mitten crab farms would be ignoring past mistakes. The bottom line is that with respect to commercially exploiting the Thames mitten crab population; we are damned if we don't and damned if we do. Doing absolutely nothing is not an option.

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# Part V
# Case Studies

# Live and Let Live: Invasive Host, *Charybdis longicollis* (Decapoda: Brachyura: Portunidae), and Invasive Parasite, *Heterosaccus dollfusi* (Cirripedia: Rhizocephala: Sacculinidae)

**Gianna Innocenti and Bella S. Galil**

**Abstract** The Levantine populations of the invasive swimming crab *Charybdis longicollis* have been parasitized by the rhizocephalan *Heterosaccus dollfusi*, itself an alien, since 1992. The parasite affects the host morphology, moulting, behaviour, causes its sterilization, and induces mortality. The high prevalence of *H. dollfusi* can be ascribed to the dense population of the host, the year-round reproduction of the parasite that promotes recurrent re-infection, and the recruitment dynamics that likely permit the synchronous development of both host and parasite. After 17 years, despite the high prevalence of the parasite and its injurious impact on the host reproduction, the invasive host-parasite pair has reached an apparent *modus vivendi*, with no evident reduction in the host population and with recurrent seasonal high rates of parasitization and multiple *externae*.

## 1 Introduction

Instances of rhizocephalans accompanying their invasive hosts are few: *Sacculina carcini* Thompson, 1836 naturally occurring in European waters (Høeg and Lützen 1985), has been introduced into Burmese waters, probably transported with its host, *Carcinus maenas* (Linnaeus, 1758), in ballast-water tanks or on the hulls of ships (Boschma 1972). *Loxothylacus panopaei* (Gissler, 1884), introduced with its host *Eurypanopaeus depressus* (Smith, 1869), was transferred with imported live oysters

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from the Gulf of Mexico to Chesapeake Bay, U.S.A. (Van Engel et al. 1966). Among the hundreds of alien species that have entered the Mediterranean through the Suez Canal and established populations along the coast of the Levant another invasive host-parasite pair was identified. The portunid crab *Charybdis longicollis* (Leene, 1938) which inhabits the Indian Ocean (Guinot 1966), the Persian Gulf (Stephensen 1946), and the Red Sea (Leene 1938), was first collected in the Mediterranean in 1954 in the Bay of Mersin, Turkey (Holthuis 1961; Lewinsohn and Holthuis 1964). Since then, it has been recorded all along the Levant coasts, from Egypt to Rhodes (Galil and Kevrekidis 2002). It is common on sandy-mud bottoms at 25–60 m and occasionally deeper, and forms as much as 70% of the benthic biomass at places (Galil 1986; Özcan et al. 2005). Of the thousands of specimens of *C. longicollis* collected off the Israeli coast none were parasitized until 1992 when a few specimens were discovered carrying the *externae* of the parasitic barnacle *Heterosaccus dollfusi* Boschma, 1960, itself an Erythrean alien, previously known from few specimens from the Gulf of Suez (Monod 1938; Boschma 1960), which was originally described from *C. longicollis* (as *Charybdis (Goniohellenus) hoplites* var. *longicollis,* see Holthuis 1961). In March 1995, *H. dollfusi* was found infesting *C. longicollis* on the easternmost part of the Anatolian coast (Øksnebjerg et al. 1997; Øksnebjerg 2000). Ever since a significant percentage of *C. longicollis* population along the Levant coast has been parasitized by *H. dollfusi* (Innocenti and Galil 2007). The parasite causes sterilization, morphological and behavioural feminization, cessation of molting and by placing high energetic demands on the host, induces mortality (Galil and Lützen 1995; Innocenti et al. 1998; Galil and Innocenti 1999; Innocenti and Galil 2007).

Aspects of the biology, ethology and population dynamics of the invasive host-parasite pair along the Mediterranean coast of Israel have been studied since 1992.

## 2 Incidence of Parasitization

Specimens of *C. longicollis* were collected off Palmahim, Israel, from 1993 to 2009. Nearly 19,000 crabs were examined, among these, over 10,000 were either *externae*-bearing, or internally parasitized morphologically-modified crabs. The number of specimens and the incidence of parasitization were higher in the spring (May–June) than in the fall samples (August–October) ($G = 17.762$, $df = 8$, $P < 0.05$; see also Innocenti and Galil 2007) (Table 1).

*Heterosaccus dollfusi* rapidly infected the Levantine populations of *C. longicollis*, parasitizing within 2 years of its initial detection 62.6% of the Palmahim host population. Examination of the incidence of parasitization in the spring samples, before the onset of parasite-induced mortality, shows that along the central Israeli coast it has been fairly high and exhibited a long-term temporal stability.

Between April 2008 and July 2009 eight samples were collected off Ashdod, Israel. Over 11,000 crabs were examined. Among these, nearly 7,500 were either

**Table 1** Incidence of parasitization in *Charybdis longicollis* collected off Palmahim, Israel, 1993–2009; fall and spring samples

| | 1993 | 1994 | 1995 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | October | November | September | September | September | September | September | September | September | September | September | September | September | October | August |
| Unparasitized | | | | | | | | | | | | | | | |
| M+F | 444 | 116 | 115 | 328 | 499 | 56 | 103 | 186 | 251 | 456 | 102 | 179 | 301 | 368 | 480 |
| Parasitized | | | | | | | | | | | | | | | |
| MI+FI | 16 | 19 | 131 | 76 | 231 | 66 | 12 | 33 | 63 | 20 | 6 | 91 | 31 | 25 | 62 |
| ME+FE | 124 | 51 | 26 | 15 | 235 | 14 | 48 | 67 | 128 | 29 | 32 | 254 | 239 | 252 | 615 |
| **Total** | **584** | **186** | **272** | **419** | **965** | **136** | **163** | **286** | **442** | **505** | **140** | **524** | **571** | **645** | **1,157** |
| **Incidence of parasitization** | ***24.0*** | ***37.6*** | ***57.7*** | ***21.7*** | ***48.3*** | ***58.8*** | ***63.2*** | ***35.0*** | ***43.2*** | ***9.7*** | ***37.3*** | ***65.8*** | ***47.3*** | ***42.9*** | ***58.5*** |
| | 1994 | 1996 | 1998 | 2000 | 2002 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | | | | |
| | May | June | May | June | May | May | May | May | May | May | May | | | | |
| Unparasitized | | | | | | | | | | | | | | | |
| M+F | 129 | 378 | 572 | 978 | 286 | 125 | 282 | 282 | 875 | 486 | 296 | | | | |
| Parasitized | | | | | | | | | | | | | | | |
| MI+FI | 46 | 90 | 116 | 273 | 72 | 38 | 106 | 158 | 999 | 152 | 516 | | | | |
| ME+FE | 170 | 693 | 226 | 512 | 332 | 62 | 439 | 233 | 1,026 | 670 | 424 | | | | |
| **Total** | **345** | **1,161** | **914** | **1,763** | **690** | **225** | **827** | **673** | **2,900** | **1,308** | **1,236** | | | | |
| **Incidence of parasitization** | ***62.6*** | ***67.4*** | ***37.4*** | ***44.5*** | ***58.6*** | ***44.4*** | ***65.9*** | ***58.1*** | ***69.8*** | ***62.8*** | ***76.1*** | | | | |

M, F: unparasitized males and females, MI, FI: internally parasitized males and females, ME, FE: externa-bearing males and females

**Table 2** Incidence of parasitization in *Charybdis longicollis* collected off Ashdod, Israel, April 2008–July 2009

| | April 08 | May 08 | July 08 | August 08 | November 08 | December 08 | April 09 | July 09 |
|---|---|---|---|---|---|---|---|---|
| Unparasitized | | | | | | | | |
| M+F | 255 | 370 | 334 | 463 | 158 | 1,122 | 554 | 469 |
| Parasitized | | | | | | | | |
| MI+FI | 1,267 | 877 | 109 | 79 | 71 | 303 | 822 | 312 |
| ME+FE | 473 | 322 | 428 | 614 | 69 | 641 | 434 | 590 |
| **Total** | **1,995** | **1,569** | **8,71** | **1,156** | **298** | **2,066** | **1,810** | **1,371** |
| **Incidence of parasitization** | ***87.2*** | ***76.4*** | ***61.7*** | ***59.9*** | ***47.0*** | ***45.7*** | ***69.4*** | ***65.8*** |

M, F: unparasitized males and females, MI, FI: internally parasitized males and females, ME, FE: externa-bearing males and females

*externae*-bearing, or internally parasitized morphologically modified crabs. The number of specimens was smallest in the fall sample (November 2008). The incidence of parasitization was distinctly higher in the spring samples (87.2, 76.4, 69.4% in April and May 2008, April 2009, respectively) than in the fall and winter samples (47.0, 45.7% in November, December 2008, respectively) ($G = 945.138$, $df = 4$, $P < 0.001$) (Table 2).

Incidence of rhizocephalan parasitization is usually low (Lützen 1984; Hochberg et al. 1992; Shields 1992), but isolated cases of high infestation have been recorded with a local percentage of infection as high as 90% (Veillet 1945) and 95% (Høeg 1995). Hines et al. (1997) (see also Alvarez et al. 1995) reported that the Rhode River population of *Rhithropanopaeus harrisii* (Gould, 1841) was first infected with *L. panopaei* in 1989 and 2 years later, 72% were infected. Incidence of infection in the commercially valuable sand crab, *Portunus pelagicus* (Linnaeus, 1758), infected by *S. granifera* Boschma, 1973, may be as high as 29% (Thomson 1951), though usually much lower (Phillips and Cannon 1978; Weng 1987). Pillai and Thomas (1972) found that 12.2% of *P. pelagicus* (as *Neptunus*) from the Gulf of Manaar were infected by *H. indicus* Boschma, 1957. In Lake Pulicat, 17.5% of *P. sanguinolentus* (Herbst, 1783) were infected by *H. ruginosus* Boschma, 1931 (Srinivasagam 1982). Lazaro-Chavez et al. (l996) recorded that up to 51.5% of the blue crab, *Callinectes sapidus* Rathbun, 1896, in the Gulf of Mexico were infested by *L. texanus* Boschma, 1933. The greater number of remarkably high prevalence of rhizocephalan infestation takes place in enclosed bodies of water, be it a bay, a fjord or a lagoon (Hartnoll 1967; Sloan 1984; Hawkes et al. 1986; Yamaguchi et al. 1994). Thus, Veillet (1945) observed high infestation in populations isolated within inlets of the Étang de Thau, a brackish water lagoon in southeast France; Srinivasagam (1982) in a brackish lagoon in southeast India; Hawkes et al. (1986) in inlets of Glacier Bay, Alaska; Hines et al. (1997) (see Alvarez et al. 1995) in Rhode River, Chesapeake Bay, Maryland; Yamaguchi et al. (1994) in sheltered bays around Amakusa Islands, Japan; Lazaro-Chavez et al. (1996) in brackish Tamiahua Lagoon, and Alvarez and Calderon (1996) in Sontecomapan Lagoon, both in Mexico.

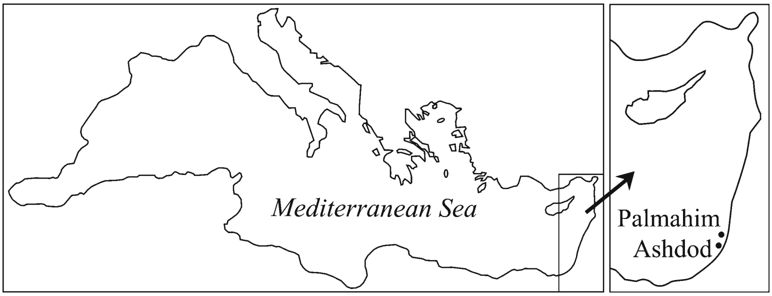

**Fig. 1** Map of the Mediterranean coast of Israel

Sheltered bays or lagoons allow the short-lived nauplii to remain within their environment. The coast of Israel, at the southeastern corner of the Mediterranean, forms a smoothly curving arc except for the indentation of Haifa Bay (Fig. 1). Yet, off the Israeli coast the incidence of parasitization has been high and fairly stable over the past 15 years (Innocenti and Galil 2007). It seems that the local environmental conditions promote the synchronous ontogenetic development of both host and parasite ensuring availability of plentiful young, recently molted prospective hosts to the short lived parasite cypris.

## 3 Effects of Parasitization on the Crabs' Secondary Sexual Characters

The abdomen of both sexes of infected C. *longicollis* is modified to such an extent that the sexual apertures remain the only reliable character to determine the host's sex. Infection of the females causes the loss of the pleopods, whereas in males the gonopods are lost or reduced, and the abdomen broadens to such a degree that it closely resembles that of an uninfected female. Modification in C. *longicollis* is initiated by young *internae* too small to be detected by the naked eye (Galil and Lützen 1995). Crabs with a modified abdomen but no visible parasites are predominantly small, most of them with CW between 15–28 mm (females) and 13–34 mm (males) (Galil and Innocenti 1999). The smallest modified female crab was 13 mm, and male crab 12 mm. The largest internally infected but visibly modified female crabs were 43 mm, and male crabs 47 mm. The modification of parasitized *C. longicollis* is much more pronounced than in other sacculinized crabs (Tattersall 1920; Day 1935; Hartnoll 1967; Weng 1987). In extent and detail it is similar to descriptions given by Matsumoto (1952) and George (1959) of *Charybdis japonica* (A. Milne-Edwards, 1861) and *P. sanguinolentus*, respectively, parasitized by two other species of *Heterosaccus*. Males or females of these genera infected by species of *Sacculina* are never modified to a similar degree. The almost total feminization of male *P. sanguinolentus* by *H. ruginosus* led Nair and Gurumani (1956) and Srinivasagam (1982) to believe that all of their parasitized crabs were females.

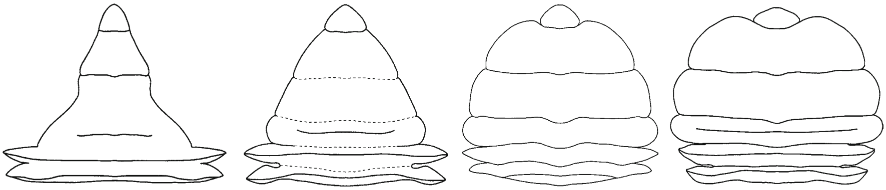

**Fig. 2** *Charybdis longicollis;* from left, abdomen of unparasitized male, internally parasitized male, externally parasitized male, unparasitized female

Unparasitized *C. longicollis* males have a narrow abdomen with a concave contour; the third, fourth, and fifth segments are fused and nonarticulate; normal copulatory pleopods are present even in the smallest males (CW 14 mm); marginal setae are sparse and very short. In infected males segments four to six of the triangular abdomen become articulated and the margins are fringed with short marginal setae. The copulatory appendages are most often absent, but remnants in various degrees of degeneration may sometimes occur. In the next stage, the sides of the abdomen are convex and fringed with long marginal setae, all abdominal segments articulate, and vestiges of copulatory appendages occur only very rarely (Fig. 2). Furthermore, the abdomen is indistinguishable in shape and setation from that of sexually mature females; copulatory appendages may occur in a reduced state, but are extremely rare; minute vestiges of up to four pairs of pleopods (similar to those in the infected females) are often present (Galil and Lützen 1995).

Unparasitized females have articulate abdominal segments and four pairs of pleopods on segments 2–5. The abdomen is roughly triangular in the smallest (CW 13–16 mm) females, but it gradually broadens until it acquires its relative maximum width at puberty. The marginal setae increase in length and abundance at each moult. Parasitized females are distinguished by the absence of normal pleopods; one or two, often asymmetrical and vestigial appendages may be present (usually on segments 2 or 3) (Fig. 3); the pleopods are replaced by one to four pairs of setate thin walled hillocks which decrease in size posteriorly (Galil and Lützen 1995).

From the reduction or absence of the gonopods in the male, absence of pleopods in the female, and the fact that none of the parasitized females carried eggs, it is evident that infection prevents both sexes of *C. longicollis* from reproducing.

"Sacculinized" males of most crab species have only moderately modified abdomens and in such species the parasites survive better on females than on males, probably because the larger abdomen of the female offers better protection than the narrow abdomen of the male (Høeg and Lützen 1995). In the present case, parasitized male and female crabs acquire a similarly broad abdomen, offering the *externae* equally good cover in both sexes. The frequency of scarred *C. longicollis* (2.3%) is much lower than in most other populations of "sacculinized" crabs (Heath 1971; Lützen 1984). This may mean that most parasites stay with the host for life and are lost only when they are damaged. George (1959) concluded the same to be true in the association between *H. ruginosus* and *P. sanguinolentus,* in which the abdomen of infected males also acquires female dimensions.

**Fig. 3** An *externa*-bearing female *Charybdis longicollis* with vestigial pleopods. Palmahim, October 2007

## 4 Effects of Parasitization on the Crabs' Size

Sacculinid-infected crabs are undersized compared with non-infected ones (Høeg 1995). Phillips and Cannon (1978) attribute the stunted size to molt-inhibition by the parasite, whereas O'Brien and van Wyk (1985) ascribe it to reduction in the number of molts and Hawkes et al. (1987) to diminished molt increments. Høeg (1995) considers that the rhizocephalans' effect on their hosts' size may also be related to size or sex dependent survival and maintains that stunted males are an indication of "feminization" of the hosts.

Carapace width measurements of *C. longicollis* specimens collected in June and November, 1987, before the parasite was first detected at Palmahim, Israel in 1992, show that the largest males were significantly larger than the largest females both spring and fall (Fig. 4). Whereas in the spring sample the size classes of male and female specimens were nearly equivalent (male median size 26.5 mm, female median size 24.1 mm, $t=2.592$, $df=140$, $P<0.01$), in the mature fall population 40.3% of the males are 30–40 mm wide, compared with 78.7% of the females, and 45.7% of males are 45 mm or larger (male median size 37.1 mm, female median size 30.2 mm, $t=5.546$, $df=179$, $P<0.01$).

Examination of crab size (CW) measurements of *C. longicollis* in the post-1992 parasitized population indicates that whereas males in the pre-1992 unparasitized population of C. *longicollis* were significantly larger than females, the size gap diminished significantly in parasitized crabs. In parasitized populations the average and maximal size of non-parasitized males is larger than parasitized males whereas average and maximal size of non-parasitized female crabs are smaller than those bearing

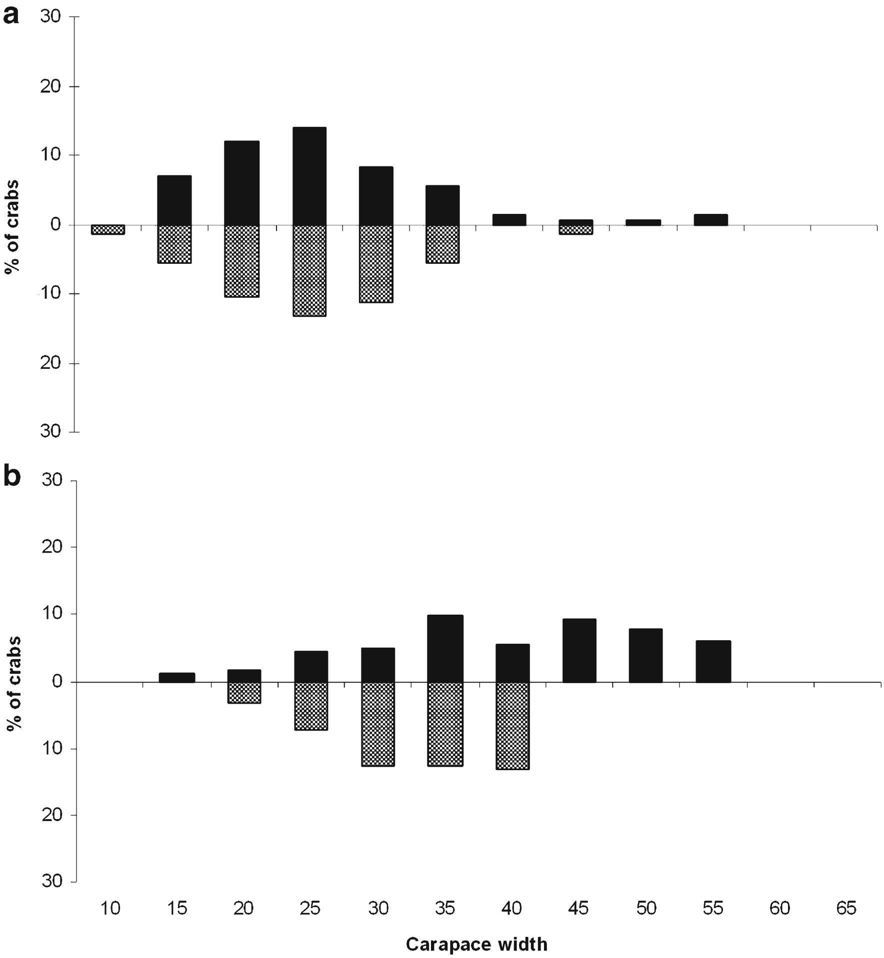

**Fig. 4** Carapace width (mm) of *Charybdis longicollis* population off Palmahim, Israel. (**a**), June 1987 (M=73 specimens; F=70); (**b**) November 1987 (M=92; F=89); ■ males, ▣ females

*externa* (Table 3). Examination of the size classes of the parasitized population collected between April 2008 and July 2009 off Ashdod, Israel (see above), reveals that spring (April 2008) sample is quite similar to the pre-1992 spring sample in the near symmetry between male and female size classes (male median size 29.0 mm, female median size 28.5 mm, t=0.531, df=253, not significant). The size classes in the summer and winter samples (August, December 2008) have shifted significantly (male median size August: 40.7 mm; December: 42.8 mm, female median size August: 35.8 mm; December: 33.4 mm, August samples: t=17.453, df=657, $P<0.01$; December samples: t=23.896, df=1,120, $P<0.01$, respectively), size classes in April 2009 recapitulate the earlier pattern: male median size is 32.8 mm and female median is 31.6 (t=5.953, df=552, $P<0.01$) (Fig. 5). Tracing the seasonal succession of size classes it is clear that many of the smaller sized parasitized crabs fail to survive.

**Table 3** Carapace width measurements (mm) of *Charybdis longicollis* collected off Palmahim, Israel, 2004, 2005, 2007, 2008

| | Average size | N | Range | | Average size | N | Range |
|---|---|---|---|---|---|---|---|
| **May 2005** | | | | **September 2004** | | | |
| M | 41.0 | 70 | 21.1–57.2 | M | 49.8 | 53 | 30.0–60.6 |
| F | 34.3 | 55 | 21.1–42.3 | F | 39.3 | 49 | 28.9–49.6 |
| ME | 36.6 | 42 | 20.6–46.3 | ME | 42.9 | 17 | 34.7–51.0 |
| FE | 37.5 | 20 | 25.9–47.0 | FE | 38.8 | 15 | 21.4–47.2 |
| **May 2005** | | | | **September 2005** | | | |
| M | 39.5 | 141 | 20.8–60.0 | M | 42.5 | 81 | 26.7–64.1 |
| F | 35.6 | 141 | 25.7–44.3 | F | 36.2 | 98 | 27.1–48.5 |
| ME | 35.4 | 309 | 23.3–52.0 | ME | 41.4 | 165 | 31.9–53.4 |
| FE | 35.2 | 130 | 26.0–45.0 | FE | 39.3 | 89 | 28.1–50.0 |
| **May 2007** | | | | **October 2007** | | | |
| M | 41.7 | 428 | 15.2–63.3 | M | 45.4 | 162 | 33.2–60.1 |
| F | 32.6 | 447 | 18.4–43.6 | F | 34.9 | 206 | 28.2–42.5 |
| ME | 33.6 | 678 | 20.4–51.9 | ME | 38.7 | 151 | 32.1–47.0 |
| FE | 33.9 | 348 | 17.5–48.9 | FE | 37.0 | 101 | 29.8–45.9 |
| **May 2008** | | | | **August 2008** | | | |
| M | 41.8 | 264 | 18.1–56.9 | M | 46.6 | 222 | 25.8–60.7 |
| F | 33.2 | 222 | 21.3–41.8 | F | 35.8 | 258 | 27.5–43.2 |
| ME | 35.8 | 409 | 23.3–49.3 | ME | 40.7 | 363 | 31.2–50.9 |
| FE | 35.6 | 261 | 24.4–49.4 | FE | 38.6 | 252 | 28.7–47.9 |

M, F: unparasitized males and females, ME, FE: externa-bearing males and females

## 5 Effects of Parasitization on the Crabs' Behaviour

Rasmussen (1959) noted that abdomen grooming behaviour in *externae*-bearing *C. maenas* of both sexes resembled that of berried females, and suggested that the stimulus for that behaviour was provided by the *interna* and was not merely tactile, as well Høeg and Lützen (1995) observed for *C. maenas* infected by *S. carcini*. Bishop and Cannon (1979) observed similar behaviour in *P. pelagicus* parasitized by *S. granifera*, as did Ritchie and Høeg (1981) in parasitized porcellanid crabs. Overstreet (1983) and Wardle and Tirpak (1991) noted the behaviour of *C. sapidus*, infested by *L. texanus,* and Gherardi and Cassidy (1995) of the hermit crab *Discorsopagurus schmitti* (Stevens, 1925) parasitized by *Peltogaster boschmae* Reinhard, 1944. Also, Bishop and Cannon (1979), who studied agonistic interactions between uninfected and infected opposite and same sex pairs of *P. pelagicus* crabs, reported that infected crabs initiated fewer encounters than uninfected crabs of comparable size and the same sex. Similarly, Wardle and Tirpak (1991) remarked that infected *C. sapidus* were "generally less active and consistently less aggressive when presented with food".

Few studies have concerned themselves with the behaviour of parasitized crabs, fewer still have employed controlled ethological experiments and the ones which did so, were all conducted on *externae*-bearing crabs (Bishop and Cannon 1979; Wardle and Tirpak 1991). The behaviour of parasitized *C. longicollis*, in different

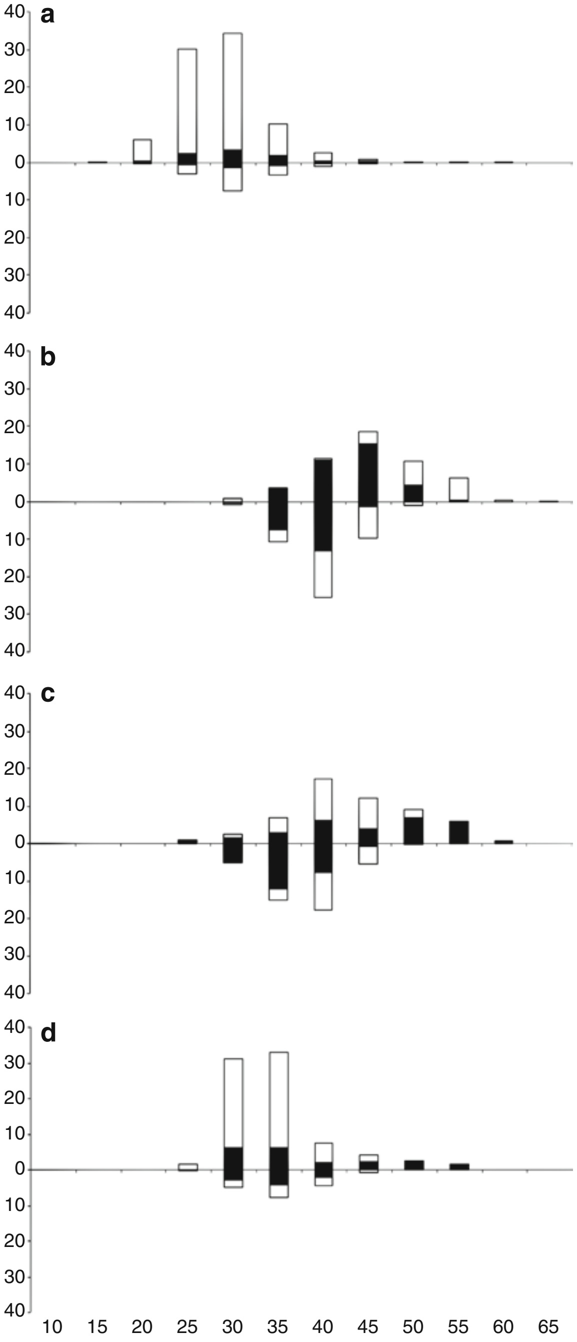

**Fig. 5** Carapace width of *Charybdis longicollis* collected off Ashdod, Israel, 2008–2009. (**a**) April 2008, (**b**) August 2008, (**c**) December 2008, (**d**) April 2009. Y axis percentage of crabs, X axis, CW size classes (in mm). Bars above: ■ unparasitized males, □ parasitized (with *externa*) males; bars ■ below unparasitized females, □ parasitized (with *externa*) females

stages of infection, was examined and compared with the behaviour of nonparasitized crabs. Mobility, rest, digging and burying; body, egg- and parasite grooming, courtship and mating were described qualitatively and analysed quantitatively under standardized conditions. Modifications of grooming, burying, courtship and mating, and agonistic behaviour have been observed in parasitized *C. longicollis* (Innocenti et al. 1998, 2003).

The presence of the *externa* induces *C. longicollis* to simulate egg-grooming behaviour: the crabs use the dactyls of the second to fourth pereopods to rub, scratch, pinch and smooth the *externa* whilst contracting the abdomen, and clean inside its mantle cavity. The *externa* grooming behaviour was obviously not observed in internally infected crabs, while a few scarred crabs flap their abdomen occasionally. *Externae*-bearing crabs spend more time cleaning and fanning the *externae* than ovigerous crabs. It is of particular interest that the parasite succeeds in inducing that behaviour in male crabs, in which grooming and fanning of the abdomen do not occur normally. This grooming behaviour serves to clean and ventilate the parasite, enhancing its survival. Indeed, Ritchie and Høeg (1981) reported the gradual death of *externae* in the porcellanid crab, *Petrolisthes cabrilloi* Glasell, 1945, parasitized by *Lernaeodiscus porcellanae* (Muller, 1852), when the hosts were prevented from grooming. Grooming behaviour appears to be controlled by the parasite, probably through hormones (Høeg 1995), as it is stimulated by the emergence of the *externa* and declines after its degeneration. Bishop and Cannon (1979) surgically removed *externae* in three crabs of unknown sex and observed that grooming behaviour declined after 2 weeks.

When non-parasitized, internally parasitized and post-parasitized (scar-bearing) *C. longicollis* crabs, were fitted with a bit of foam rubber, simulating the size and consistency of an *externa*, their behaviour was similar to non parasitized crabs, i.e. they did not perform grooming behaviour. Within minutes the non-parasitized crabs tried to pull out the artificial *externa* with their chelipeds, while some of the scar-bearing crabs were observed contracting their abdomen and cleaning the false *externa*. These preliminary findings suggest that in uninfected crabs, grooming behaviour is apparently not stimulated by the physical presence of *externa*; however, that presence may elicit grooming behaviour in crabs recently freed from the parasite (Innocenti et al. 1998).

Burying behaviour is common in non-parasitized crabs. Digging movements anticipate the burying of the crab, the crab sinks very quickly, with the fifth pereiopods heaping sediment over the carapace until it is completely concealed. Compared with internally parasitized and post-parasitized crabs, crabs bearing mature *externa* dig in an uncoordinated manner, gathering the sand less efficiently, barely bury themselves. Similar modification was recorded by Wardle and Tirpak (1991) in *C. sapidus* parasitized by *L. texanus*.

No traces of courtship and mating behavioural patterns (i.e., grasping, rocking or shaking) were observed in internally, externally or post-parasitized crabs.

The behaviour of uninfected *C. longicollis* male crabs contained more aggressive elements than that of uninfected females, and the agonistic behaviour patterns of uninfected males differed significantly from those of uninfected females, whereas the behaviour patterns of infected males and females were comparable. In encounters between infected males, markedly fewer and less aggressive elements were displayed than in encounters between uninfected males, whereas in encounters between infected females, more aggressive elements were displayed than in encounters between uninfected females. The feminized agonistic behaviour of male crabs parallels the feminization of the secondary sex characters of parasitized *C. longicollis* (see above). It is also suggested that the presence of the parasite reduces belligerence in male crabs, enhancing injury avoidance to the highly susceptible *externa* (Innocenti et al. 2003).

## 6 Multiple Parasitization

Sacculinids commonly occur singly on the host, but two or more per host are occasionally found. In Boschma (1960) original material there were two *C. longicollis,* each with a single *externa*, and two with two *externae* each. The high number of *externae* per host in our material (up to eight) is unusual and has been recorded only for *L. texanus* (see Reinhard 1950; Pearse 1953), *Sacculina triangularis* Anderson, 1862 (see Bocquet-Védrine 1959), S. *hartnolli* Boschma, 1965 (see Hartnoll 1967), and *Sacculina* sp. (Yamaguchi et al. 1994). In sacculinids, multiple *externae* may arise either from plural infection of cypris larvae (Rainbow et al. 1979) or from an occasional division of a single tumour into two nuclei (Delage 1884; Smith 1906; Perez and Basse 1928; Reinhard 1954). In the former case, their frequency is dependent, in the latter case independent, of the incidence of parasitization. It seems that the parasite avoids settling on an already parasitized host when unparasitized crabs are plentiful (Thresher et al. 2000), and only does so when the chances of encountering an unparasitized host are greatly reduced, as reported for *Lithodes aequispina* (Benedict, 1894) parasitized by *Briarosaccus callosus* Boschma, 1930 (Sloan 1984), and for the blue crab *Callinectes* ssp. infected by *L. texanus* (see Alvarez et al. 1999, 2001; Alvarez and Calderon 1996; Høeg 1995).

Multiple parasitization has been common in the Palmahim population of *C. longicollis*: nearly 40% of the *externae*-bearing hosts sampled between 1994 and 2009 harboured more than one *externa*, and over 17% bore three *externae* or more (Fig. 6). The percentage of specimens bearing three or more *externae* is five times as high in spring as in fall samples (Fig. 7).

The highest number of *externae* per host in the Palmahim population was eight, and has been recorded only in four instances, and only from small crabs (CW 23.5–32.8 mm), whereas two and three *externae* were recorded for nearly the whole size range (Fig. 7). The pattern that emerges from the examination of the percentage of *externae*-bearing hosts bearing more than a single *externa* is that it increases when the incidence of parasitization rises above 50% (May 2002, percentage of multiple *externae* 47.6%/ incidence of parasitization 58.6%; May 2004, 37%/44.4%; May 2005, 58%/65.9%; May 2006, 52%/58.1%; May 2007, 61%/69.8%; May 2008, 51%/62.8%; May 2009, 55.4%/76.1%).

Moreover, the higher the percentage of parasitization, the higher the percentage of multiple *externae* per host. Examination of the samples collected off Ashdod

**Fig. 6** *Charybdis longicollis* bearing 6 *externae*, collected off Palmahim, Israel, May 2005

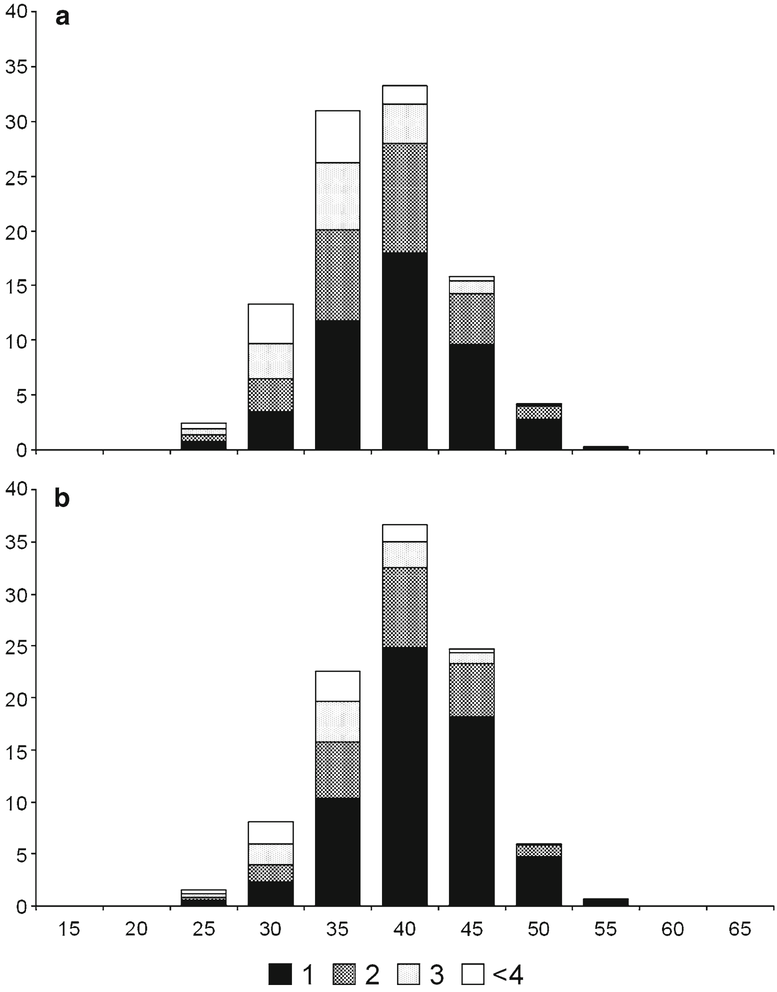

**Fig. 7** Percentage of multiple *externa* in *Charybdis longicollis* collected off Palmahim, Israel, 1998–2008; X axis, CW size classes (in mm) respectively, (**a**) spring; (**b**) fall

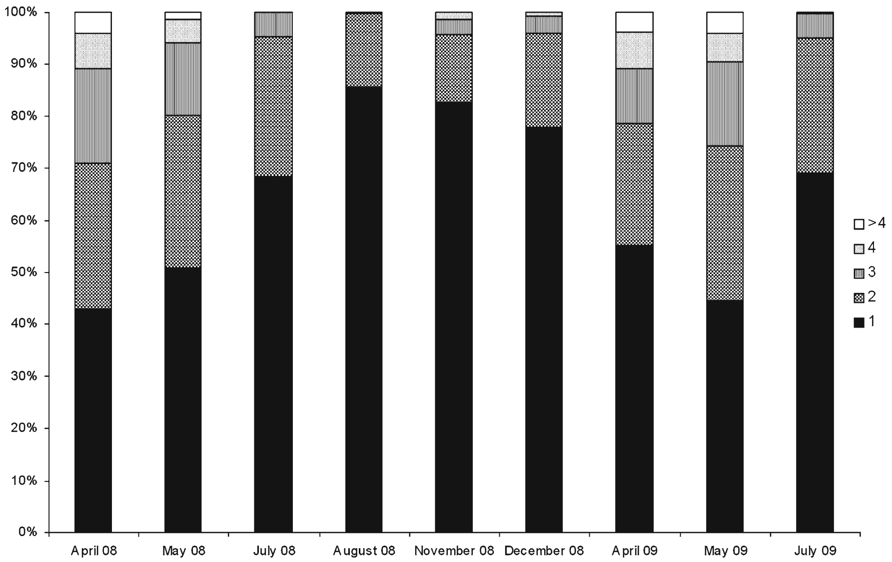

**Fig. 8** Percentage of multiple *externa* in *Charybdis longicollis* collected off Ashdod, April 2008–July 2009

between April 2008 and July 2009 shows that the percentage of multiple *externae* bearing hosts stood at 57%, 50% and 45% in the spring samples with their higher incidence of parasitization (87.2%, 76.4%, 69.4% in April and May 2008, April 2009, respectively), as compared with 14 and 17% for the fall and winter samples (47.0%, 45.7%, November, December 2008, respectively). In fact, four or more *externae* per host were encountered only in the spring samples (Fig. 8).

Almost without exception, multiple *externae* are found on small-size crabs, presumably because by placing an unacceptably high nutritional demand on the host, multiple *externae* weaken it and in many cases cause its untimely death.

## 7 Incidence of Epibionts on Parasitized Crabs

The presence of epibionts is determined by the host's moult interval, behaviour pattern of the host and energy costs to the host (Phillips and Cannon 1978; Bishop and Cannon 1979; Abello et al. 1990; Miller et al. 2006). Epibionts in parasitized crabs burden their host by hampering movement thus increasing its vulnerability to predation (Overstreet 1983; Gaddes and Sumpton 2004). Because moulting and burying protect against fouling epibionts, parasitized crabs are expected to bear more epibionts than unparasitized ones (Gili et al. 1993). Moreover, it has been observed that parasitized crabs bearing more epibionts spend more time in grooming (Bishop and Cannon 1979). According to Miller et al. (2006), 85.4% of

**Fig. 9** *Charybdis longicollis* fouled by *Hydroides operculatus* and the turtle barnacle, *Chelonibia patula* Palmahim, May 2007

the *C. japonica* individuals collected in spring were fouled by large numbers of serpulid polychaetes, the fouling more abundant in males than females. They argued that more epibionts could be expected in larger specimens because their intermoult period is longer. Similar results were reported for *Lithodes ferox* Filhol 1885, where most female specimens with carapaces longer than 70 mm bore the stalked barnacle *Poecilasma kaempferi* Darwin, 1852 and the hydroid *Stegopoma plicatile* (Sars, 1863) (Abello and Macpherson 1992), and for *C. maenas* where the prevalence of barnacles and the serpulid polychaete *Pomatoceros triqueter* (Linnaeus, 1767) on parasitized crabs was higher than for unparasitized ones (Mouritsen and Jensen 2006).

Both unparasitized and parasitized *C. longicollis* crabs have been noted to bear epibionts: the Erythrean alien serpulid polychaete, *Hydroides operculatus* (Treadwell, 1929) (Galil and Lützen 1995), the acorn barnacle, *Balanus trigonus* Darwin, 1854, borne by 5% of the *externae*-bearing crabs in Haifa Bay, Israel (Galil and Innocenti 1999), and the turtle barnacle, *Chelonibia patula* (Ranzani, 1818). The serpulid worms occurred mainly on the thoracic sternites, to a lesser degree dorsally on the carapace, and occasionally on the thoracic legs (Figs. 9 and 10).

The frequency of epibionts in *C. longicollis* was low in both unparasitized and parasitized crabs in spring (6.7, 1.9% respectively), whereas in fall, nearly a third of the parasitized crabs bore serpulids compared with only 1% of the unparasitized crabs. When the "load" of epibionts was scored (as follows: 1 = up to 2, 2 = up to 5, 3 = over 5 epibionts), it became apparent that though in fall the number of epibiont-bearing crabs was higher, the proportion of crabs bearing over five epibiotic specimens was higher in spring (Innocenti & Galil 2010).

Our results support the existence of a relationship between host size and number/frequency of epibionts: unparasitized males (Palmahim, May, 2007) bear a higher load of epibionts than unparasitized females, probably reflecting size differences (average CWM 51 mm vs. CWF 32.5 mm) and possibly different intermoult periods. Epibiont and *externae*-bearing male crabs were undersized (average CW 43 mm), whereas epibiont and *externae*-bearing females were larger

**Fig. 10** *Charybdis longicollis* heavily fouled by *Hydroides operculatus* (below) and the turtle barnacle, *Chelonibia patula* (above) Palmahim, May 2007

(average CW 38.7 mm) than unparasitized females and epibiont-bearing internally parasitized females (average CW 33.8 mm) (Innocenti & Galil 2010).

Parasitized crabs with CW smaller than 30.9 mm and unparasitized crabs smaller than 37.4 mm bore no epibionts. The highly infected (>70%) males and females in the spring sample have a lower incidence of epibionts (1.8, 2.0%, respectively). The only specimens bearing multiple *externae* (4, 5 ext., CW 42, 41.5 mm respectively), carried a significantly lower number of epibionts ($G = 13.691$, $df = 2$, $P < 0.01$). It may be that the energy cost of bearing epibionts in addition to multiple *externae* is too large, and such burdened individuals are more likely to perish. The epibiont load of unparasitized crabs in the fall sample is low and probably reflects the short moult interval, whereas the parasitized crabs have a high epibiont prevalence (34.1%) that reflects the rhizocephalan-influenced behavioural changes in the host in limiting grooming and burying. Similar results were recorded by Gaddes and Sumpton (2004) for *P. pelagicus* parasitized by *S. granifera* and fouled by the epizoic stalked barnacle *Octolasmis* ssp.

## 8 Developmental Stages of *Heterosaccus dollfusi*

*Heterosaccus dollfusi* passes through a sequence of developmental stages starting with infection of the host crab by a female cypris larva and terminating with the death of the parasite. Infection results in the formation of an *interna* within the crab's hemocoelic spaces (Høeg and Lützen 1995). The presence of an *interna* can be easily recognized in *C. longicollis* as even at this early stage of parasitization there is a pronounced modification of the abdomen in both sexes. Within the host's abdomen the *interna* forms a bud, which will become the *externa* or the reproductive body of the parasite. The bud, or nucleus, is squeezed between the hindgut and the membranous ventral cuticle of the second or third abdominal segments and is visible through the integument as a pale circular area, approximately 1.5 mm in diameter. When mature, the nucleus breaks through the host's skin. It forms a whitish flattened semicircular disc (up to 2 mm) attached by a short stalk. Emergence of nuclei usually takes place when the crab is comparatively soft-shelled. Small virgin *externae* are considered immature, as long as they lack the presence of male cells in the receptacles (Galil and Lützen 1995; Høeg and Lützen 1995). Immature *externae* of *H. dollfusi* are at first flat and milky-white, but with maturity become increasingly distended and turn cream-colored tan; they may reach a maximum size of 17 mm, but in cases of multiple parasitization of a host, the crowded *externae* develop into the next stage at a far smaller size. The *externa* is considered mature after it has produced its first batch of eggs. This normally happens at a size of 12–13 mm, but in cases of multiple parasitization specimens of 5–6 mm can already be mature. With age, the cuticle of the *externa* turns from yellowish gray through shades of brown into dark brown and at the same time gradually becomes thicker, wrinkled and worn. When the *externa* dies, it withers and drops off, leaving a circular, dark scar of approximately 2.5 mm large, marking the base of the lost stalk of the *externa*. Nuclei occur almost exclusively in the stage immediately following the moult, and so do the large majority of immature *externae*. Old *externae* and presence of scars are always associated to intermoult periods (Høeg et al. 2005). The proportion of nuclei and immature *externae* was twice as large in spring as in fall, whereas mature *externae* and scars were proportionately much more numerous in fall samples. Throughout the year, over 4/5 of apparently mature *externae* were ovigerous. The ovaries of mature *externae* were always full of growing oocytes, permitting repeated ovipositions during the lifetime of the *externa*. Since 1 or 2 days may pass between emission of nauplii and the next oviposition, it is evident that practically all *externae* are reproducing during both spring and fall.

No ageing *externae* were found on freshly moulted crabs, implying that *externa*-bearing crabs are prevented from moulting. Thus the size of an *externa*-bearing crab indicates the size and age of the host at the time the nucleus emerged. Our studies show that emergence of *H. dollfusi* takes place over a wide range of host sizes, from carapace width of 14.8 mm to 61.5 mm in males. Infection therefore occurs across a wide range of sizes, but is much more frequent on smaller-sized crabs (Fig. 11). Differences in the relative number and age of *externae* in spring and fall indicate that emergence occurs mostly in spring, presumably continuing

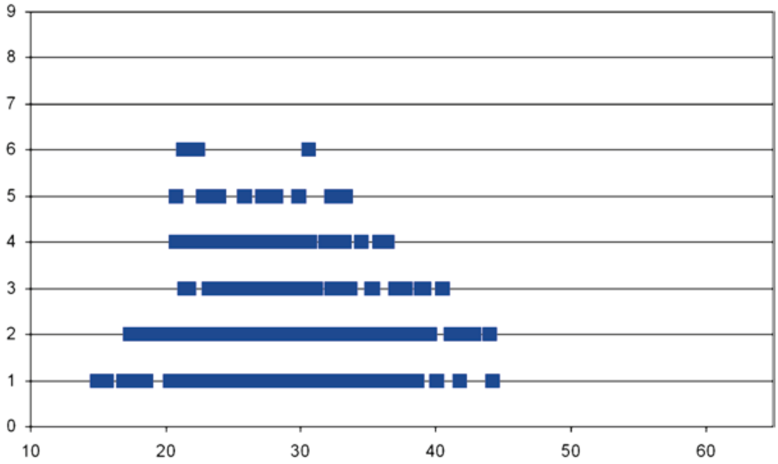

**Fig. 11** Number of *externae* borne by size classes of *Charybdis longicollis* collected off Ashdod, Israel, April 2008. Y axis number of *externae*, X axis, CW size classes (in mm)

throughout the summer, and decreases in the fall. The presence of many mature *externae* makes it likely that a number of *H. dollfusi* live through autumn and winter until next spring in order to produce the male cyprids needed for the maturing of the *externae* that emerge during spring (Galil and Lützen 1995; Høeg and Lützen 1995; Høeg et al. 2005). These are perhaps represented by the few old *externae* present in the spring sample.

## 9 Live and Let Live or, Are Rhizocephalan Barnacles Efficient Biocontrol Agents?

Absence of natural enemies, be it competitors, predators, pathogens, or parasites, is one of the explanations given for the success of alien biota (Wolfe 2002; Torchin et al. 2003). Diminished parasitization of alien species has been attributed to uninfected life-history stages of the originator inoculum, the small numbers of the founding population, the absence of intermediate hosts in the new locale, and host-specificity of native parasites that forestall infection of alien hosts (Hines et al. 1997; Thresher et al. 2000). Yet, though parasite species richness may be lower in alien hosts in their new range, the incidence of parasitization may be many times higher (Galil and Lützen 1995; Hines et al. 1997; Kruse and Hare 2007). Invasive species management benefits from higher infection values by utilizing parasites from the host's home range to reduce the host's populations densities (Hoddle 2004). It has been suggested that biocontrol, involving the introduction of a predator, parasite or pathogen, may present an option for marine pests management (Thresher et al. 2000). Kuris (1974, 1997) suggested parasitic castrators, specifically rhizocephalan barnacles, may be important regulators of host population density, since they inflict reproductive death on their hosts, and proposed their use as control agents for invasive marine decapod crustaceans, provided they are specific to the target host and effectively regulate its population density. Few studies, however, have documented the population dynamics of rhizocephalan barnacles and their hosts; fewer still described the population dynamics of alien rhizocephalan barnacles and their hosts in the region of their introduction (but see Hines et al. 1997; Innocenti and Galil 2007).

The Erythrean invasion presented us with an interesting “field experiment”. *Charybdis longicollis* entered the Mediterranean over half a century ago, but individuals harbouring *H. dollfusi* were collected long after the host crab Mediterranean populations increased in density, affording the parasite increased transmission efficiency. Indeed, though *H. dollfusi* has limited dispersal capabilities, it rapidly infected the Levantine populations of *C. longicollis* (see above). Incidence of parasitization in the latest spring samples exceeds two thirds of the host population and the parasite had not been detected so far in any other portunid crab species inhabiting the Levantine sublittoral, alien or native, including the congeneric *Charybdis helleri* (A. Milne Edwards, 1867), *Portunus segnis* (Forskål, 1775), and the native *P. hastatus* (Linnaeus, 1767). But is it an efficient control agent?

In its second decade in the Levantine Sea, the population of *H. dollfusi* seems stable: despite the prevalence of the parasite and its injurious impact on the host reproduction, the Erythrean invasive host-parasite pair reached a *modus vivendi* with no reduction in the host population, and continuing high rates of parasitization. It is suggested that the high fecundity of the host, the “size refuge” formed by parasite-free larger males, and the “open” recruitment dynamics of *C. longicollis,* keep its population density high enough for *H. dollfusi,* with its “closed” recruitment dynamics, to maintain its pandemic infection rates. This “experiment” acted out along the Levant coast demonstrates that a parasitic rhizocephalan barnacle may not reduce the abundance of an invasive decapod host with widely dispersed planktonic larvae despite high infection rates. It is proposed that these results bear important implications for attempts to utilize rhizocephalan barnacles for biological control of invasive decapods.

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# Invasion History and Success of the American Blue Crab *Callinectes sapidus* in European and Adjacent Waters

**Stefan Nehring**

**Abstract** The first record of the American blue crab *Callinectes sapidus* Rathbun, 1896 from Europe was collected in 1900 on the Atlantic coast of France. Subsequently specimens were detected in the North Sea (1932), Mediterranean Sea (1949, but probably as early as 1935), Baltic Sea (1951), Black Sea (1967), and possibly in the Sea of Azov (1967). It seems that multiple independent introductions may have taken place with ballast water is the most likely introduction vector. In some cases accidental release from holding tanks or intentional release from fishery activities could be involved. Several records may likely be explained also by long-distance migrations of specimens from their primary locations of introduction. But not every introduction was successful over time. Among insufficient habitats and environmental pollution, too low water temperatures seem an important factor for the non establishment of *C. sapidus* especially in northern Europe and in the Black Sea. The American blue crab may benefit from global warming, and there is increasing concern about its ecological and economic impacts. For a definitive assessment an adequate quantification and comparison of documented and potential effects of *C. sapidus* is of considerable importance. Such ambitious task has not been carried out so far.

## 1 Introduction

The American blue crab *Callinectes sapidus* Rathbun, 1896, is native to the Atlantic coast from Nova Scotia, Canada to northern Argentina (Food and Agriculture Organization 2007). Records north of Cape Code, Massachusetts, however, occur only during favourable warm periods (Williams 1984). It is most abundant from

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Texas to Massachusetts Bay, where it forms the base of an important commercial and recreational fishery (Hill et al. 1989). The species lives in estuaries and marine embayments from the water's edge to approximately 90 m, mainly in the shallows to depth of 35 m, on muddy and sandy bottoms. It is extremely euryhaline. Within the native range crabs occupy water ranging from a near-ocean salinity of 34 psu to freshwater in rivers as far as 195 km upstream from the coast. After mating in the upper reaches of estuaries, females move seawards or to nearshore coastal waters to spawn (Hill et al. 1989).

Its presence in high numbers next to well travelled shipping routes made *C. sapidus* a candidate for passive dispersal with shipping. As it is a highly valued seafood, it is conceivable that *C. sapidus* may be intentionally released to form the nucleus of a breeding population of commercial value. Therefore it may have not been a complete surprise to learn that over the past century blue crabs have been observed in Africa, Asia, Europe, far from their native range (e.g., Williams 1974; CIESM 2008). Despite the increasing spread and rising invasion rate, no comprehensive review of the introduction of *C. sapidus* exists. A project inventorying invasive species, funded by the European Commission (DAISIE 2009), attempted to document the species spatial and temporal spread across Europe in the form of a searchable database. However, the data was limited and insufficient. We aim in this chapter to review the presence of *C. sapidus* in European waters and surrounding seas (Fig. 1). The species' possible origin, vectors of introduction, and its potential as an invasive are discussed.

## 2 Spatial and Temporal Trends in European and Adjacent Waters

### *2.1 Atlantic Ocean (Inclusive of English Channel)*

*France* Bouvier (1901) was the first to record *C. sapidus* in Europe. A port official had found, probably in 1900, a live adult male crab in a freshwater basin inside the harbour of Rochefort on the Atlantic coast of France. Not until 60 years later, was a second adult male specimen collected nearby, by a plaice fisherman, in the outer estuary of the River Gironde near Verdon (Amanieu and Le Dantec 1961). Most French records of the species stem from the Seine estuary, Normandy: in the summer of 1973 or 1974 a specimen was observed at Deauville (Vincent 1999), a few specimens were captured by fishermen in the outer Seine estuary and two were collected live in Le Havre harbour (Vincent 1986, 1999), in October 1996 a dead specimen was washed ashore at the Cap de la Hève (Vincent 1999). The most recent record dates back to September 2003 when a specimen was caught near Courseulles-sur-mer (ICES WGITMO 2004). All the above mentioned specimens, but one of indeterminate sex, were males. Few female crabs were recorded: a single specimen was captured at Malo-les-Bains, near Dunkirk, on 17 October 1984, and in September and October 1995 two females, one ovigerous, were collected

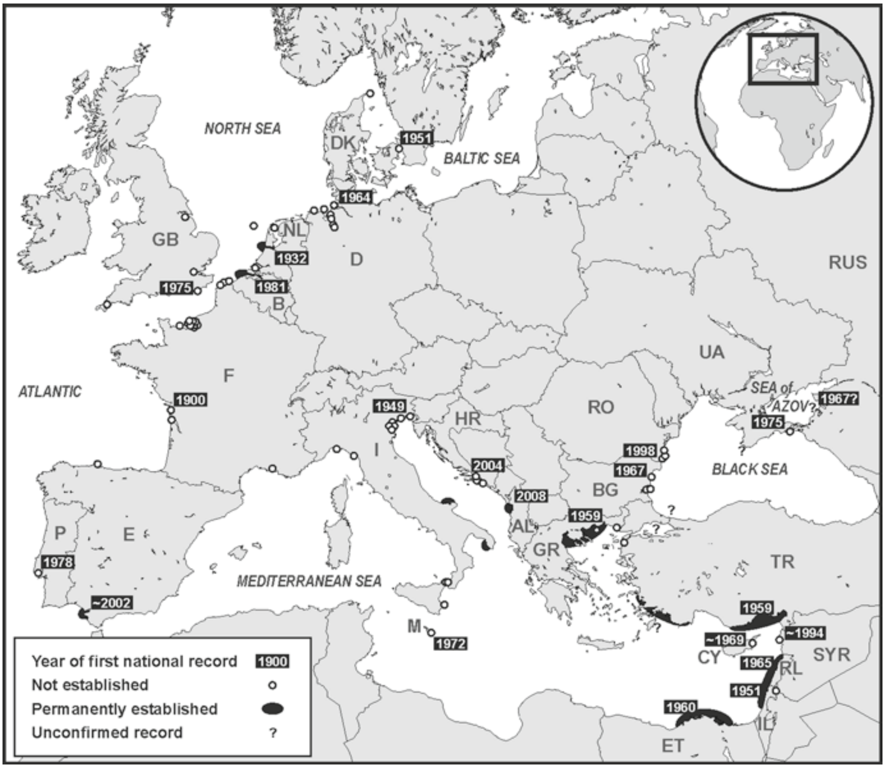

**Fig. 1** Occurrence and year of first legitimized national records of *Callinectes sapidus* Rathbun in European and adjacent waters. Not established: usually single record; permanently established: data support a recent establishment; unconfirmed record: record could not be verified (References see text)

nearby at Gravelines and Bray-Dunes respectively (Vincent 1999). Between 1995 and 2001 several adult specimens were collected along the coast of northern France, including ovigerous females, but no details were kept (ICES WGITMO (2001)). Because of the irregular and sporadic records, *C. sapidus* is considered not to have established a population along the French Atlantic coast, and the rare occurrence of ovigerous females near the Belgian border could be ascribed to established populations there (see following).

*Great Britain* The first British record of *C. sapidus* was trawled off Littlestone-on-Sea, Kent, in September 1975 (Ingle 1980, Clark 1984). On 24 February 2010 a live adult female crab was caught in the Fal estuary, south of Turnaware point (P.F. Clark pers. comm.). Other records from the UK were collected from the North Sea (see following).

*Portugal* The only known record of the species is an adult female specimen collected in January 1978 in the outer estuary of the Tajo at Paco de Arcos, near Lisbon (Gaudencio and Guerra 1979).

*Spain* The species was mentioned as occurring in the estuary of the Guadalquivir, on the southern Atlantic coast of Spain (WWF/Adena 2002). It seems that the species has become established in the Guadalquivir estuary since 2005, though no details were given (ICES WGITMO 2007).

In northern Spain an immature female specimen was collected on 22 September 2004 from the grille of the intake cooling water pipe at a power plant at Port of El Musel, Gijón (Cabal et al. 2006).

## 2.2 North Sea

*Belgium* The first Belgian record of *C. sapidus* dates from November 1981. A dead specimen was discovered in the cooling water system of a chemical plant at Antwerp which water originate in the River Scheldt (Adema 1991). The first live specimen was found by a child on August 1984 at Knokke-Heist, near the harbour of Zeebrugge (Rappé 1985). In October 1993 a male specimen was collected in the artificially heated waters of the cooling system of the nuclear plant at Doel on the inner Scheldt estuary (Van Damme and Maes 1993). At the same site a single blue crab was detected between July 1994 and June 1995 (Maes et al. 1998).

Between 1995 and 2001 several crabs, including ovigerous females, were found in Belgian coastal waters, though no additional information is given (ICES WGITMO 2001). In November 2002 an adult male crab was fished off Oostende (ICES WGITMO 2003). Between August and November 2004 an adult male and three female specimens, one of which ovigerous, were caught by shrimp fishermen in the Western Scheldt estuary and transferred to public aquaria (Kerckhof and Haelters 2005). Between July and October 2006 at least seven female specimens including several ovigerous specimens were brought in by shrimp fishermen. They related that additional specimens have been fished, and indeed, several dried specimens are on exhibit in the Nieuwpoort fishmarket (ICES WGITMO 2007, F. Kerckhof pers. comm.). It seems plausible that since the 1990s a resident population exists in the coastal waters and in the Scheldt estuary (ICES WGITMO 2001; Kerckhof et al. 2007), perhaps connected with the established population in the Dutch part of the Western Scheldt estuary (see following).

*Germany* The first record from Germany was a specimen caught in the outer estuary of the Elbe near Cuxhaven in September 1964 (Kühl 1965). Several records stem from the Weser estuary: a specimen was caught, probably in 1965, near Blexen, between the outer and inner Weser estuary (Nehring et al. 2008), two specimens were found in 1990 in the cooling water inlet of a power station at Bremen harbour on the inner Weser estuary (Nehring et al. 2008), and in November 1998 an adult was caught in an eel pot together with several Chinese mitten crabs (*Eriocheir sinensis* H. Milne Edwards, 1853) in the inner part of the Weser estuary (Geiter 2000). All but one crab of undetermined sex were male crabs. The first recorded adult female was caught by a shrimp fisherman in the outer Weser estuary on 20 July 2007 (Nehring et al. 2008). The most recent female specimen was

**Fig. 2** Mature female of *Callinectes sapidus* Rathbun, 1896 caught in the German Wadden Sea on 26th of Mai 2008. Carapace width 16.5 and 12.5 cm excluding the longest lateral spines. The carapace is covered by specimens of the circumpolar barnacle *Balanus crenatus* Bruguière, 1789 (Photo by M. Kröger)

collected on 26 May 2008 by a shrimp fisherman in the East Frisian Wadden Sea at the Accumersieler Balje, the tidal inlet between the German islands Baltrum and Langeoog (Fig. 2). The female, kept in a public marine aquarium at 30 psu and 19°C, laid on the14th day millions of eggs, which hatched after 2 weeks (Nehring and van der Meer 2010). As a successfully reproducing population had not been observed so far, *C. sapidus* is considered as non established alien species (Gollasch and Nehring 2006; Nehring and van der Meer 2010). Crabs found on the German North Sea coast may stem from established populations of the species in the Netherlands (see following).

*Great Britain* On 18 August 1982 a male was collected by an angler from Dunham Bridge, approximately 38 miles up the River Trent, a tributary of the Humber (Clark 1984). A single specimen was caught, probably in 2000, by an eel fisherman in the River Thames near Erith (P.F. Clark pers. comm.).

*The Netherlands* The first Dutch records consist of two female specimens, one taken on 10 September 1932 in the River Zaan near Zaandam, northwest of Amsterdam, and the other collected in December 1934 in Amsterdam harbour (Den Hartog and Holthuis 1951). The authors mention two boiled specimens, male and female, washed ashore near Vlissingen on August 1950. A live specimen was collected from the Noordzeekanaal at Nauerna in July 1951, and four dead specimens washed ashore at Schiermonnikoog on 7 May 1967 (Holthuis 1969). Both live and dead crabs have been found sporadically in Dutch coastal waters over the next decades: dates, locations, sex and conditions are summarized by Adema (1983, 1991), Craeymeersch and Kamermans (1996), ICES WGITMO (2000, 2001, 2006) and Wolff (2005). It should be noted that ovigerous females were found in 1982, 1999 and 2000. In the ports of Amsterdam, Hoek van Holland and Rotterdam specimens of *C. sapidus* are recorded each year since 1995, though detailed information is lacking. In 2002 a first blue crab was observed by a diver in the Eastern Scheldt estuary near the storm surge barrier (Anonymous 2003). The frequency and the increased number of records, including ovigerous females, suggest that *C. sapidus* has become established in the Western Scheldt estuary and adjacent waters as well as the Noordzeekanaal between Amsterdam and the North Sea since the 1990s (ICES WGITMO 2000,ICES WGITMO 2001;Wolff 2005). It is likely the population in the Western Scheldt estuary is part of the established population found in the Scheldt estuary and coastal waters of Belgium. The recent occasional records in the Dutch Wadden Sea and the German North Sea coast could be connected with the established population in the Noordzeekanaal.

## 2.3 Baltic Sea

*Denmark* Only two records are known from Danish waters: on 20 September 1951 a female was captured by a plaice net northeast of Copenhagen and kept alive for a year in a public aquarium (Wolff 1954), in 2007 an adult male was caught off Skagen, Northern Jutland, between the Kattegat and the Skagerrak (Tendal and Flintegaard 2007).

## 2.4 Mediterranean Sea

*Albania* The first record dates to 2008: a female crab was found in Patok Lagoon, near the border with Montenegro (White et al. 2009). Referring to pers. comm. with local fishermen, *C. sapidus* was probably introduced in 2006 (Beqiraj and Kashta 2010). In the first years the species was not abundant, while during 2009 its abundance was highly increased. During April and October 2009 a daily average of 40–50 individuals were caught in a 300 m gillnet (Beqiraj and Kashta 2010). The authors conclude that there is a self-maintaining population in Patok Lagoon.

*Croatia* The first record was a male crab collected from a fish trap set in the Neretva estuary in October 2004, another specimen was collected by gillnet in the same location on 6 December 2006. On 15 October 2004 two females and two males were caught in a hypersaline lagoon on the Pelješac peninsula near Ston (Onofri et al. 2008). The authors suggest sufficient information has not been gathered yet to deduce whether *C. sapidus* has established a population in the area.

*Cyprus* Demetropoulos and Neocleous (1969) reported occasional occurrence of the crab along the southeast coast of Cyprus, between Cape Andreas and Cape

Greco. Lewinsohn and Holthuis (1986) reported one preserved and two live specimens from Cypriot waters, though no dates or localities were given. No other Cypriot records of this species are known.

*Egypt* Banoub (1963) reported that blue crabs had been first recorded in the 1940 fisheries statistics of Lake Menzela. However, at that time the catches of *C. sapidus* had not been split from those of swimming crabs of the *Portunus pelagicus* species complex, and this confusion has persisted in literature (Williams 1974; Lai et al. 2010). The first confidently identified specimens of *C. sapidus* were collected in Lake Edku in January 1960 (Banoub 1963). In the 1960s it was mostly caught by fish-traps in the brackish Nile delta lakes and only rarely from the adjacent coast (Ramadan and Dowidar 1972). Their annual catch peaked in 1964 (2,413 tons), subsequent catches plummeting: in 1971 only 8 tons were fished, possibly because the construction of the High Dam at Aswan altered the hydrology of the delta (Ramadan and Dowidar 1972). The decline worsened in the following years, but has since the 1980s partially recovered (Abdel-Razec 1987). Though no records have been published in recent years, it is believe that population persists.

*France* A single record is known from the French Mediterranean coast: on 1 October 1962 a single specimen was found in the Etang de Berre, near Marseille (CIESM 2008; H. Zibrowius pers. comm.).

*Greece* A survey among fishermen implied that at least since 1935 the crabs have occurred in the Gulf of Thessaloniki, and that since 1952 they have been sold regularly at the markets of Athens, Kavala, Piraeus and Thessaloniki, but catches have dwindled since 1963 probably due to overfishing and pollution (Georgiadis and Georgiadis 1974). In 1971 a single dead specimen was found in the Gallikos estuary, and nearby a fisherman caught 4 kg blue crabs. In the region of Alexandropolis and the lagoons of Thraki the crabs disappeared between 1978 and 1982, probably for similar reasons (Enzenroß et al. 1997). However Serbetis (1959) maintains that *C. sapidus* was first observed in 1948 in the Peneios estuary, in the Gulf of Thessaloniki, and has spread only since 1954 in the northern Aegean Sea. The first confidently identified specimens, an adult and a juvenile female, were collected on 29 June 1959 near Porto Lago harbour, on the Aegean coast (Holthuis 1961). Between March 1963 and May 1965 many live and dead specimens were observed in the estuaries and the lagoons of the northern Aegean Sea (Kinzelbach 1965). Unlabelled and badly preserved specimens were reported from a collection on Rhodes (Kinzelbach 1965), and a single unconfirmed record from the southern Aegean Sea exists (Kevrekidis and Galil 2003).

Specimens infested with a rhizocephalan parasite were rejected by the housewives shopping for seafood (Kinzelbach 1965). Boschma (1972) identified the parasite, without examination, as *Loxothylacus texanus* Boschma, 1933, known from the American populations.

Though the population of *C. sapidus* has been decimated, it is considered as established especially in the northern Aegean Sea (Pancucci-Papadopoulou et al. 2005).

*Israel* The first Israeli records, three males and a female, were collected on November 1951 in the Heftsi-Bah estuary, near Hadera (Holthuis and Gottlieb 1955). These authors reported the finding of many specimens from the Na'aman estuary, near Acre, the Dalia estuary, near Tantura, and in Haifa Bay, and proposed that their abundance and the presence of ovigerous females indicate that *C. sapidus* has become established along the coast. In the following decades blue crabs had been regularly collected along the Israeli coast near estuaries and in brackish fish ponds (Snovsky and Galil 1990). Analysis of zooplankton samples collected along the coast between the years 1961 and 1968 showed blue crab larvae peak in April and are less abundant in May, July and September (Galil 1993). The larval contingent clearly demonstrates that *C. sapidus* has indeed assimilated within the local coastal fauna.

Though unable to reproduce in freshwater, the crab has been reported from inland water: a single adult specimen was collected by gillnet in the Sea of Galilee on October 1989 (Snovsky and Galil 1990). The authors assume that its occurrence in the freshwater lake was an accidental introduction with mugilid juveniles transported from the Mediterranean Sea to stock the lake.

*Italy* The first record of *C. sapidus* in the Mediterranean Sea is commonly ascribed to Giordani Soika (1951) (e.g., by Enzenroß et al. 1997; CIESM 2008). That author reported two specimens: an adult female collected off Caorle, north of Venice in December 1949, and a adult male from the lagoon of Venice, near Fusina, collected on 10 October 1950; he identified as *Neptunus pelagicus* A. Milne-Edwards, 1861 (syn. *Portunus pelagicus* (L.)), but which have been later identified by Holthuis (1961) based on Giordani Soika's description and illustration as *C. sapidus*. Mizzan (1993) identified two specimens of *C. sapidus* labelled as *N. pelagicus* he found in the zoological collections of the Natural History Museum of Venice as those originally recorded by Giordani Soika. However, the sampling sites and dates of the specimens differ from those stated by Giordani Soika (1951) the female crab was collected near Marina di Grado on 4 October 1949, and the male in Venice lagoon on 8 October 1950. Since that female was collected earlier than the one cited by Giordani Soika, it seems that the first confirmed record of the Mediterranean should be ascribed to Mizzan (1993), though there are claims to its presence in the Aegean as early as 1935. Additional specimens were collected in the lagoon in October 1991 and 1992 (Mizzan 1993), though not in the following years, so Mizzan (1999) concluded that *C. sapidus* has not established a population there. In the collections of the Museum, Mizzan (1993) also found out a male of *C. danae* Smith, 1869 which is native to Western Atlantic from Florida to Argentina (Rathbun 1930). It had been caught in Venice Lagoon on 6 September 1981.

Blue crabs have been recorded from the brackish lagoons on the Adriatic coast of Apulia: from Varano lagoon in the summer of 2007 and from Lesina lagoon between June and October 2007 (Florio et al. 2008). A specimen was collected also near Lecce on the Salento peninsula where it was caught by fishermen in January 2001. Subsequent records attest to the gradual increase of population and it's attraction to many stakeholders (Gennaio et al. 2006). It seems that *C. sapidus* endures in these large brackish basins in southern Italy.

Ghisotti (1966) and Torchio (1967) had published records of *C. sapidus* from Sicily, however, the specimens were sent for verification and identified as *N. pelagicus* (Holthuis 1969). Shortly thereafter, in spring 1970, a female *C. sapidus* was found near the harbour of Messina, and another female was fished nearby in autumn 1972 (Cavaliere and Berdar 1975). Trawling surveys off the eastern coast of Sicily between 1988 and 1990 collected *C. sapidus* though details are missing (Franceschini et al. 1993). Pipitone and Arculeo (2003) doubt the establishment of the species in Sicilian waters.

Only three specimens are known from the Ligurian Sea: two specimens from the port of Genoa and the surrounding waters collected in 1962, and a large male caught in a fish trap near La Spezia, in the Gulf of Genoa in 1965 (Tortonese 1965).

*Lebanon* The first record collected from St. George Bay, Beirut, in 1965 and consisted of 1 male and 12 females, 3 ovigerous (George and Athanassiou 1965). The authors judged the crab quite abundant as it featured prominently in the local fish markets and roadside stands. Local fishermen claimed the species had been in Lebanon for at least the previous 5 years (George and Athanassiou 1965). This information corresponds with an unverified observation by the authors that a throw net fisherman caught blue crabs on 17 February 1964 in the Kebir estuary, in northern Lebanon. Shiber (1981) examined a specimen which was collected off Antelias, near Beirut, on 15 April 1965. Serbetis (1959) reported blue crabs from the markets of Beirut, but Holthuis (pers. comm. in Shiber 1981) suggested that the colour of his specimens indicates they may have been *N. pelagicus*. The frequent records in the 1960s have allowed an established population in the coastal waters of Lebanon (George and Athanassiou 1965). Though no recent records are known, it may still exists there, as it does off the Israeli coast.

*Malta* Two male specimens were trapped in Marsaxlokk Bay on 20 November 1972 (Schembri and Lanfranco 1984). No other Maltese specimens have been found (P.J. Schembri pers. comm.).

*Syria* Saker and Farah (1994, cited by CIESM 2008) report the species off Lattakia, though no details were given and no information about the status of the population of this species is available. Today blue crabs are sold in Syrian markets, however, their origin is unknown (P.Y. Noël pers. comm.). Possibly the population is connected with the established populations along the Lebanese and Turkish coasts.

*Turkey* Artüz (1990) affirmed *C. sapidus* was introduced intentionally between 1935 and 1945 into the northern Aegean Sea, particularly into the Gulf of Saros (Turkey) and in the Gulf of Thessaloniki (Greece). It initially did well but was later displaced to the southern Aegean and gradually came to occupy the Turkish Mediterranean coast. Serbetis (1959) mentioned that the crabs were caught in a lagoon on the Turkish coast off Samos in 1947. However, the narrative of intentional introduction has not verified. The first specimens of *C. sapidus* firmly recorded from Turkey were four males and two females collected in brackish Lake Akyatan near the border with Syria in May 1959 (Holthuis 1961).

The distribution and abundance of records between 1985 and 1995 show that it was well established in at least 15 lagoons, estuaries and bays on the Levantine and Aegean coasts (Enzenroß et al. 1997). In most locations the crabs were fished commercially. In the early 2000s about 200 tons were sold annually, but since 2003 its catches diminished substantially to only 17 tons in 2008 (Anonymous 2009). Overfishing, pollution, epidemic or combinations thereof are blamed: the "black spot disease" was observed in spring 1995 at some locations (Enzenroß et al. 1997).

References to the presence of the species in the Sea of Marmara remain as yet unconfirmed (e.g., Zaitsev and Öztürk 2001; Tuncer and Bilgin 2008). Müller (1986), referring to Georgiadis and Georgiadis (1974), assumed that the crabs offered for sale in the fish markets of Istanbul had been fished in the Marmara Sea. However, they were in all likelihood fished in the Aegean Sea or imported from Greece. Though recently, in November 2008, an adult female was collected with gillnet off Canakkale, the Dardanelles (Tuncer and Bilgin 2008).

## *2.5 Black Sea*

*Bulgaria* The first record in the Black Sea was an adult female caught in October 1967 in the western part of Varna Bay, near Asparuchowo (Bulgurkov 1968). In 1984, a second specimen was found (Zaitsev and Öztürk 2001). The most recent record dates to August 2006. A single specimen was caught by a fisherman in his net while fishing off Burgas (Anonymous 2006). The intermittent records may signify the species has not yet established a population.

*Romania* On 23 August 1998 an adult male was collected off Mangalia, near the border with Bulgaria and an adult female caught in a tuna trap on 8 October 1999 nearby (Petrescu et al. 2000). Another female was captured off Agigea in 2000 (Micu and Micu 2006). The authors conclude that there is no self-maintaining population along the Romanian coast of the Black Sea.

*Turkey* Özturk (pers. comm. in Zaitsev and Mamaev 1997) recorded the species from the Bosphorus. But a more recent check-list of the crustacean fauna of the Bosphorus fails to list it (Balkis et al. 2002).

*Ukraine* The first record is based on a male specimen caught in the Kerch Strait near Bolshoi Utrish Cape in June 1975 (Monin 1984). In 1980s *C. sapidus* was recorded at the Crimean coast (Revkov 2003). It has been recently reported increasingly abundant nearshore off Sevastopol (Shiganova 2008), but the report could not be verified. It remains unclear whether the species had established a population in the area.

## *2.6 Sea of Azov*

*Russia Callinectes sapidus* was recorded in the Sea of Azov in 1967 (DAISIE 2009), though the record remained unverified.

## 3 Pathways of Introduction

Although *C. sapidus* has been repeatedly collected over the past century in many locations in European seas, it is unknown how the species had arrived in Europe. It is proposed that multiple independent introductions had taken place, possibly utilizing different pathways, even to the same sites.

Already Bouvier (1901), who published the first occurrence of the species in Europe, has speculated on the manner of its arrival. The specimen could have arrived in the harbour of Rochefort through shipping, in a ship's boat or in a corner full of water, or in vessels' fouling community. However, it is unlikely the crab with its affinity to brackish water would cross oceans on ships' hulls or as suggested by Wolff (1954) with floating seaweeds. The later pathway would also fail to explain the presence of the crabs in remote areas such as the northern Adriatic, eastern Mediterranean or Black Sea. Transport in ballast tanks is considered the most likely vector because, in its native range, *C. sapidus* is abundant next to major shipping routes and had been found in its introduced range initially in or nearby ports, where ballast water are discharged (cf. Wolff 1954; Holthuis and Gottlieb 1955). Direct evidence was supplied recently, when three living specimens had been found in ballast tanks but none on ships' hulls (Gollasch 1996). During ballast intake, juveniles, or more likely, planktonic larvae, maybe by swept in with the water (Holthuis and Gottlieb 1955; Mizzan 1993). As the larval development of *C. sapidus* lasts from about 37–69 days (Hill et al. 1989), long enough to make vessel transport plausible. In other cases, different transport mechanisms could be involved. The species, commercially valuable (from *sapidus* (Latin) = "savory"), may have been introduced intentionally or has been accidentally released from holding tanks in which live crabs had been imported for human consumption or for the aquarium trade (ICES WGITMO 2006). Records of intact but boiled specimens on the Dutch North Sea coast (Wolff 2005), seem to indicate that *C. sapidus* is consumed aboard vessels, and it is possible that leftovers (boiled or live specimens) were thrown overboard (cf. Nehring et al. 2008).

*Callinectes sapidus* is most valuable in commercial fisheries, providing a highly acceptable, nutritious product worth several million dollars annually in the USA alone. Consequently the intentional release of blue crabs into Europe to support a fishery should not be excluded as suggested by Artüz (1990) it for the northern Aegean Sea. However, our knowledge about worldwide transfers of blue crabs (and other alien species) inclusive evidences for their ultimately fates is extremely limited so far. An improvement of providing of specific data is indispensable for a forward-looking alien management.

Beyond the initial human-mediated introduction, the rapid and widespread dispersal from the areas of introduction may also be an important factor in arriving new habitats in broader environs. Among larval transport by water currents, occasional records of adult blue crabs in new areas may likely be explained in some cases by long-distance migrations of blue crabs from areas of their established populations – like in case of records of adult specimens of the Chinese mitten crab *Eriocheir sinensis* in the Baltic (Ojaveer et al. 2007). Hill et al. (1989) underline that adult blue crabs are excellent swimmers and can migrate long distances over the sea bottom (Stimpson erected the Genus *Callinectes* in 1860 and derived it from *calos* (Greek) = *strenuus* (Latin) = "strenuous" and *nectes* (Greek) = *natator* (Latin) = "swimmer"). Especially female blue crabs can move several hundred kilometers (Hill et al. 1989), wherein just fertilized or ovigerous females have an enhanced potential for bio-contamination of new habitats. A passive dispersal of juvenile or adult specimens of *C. sapidus* as hitchhikers on ships' hulls is also possible, but probably for relatively short distances only.

In general, the invasion history of *C. sapidus* in European and adjacent waters is unknown in detail up to now. However, identification of source populations and reconstruction of possible pathways of invasion are key issues in our understanding of the invasion process and especially in the design of effective measures to minimise introduction and spreading of alien species. Molecular markers provide effective tools to investigate invasion histories, as actually shown for the occurrence of *E. sinensis* in European and North American waters (Hänfling et al. 2002). Conducting genetic analyses based on older voucher as well as on living specimens from different native and non native occurrences would be an important step for understanding the invasion history of *C. sapidus* in its introduced range.

## 4 Factors for Establishment

Brackish waters are characterized by the lowest number of indigenous species ("Artenminimum" *sensu* Remane 1934) and seem to have many open ecological niches (Nehring 2006). But brackish waters are often exposed to intensive international ship traffic, one of the most important vectors for aquatic alien species. Thus, these habitats have the highest potential for species introductions (Nehring 2006). *Callinectes sapidus* is a typical brackish water species, necessitates the presence of estuaries or lagoons which are necessary environments for the completion of its life-cycle. It tolerates salinities ranging from freshwater to hypersaline, but growth of megalopae and small juvenile crabs may be normal at salinities of 5 psu (Hill et al. 1989). Blue crabs are more tolerant of low temperatures than are many other species of fishes and shrimp, however, according to laboratory experiments development of blue crab larvae requires water temperatures of more than 21°C (Hill et al. 1989). So it's no wonder that since 1900 *C. sapidus* could establish populations in several utilizable European and adjacent waters, in some cases supported by waters artificially warmed by power plants (Table 1). But not every introduction was successfully in the long run. Among insufficient habitats and environmental pollution, too low water temperatures seem an important factor for the non establishment of *C. sapidus* especially in northern Europe and in the Black Sea. However, indications suggest that water temperatures will become warmer due to continuing climate change (e.g., Mackenzie and Schiedek 2007). In consequence, the temperature regime will probably become more favourable for blue crabs in not yet occupied areas in the near future.

**Table 1** Occurrence of *Callinectes sapidus* Rathbun in European and adjacent waters. Status: recorded along most of the coasts (+++), in part of the area (++), at one or a few localities (+)

| Country | Region | First legitimized record | Status | Establishment | Main reference |
|---|---|---|---|---|---|
| Albania | Mediterranean Sea | 2008[a] | + | Since 2006[a] | Beqiraj and Kashta (2010) |
| Belgium | North Sea | Nov 1981 | ++ | Since 1990s | Kerckhof et al. (2007) |
| Bulgaria | Black Sea | 2 Oct 1967 | + | None | Petrescu et al. (2000) |
| Croatia | Mediterranean Sea | 1 Oct 2004 | + | None | Onofri et al. (2008) |
| Cyprus | Mediterranean Sea | ~1969 | + | None | Lewinsohn and Holthuis (1986) |
| Denmark | Baltic Sea | 20 Sep 1951 | + | None | Tendal and Flintegaard (2007) |
| Egypt | Mediterranean Sea | Jan 1960[b] | ++ | Since 1940[b] | Abdel-Razec (1987) |
| France | Atlantic Ocean | 1900 | + | None | Vincent (1999) |
| France | Mediterranean Sea | 1 Oct 1962 | + | None | CIESM (2008) |
| Germany | North Sea | 12 Sep 1964 | + | None | Nehring et al. (2008) |
| Great Britain | Atlantic Ocean | Sep 1975 | + | None | Clark (1984) |
| Great Britain | North Sea | 18 Aug 1982 | + | None | Clark (1984) |
| Greece | Mediterranean Sea | 29 Jun 1959[c] | ++ | Since 1935[c] | Pancucci-Papadopoulou et al. (2005) |
| Israel | Mediterranean Sea | 21 Nov 1951 | +++ | Since 1950s | Holthuis and Gottlieb (1955) |
| Italy | Mediterranean Sea | 4 Oct 1949 | ++ | Since 2000 | Florio et al. (2008) |
| Lebanon | Mediterranean Sea | 11 Feb 1965 | +++ | Since 1965 | Shiber (1981) |
| Malta | Mediterranean Sea | 20 Nov 1972 | + | None | Schembri and Lanfranco (1984) |
| Portugal | Atlantic Ocean | 1 Jan 1978 | + | None | Gaudencio and Guerra (1979) |
| Russia | Sea of Azov | 1967? | ? | None | DAISIE (2009) |
| Spain | Atlantic Ocean | ~2002 | + | Since 2005 | ICES WGITMO (2007) |
| Syria | Mediterranean Sea | ~1994 | ? | Unknown | CIESM (2008) |
| The Netherlands | North Sea | 10 Sep 1932 | ++ | Since 1990s | Wolff (2005) |
| Turkey | Mediterranean Sea | 18 May 1959[d] | ++ | Since 1940s[d] | Enzenroß et al. (1997) |
| Turkey | Black Sea | ? | (?) | None | Zaitsev and Mamaev (1997) |
| Ukraine | Black Sea | Jun 1975 | + | Unknown | Monin (1984) |

[a] Probably introduced 2006

[b] Probably introduced longer or shorter before 1940

[c] Probably introduced 1935

[d] Probably introduced between 1935 and 1945

*1967?* first legitimized record in 1967 unverified, *?* status unknown, (*?*) first legitimized record unknown

## 5 Ecological and Economic Impacts

Together with r-selected life history traits (high fecundity and dispersal capacity, fast growth), the broad environmental tolerances predispose *C. sapidus* as a likely successful invader (Hill et al. 1989). Blue crabs perform a variety of ecosystem functions and can play a major role in energy transfer within estuaries and lagoons. At various stages in the life cycle, blue crabs serve as both prey and as consumers of plankton, small invertebrates, fish, and other crabs. They are important detritivores and scavengers and, if food is in short supply, even also cannibals (Hill et al. 1989). They are aggressive towards other species, and compete with other crabs for food and space (Gennaio et al. 2006; Nehring et al. 2008). *Callinectes sapidus* is also a host to several parasites and diseases, some with a high potential to cause mass mortalities (Messick and Sindermann 1992). Thus the introduction of blue crabs can have significant consequences to the ecology of the invaded environments. Despite the nomination of *C. sapidus* as one of the 100 'Worst Invasive Alien species in the Mediterranean' (Streftaris and Zenetos 2006), up to now the definite long term impacts of *C. sapidus* to non-native environments are unknown although since decades this alien species has established distinct permanent populations especially in the eastern Mediterranean Sea where particularly high abundances of blue crabs could be observed. Intensified research in this field should be undertaken.

*Callinectes sapidus* supports an important fishery in its native range along the Atlantic coast of North-America as well as in its introduced range in the eastern Mediterranean Sea. However, due to climate change and its supposed positive effects on the occurrence of blue crabs, *C. sapidus* might well become a candidate for a target species in commercial fishery elsewhere. This could be a real scenario for example in the Adriatic Sea, at the European Atlantic coast and in the North Sea. Otherwise in this context it will be an interesting question whether *C. sapidus* will significantly reduce stocks of the introduced Pacific oyster (*Crassostrea gigas*), which is commercially used in several European countries because adult blue crabs prefer molluscs such as oysters as their primary food sources (Hill et al. 1989). Blue crabs are reported to mutilate fish caught in traps and trammel nets, and tear those nets (Banoub 1963; Beqiraj & Kashta 2010). The occurrence of *C. sapidus* could be also an important harmful factor in the human health system as well as in the tourism sector because blue crabs have been implicated as carriers of strains of the bacterium *Vibrio cholerae* which are responsible for outbreaks of human cholera (Hill et al. 1989). However, comprehensive analyses about the economic benefits and disadvantages of *C. sapidus* in its introduced range are not done so far. This should be put into action now.

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# The Introduced American Lobster, *Homarus americanus* in Scandinavian Waters

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**Abstract** Transport of live American lobsters to Scandinavia serves as a vector of introduction as specimens inevitably escape or are released into local waters. The presence of live American lobster in Norwegian waters has raised concerns about disease transfer, ecological interactions and hybridisation with the European lobster. Since 2000, 91 specimens were collected. These were morphologically examined, as well as analysed for genetic characteristics. Diagnostic DNA methods based on microsatellites were developed and have been in use since 2000 to resolve problems stemming from overlapping morphological characters. Based on DNA profiles, 24 of the 91 were identified as American lobsters, in Norway found from Oslofjord in the eastern part and along the southern and western coastline north to the Møre region. Recently American lobsters were also found in Danish and Swedish waters. The remaining specimens, though morphologically similar to the American lobster, had a typical DNA profile of the European species. Several American lobster specimens were egg-carrying, but so far, no evidence for hybridisation has been found. The local lobster fishery should be carefully monitored to detect specimens *H. americanus*, and signs of Gaffkemia and shell disease in the native population investigated. Tighter controls should be enforced on holding live imports to reduce the likelihood of escape and release.

**Keywords** American lobster • Scandinavia • DNA identification • Geographic distribution • Interspecific competition • Disease transfer

## 1 Introduction

The two species of clawed lobster, *Homarus americanus* H. Milne Edwards, 1837 and *H. gammarus* (Linnaeus, 1758), are similar in morphology, life history pattern and ecological preferences. They are however separated geographically

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by the Atlantic Ocean. In the western Atlantic, the harvest of American lobster increased substantially in the 1980s to 70,000–80,000 metric ton annually, while the annual fishery for lobsters in the eastern Atlantic is only 2,500–3,000 metric ton. The fishery of the native lobster, *H. gammarus*, has a long tradition in Norway, especially along its southern coast (Appelöf 1909; Agnalt et al. 2007; Agnalt 2008). Large fluctuations in the harvest have been observed, but before the World War II the landings contributed from 30% to 40% of the total harvest of lobster in Europe (Dow 1980; Browne et al. 2001; Agnalt et al. 2007). The Norwegian lobster fishery collapsed between 1960 and 1970, and the official harvest has remained at 30–50 ton annually. In Norway, the native lobster populations are close to depletion (Agnalt et al. 2007).

Along with the decrease in the lobster fishery, importation of live American lobster, *H. americanus*, from the United States and Canada has increased. Such import started already in the late 1950s, and from 1999 onward, about 250 ton have been imported annually to the Scandinavian countries (van der Meeren et al. 2004). The importation of live specimens unavoidably leads to unintentional releases into the wild (Carlton 1985, 2002). The presence of American lobster specimens in Scandinavian waters may raise the risk of disease introductions that may affect populations of the native lobster (Staveland and Kjos-Hansen 1978; Egidius 1978).

Many introduced crustacean species have successfully adapted to their new environment. The red king crab, *Paralithodes camschaticus* (Tilesius, 1815), was transferred from Sea of Japan to the northeast Atlantic in the 1960s and 1970s, in order to establish a new commercial fishery (Orlov and Karpevich 1965; Orlov and Ivanov 1978). The species has since greatly increased its abundance and expanded its range (Kuzmin et al. 1996; Sundet and Hjelset 2002; Nilssen and Sundet 2006; Hjelset et al. 2009). Potential ecological impacts were discussed in Jørstad et al. (2002), and more detailed studies were carried out, focusing on predation on benthic fauna such as e.g., scallops, *Chlamys islandica* (Jørgensen 2005; Jørgensen and Primicero 2007). Another example is the green crab, *Carcinus maenas* (Linnaeus, 1758), that has been unintentionally worldwide introduced (Grosholz and Ruiz 1996; Furlani 1996). This crab too seems to adapt rapidly to new environments, and aggressively competes for food, shelter and habitat with significant ecological consequences (Cohen et al. 1995; MacDonald et al. 2007; Tanner 2007; Griffen and Byers 2009), including competition with juvenile American lobster (Williams et al. 2006; Rossong et al. 2006).

Initially, the main concern regarding the commercial import of American lobster (see Fig. 1 for distribution areas) into Europe was the risk of disease transfer to the native lobster (Håstein et al. 1977; Egidius 1978). Recently, concerns have been expressed also regarding interspecific competition since both habitat and food preferences are similar. If established as a viable and reproductive species in Europe, the larger size American lobsters will represent a threat to the European lobster as well as other crustacean such as Norway lobsters (*Nephrops norwegicus*) and crab species (van der Meeren et al. 2000; Jørstad et al. 2007). The ecological consequences of permanent establishment are uncertain. In this contribution we summarize our findings from 2001 to 2009, and discuss the problems of Gaffkemia and shell disease, the likelihood of hybridization, interspecific competition and potential ecological effects.

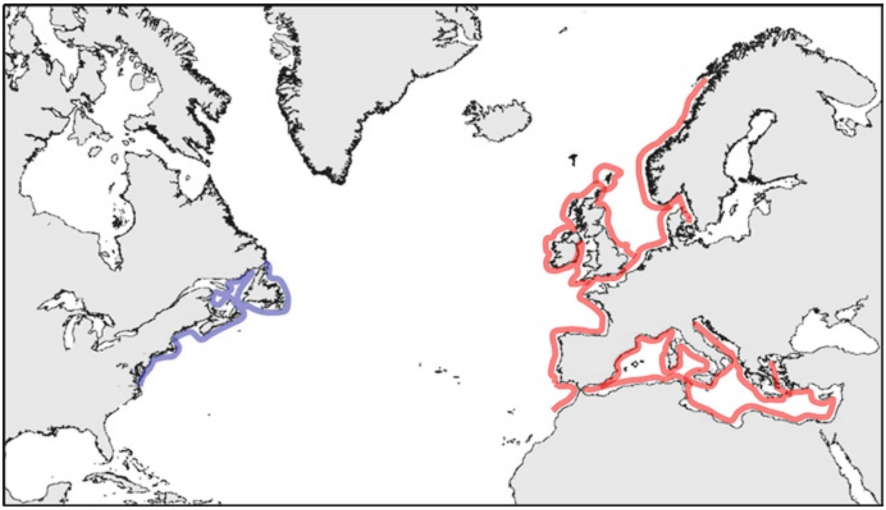


**Fig. 1** Natural geographic distributions areas for American lobster, *Homarus americanus* (in *blue*) and European lobsters, *Homarus gammarus* (in *red*)

## 2 Morphological and Genetic Differences

The first American lobster was caught in the Oslofjord in 1999 (van der Meeren et al. 2000). The classification was based on morphological characterization, mainly colour and presence of ventral rostral spines. *Homarus americanus* is characterized by "Color dark bluish green to brownish olive mottled with very dark greenish black spots, often almost black, pleura with reddish tips", while *H. gammarus* is "often bluish to bluish black dorsally, with white tracings or mottlings on the carapace and the abdomen dorsally. Chelipeds have white tubercles; chelae may be suffused with orange tints and walking legs are lighter blue. The whole body may be much lighter in colour, and under parts may appear yellowish or white" (after Williams 1995). The most obvious morphological difference is the presence of a well-developed subrostral tooth or spine on the ventral rostral margin of *H. americanus* that is absent from *H. gammarus* (Holthuis 1991).

The morphological characteristics, including colour variation of European lobster populations have been observed (Ferguson 2002; Agnalt 2008). Significant colour variations were demonstrated, including colour patterns comparable to American lobsters. The typical colour pattern for American and European lobsters from Norway are shown (Fig. 2). Intermediate colour patterns occur (Fig. 2b). Some European lobsters are, however, quite similar in appearance to the American species, and the presence of subrostral spines is not a definitive character (Devescovi and Luca 2000) Therefore, development of genetic methods was needed to tell the species apart (Jørstad et al. 2007).

Genetic differences, as differences in allele frequencies, have been described for allozymes (Hedgecock et al. 1977) and microsatellites (Tam and Kornfield 1996;

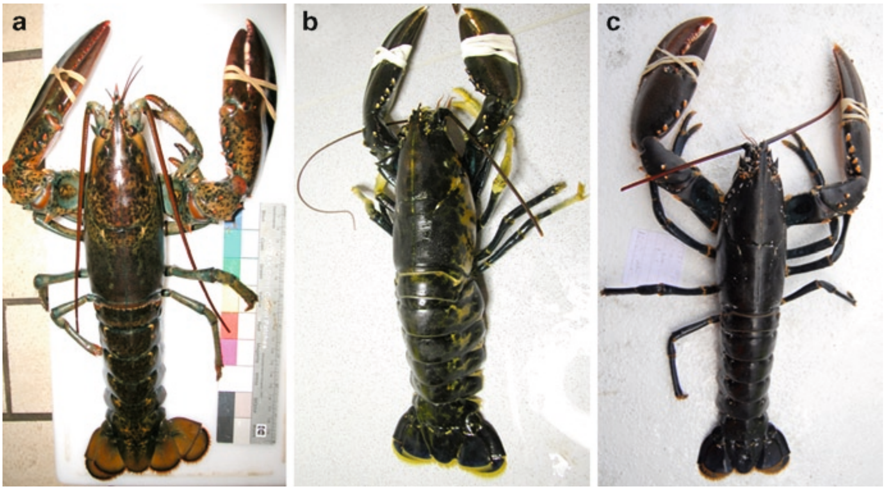


**Fig. 2** Examples of morphological color patterns in *Homarus* found in Norwegian waters. (**a**) *Homarus americanus*, normal pigmentation. (**b**) Intermediate form or "odd-looking" lobster. (**c**) *Homarus gammarus*, normal pigmentation in Norway

Ferguson 2002). Screening for diagnostic markers (Jørstad et al. 2007) has identified three microsatellite DNA loci that distinguish the two species. Recently, two more loci have been found with almost no overlapping of microsatellite DNA fragment sizes, providing a diagnostic tool for species identification as well as for detection of hybrids. This is illustrated in Fig. 3 where three lobsters, corresponding to the three morphological colour pattern categories (shown in Fig. 2), were analysed for the two most diagnostic loci (*Hgam98*, Fig. 3a and *Hgam232*, Fig. 3b). As shown in the diagrams of fragment sizes (profiles), there are large differences, and no overlapping alleles have so far been detected between the species. These microsatellite loci are considered as diagnostic, and they also provide a genetic tool to detect hybrids.

These loci have been used in the monitoring and identification program described below.

## 3 Sampling and Genetic Analysis of "Odd-Looking" Lobsters

After the first observations of American lobsters in Oslofjord in 1999, Bergen Aquarium in cooperation with Institute of Marine Research (IMR) designed a collection and reporting program (van der Meeren et al. 2000). Information about American lobsters, including morphological description and colour patterns, was disseminated to the media and by leaflets to Norwegian fishermen. Following that campaign, "odd-looking" lobsters were delivered to Aquaria in Bergen, Drøbak, Kragerø and Ålesund, and to IMR, where they were kept alive. Measurements and sampling were carried out as described in Jørstad et al. (2007).

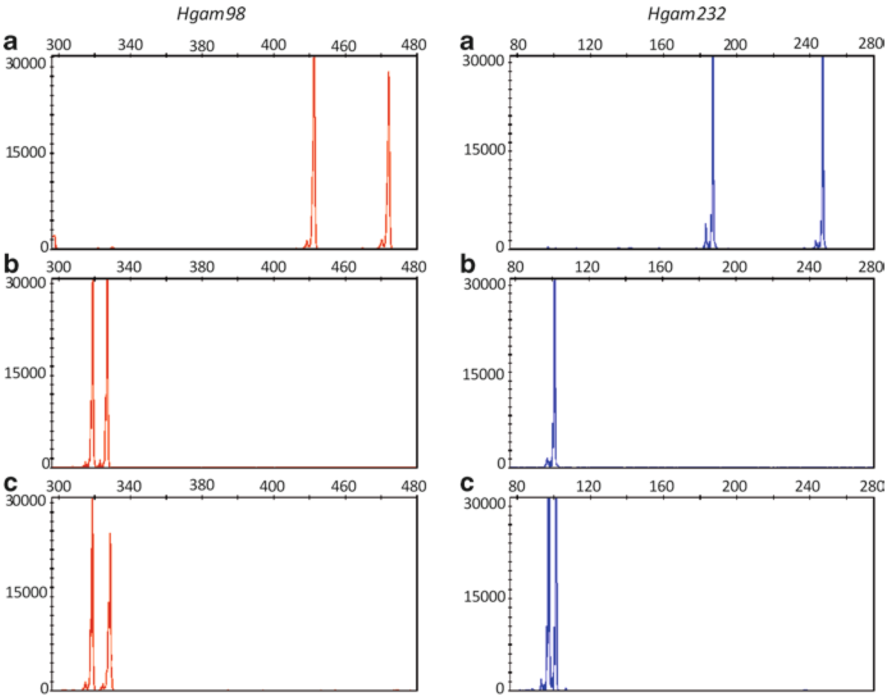


**Fig. 3** Diagram of microsatellite DNA fragments sizes from ABI sequencer for two different loci (*Hgam98* and *Hgam232*). The diagram (**a**), (**b**) and (**c**) correspond to lobsters with the morphological color patters shown in Fig. 2

Except for the two specimens of American lobster caught near Ålesund in 2006 (Table 1, nos 14 and 15), their sizes is quite uniform, mainly between 85 and 120 mm carapace length. This may signify capture soon after their release/escape, since sampling a well established lobster population in Norway one would expect a wider size range (Agnalt et al. 2004).

The first results from the investigation from 2001 to 2005 have been reported by Jørstad et al. (2007). In this period 45 "odd-looking" lobsters were sampled/collected at different locations from Oslofjord, along the Skagerak coast and in western Norway up to Ålesund. DNA was extracted using the Qiagen Dneasy 96 Tissue Kit. Initially 13 microsatellite loci were used in the comparison between reference samples of the two species. The *H. gammarus* specific primers were developed at Queen's University Belfast (Ferguson 2002), and the PCR products were analysed at the IMR. This investigation identified three microsatellite loci (*Hgam98*, *Hgam197* and *Hgam 47b*) that were diagnostic to distinguish the species. Genetic analyses of the collected "odd-looking" lobsters were based on these three microsatellite loci. Nine of the 45 lobsters examined were identified as *H. americanus* by their DNA profiles (Jørstad et al. 2007). The remaining specimens had microsatellite DNA fragments (all three loci) typical for *H. gammarus*, and none of the lobsters in this first group were hybrids.

**Table 1** Summary information for *Homarus americanus* occurrence in Scandinavian waters

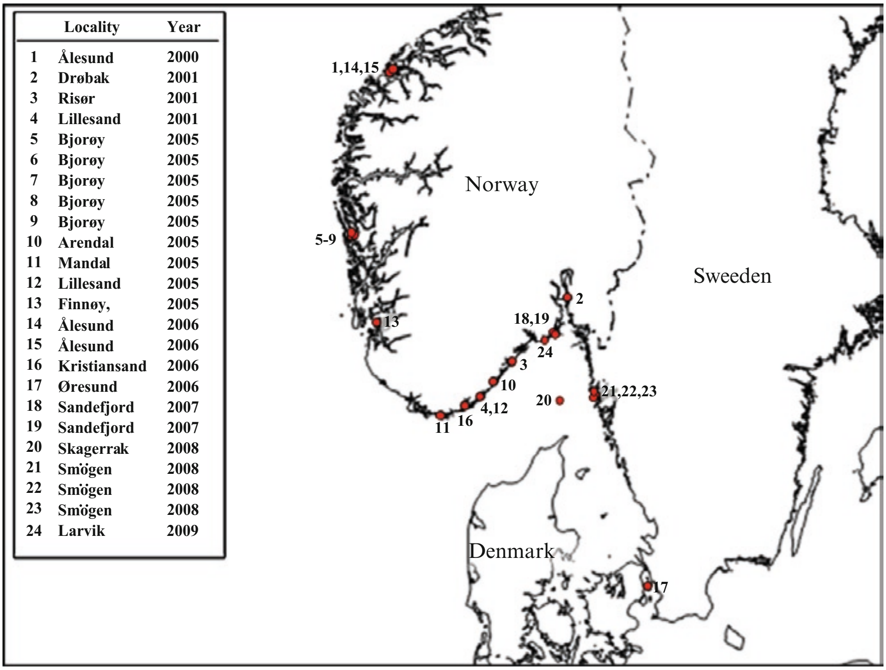
| No. | Locality | Date | Year | Sampling place | Carapax length (mm) | Sex 1 = female 2 = male | Total length (mm) | Weight (g) | External eggs |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Ålesund | 08.12. | 2000 | Bergen Aquarium | 98 | 2 | 287 | 609 | |
| 2 | Drøbak | 10.01. | 2001 | Drøbak Aquarium | 90 | 1 | 270 | 570 | |
| 3 | Risør | 10.01. | 2001 | Risør Aquarium | 93 | 1 | 277 | 640 | Yes |
| 4 | Lillesand | 10.01. | 2001 | IMR, Flødevigen | 104 | 1 | 303 | 915 | Yes |
| 5 | Bjorøy | 28.08. | 2005 | IMR, Bergen | 87 | 1 | 255 | 515 | |
| 6 | Bjorøy | 04.09. | 2005 | IMR, Bergen | 89 | 1 | 250 | 533 | Yes |
| 7 | Bjorøy | 04.09. | 2005 | IMR, Bergen | 87 | 2 | 245 | 488 | |
| 8 | Bjorøy | 12.10. | 2005 | IMR, Bergen | 88 | 1 | 255 | 537 | Yes |
| 9 | Bjorøy | 15.10. | 2005 | IMR, Bergen | 98 | 2 | 270 | 802 | |
| 10 | Arendal | 28.11. | 2005 | IMR, Bergen | 98 | 1 | 305 | 1,064 | |
| 11 | Mandal | 28.11. | 2005 | IMR, Bergen | 108 | 2 | 255 | 632 | |
| 12 | Lillesand | 28.11. | 2005 | IMR, Bergen | 90 | 1 | 335 | 1,309 | |
| 13 | Finnøy, Haugøy | 09.12. | 2005 | Finnøy | 120 | | | | |
| 14 | Ålesund, Hessafjord | 15.02. | 2006 | Atlanterhavsparken | 150 | 2 | 390 | 3,300 | |
| 15 | Ålesund, Havn | 15.02. | 2006 | Atlanterhavsparken | 155 | 2 | 410 | 3,300 | |
| 16 | Kristiansands fjorden | 21.10. | 2006 | IMR, Flødevigen | 100 | 1 | 285 | 744 | |
| 17 | Øresund, Danmark | 15.12. | 2006 | Øresund Aquarium | 111 | 2 | 315 | 1,250 | |
| 18 | Sandefjord | 28.09 | 2007 | IMR, Bergen | 88 | 1 | 260 | | Yes |
| 19 | Sandefjord | 01.10. | 2007 | IMR, Bergen | 91 | 2 | 255 | | |
| 20 | Skagerrak | 05.06. | 2008 | Svensk Fisk, Gøteborg | 105 | 1 | | | |
| 21 | Smögen, Sweeden | 26.09. | 2008 | Fiskeriverket, Lysekil | 84 | 2 | | | |
| 22 | Smögen, Sweeden | 23.10. | 2008 | Fiskeriverket, Lysekil | 80 | 1 | | | |
| 23 | Smögen, Sweeden | 28.10. | 2008 | Fiskeriverket, Lysekil | 84 | 2 | | | |
| 24 | Larvik, Viksfjord | 09.10. | 2009 | Larvik | | 2 | | 2,300 | |

The different individuals are given number according to date of catch and the locality. Measurements were carried out on specimens received by IMR. All specimens were identified by DNA profiles. Sample no 17 (Øresund) was provided by Jens Petter Jeppesen, Øresund Aquarium, while nos 20, 21, 22, 23 were provided by Vidar Øresland and Mads Ulmestrand, Lysekil

Since 2005, lobster fishermen have kept on delivering “odd-looking” lobsters to IMR. The total material at present (2000–October 2009) consist of 91 “odd-looking” lobsters. DNA profiling using the methods described above has positively identified 24 specimens as *H. americanus*. The remaining 69 specimens of “odd-looking” lobsters were *H. gammarus*. As shown in Fig. 3, several specimens of *H. americanus* have recently also been found in Danish and Swedish coastal areas. One lobster was caught in Øresund in 2007 and four lobsters in Lysekil (see Table 1 for contact persons). Samples were collected and the DNA analyses were run at the IMR laboratory. The samples from the last part of the period were also analysed for a new diagnostic loci, *Hgam232*, as demonstrated in Fig. 3.

The sexes are almost equally represented among the *H. americanus* individuals collected in Scandinavian waters, (Table 1). Berried females are protected in the United States and Canada, so the eggs of the five berried females were possibly extruded in transport or later by females that had mated before capture, or mating had occurred during transport or once released into Norwegian waters. DNA analyses of eggs from the five females analysed so far (Table 1), revealed alleles only found in *H. americanus*.

There are three areas where *H. americanus* specimens had been captured within a restricted space and time (Table 1, Fig. 4). In 2005 fishermen caught five *H. americanus*



| | Locality | Year |
|---|---|---|
| 1 | Ålesund | 2000 |
| 2 | Drøbak | 2001 |
| 3 | Risør | 2001 |
| 4 | Lillesand | 2001 |
| 5 | Bjorøy | 2005 |
| 6 | Bjorøy | 2005 |
| 7 | Bjorøy | 2005 |
| 8 | Bjorøy | 2005 |
| 9 | Bjorøy | 2005 |
| 10 | Arendal | 2005 |
| 11 | Mandal | 2005 |
| 12 | Lillesand | 2005 |
| 13 | Finnøy, | 2005 |
| 14 | Ålesund | 2006 |
| 15 | Ålesund | 2006 |
| 16 | Kristiansand | 2006 |
| 17 | Øresund | 2006 |
| 18 | Sandefjord | 2007 |
| 19 | Sandefjord | 2007 |
| 20 | Skagerrak | 2008 |
| 21 | Smögen | 2008 |
| 22 | Smögen | 2008 |
| 23 | Smögen | 2008 |
| 24 | Larvik | 2009 |

**Fig. 4** Detection of *Homarus americanus* in the commercial fisheries in Scandinavian waters in the period from 2000 to 2009. The capture locations are given in red spot and number according to Table 1. All specimens have been identified by DNA profiling based on diagnostic loci

in the Bjorøy Island area south of Bergen on the west coast of Norway, and three specimens were detected at Smogen near Lysekil in Sweden in autumn 2008. A similar situation was observed in the Larvik region recently (2009). These concentrations are possibly a result of accidental release or escape from lobster storing facilities.

## 4 Competition and Hybridization: In the Lab and in the Wild

Since homarid lobsters are commercially valuable, they have been farmed and transplanted since the nineteenth century (Nicosia and Lavalli 1999). Efforts of transplanting *H. americanus* to the NE Pacific coast of America, where suitable environmental conditions exist, date back to 1870s–1890s (see Nicosia and Lavalli 1999 and references therein). However, no information is available on the fate of these early transplantations. Study of transplantations from the east coast in the 1960s showed that *H. americanus* would grow, survive, reproduce, and behave normally in Pacific waters. Studies of interspecific competition showed that the native *Palinurus interuptus* may be displaced by *H. americanus* and further transplantations were therefore discontinued (Krekorian et al. 1974).

A similar concern is expressed in connection with the introduction of *H. americanus* in European/Scandinavian waters. Due to the assumed larger size of the American species, it was believed that the European species could be outcompeted with respect to food and shelters. Both species are highly aggressive and have developed a hierarchy dominance system (for review see Skog 2008), between as well as within the sexes. A study of the sexual behaviour of males of the two species exposed to *gammarus* females showed that only *H. gammarus* males exhibited sexual interest/behaviour and mating (van der Meeren et al. 2008). The observations indicated some kind of species specific mating preference, at least under the experimental conditions used. The results obtained may alternatively be explained by stress of transportation impact on the sperm production for *H. americanus* males (Talbot et al. 1983) and insufficient acclimation. Since successful mating has occurred in laboratory or hatchery settings, the likelihood remains that it may happen in the wild as well.

In USA and Canada much of the research on lobsters in the 1970s and 1980s was focused on developing lobster farming (Carlberg et al. 1979; Aiken and Waddy 1995; Nicosia and Lavalli 1999). Hybrids were of special interest since they were thought to combine favourable parental traits. Carlberg et al. (1978) successfully mated *H. gammarus* females with American males and produced viable hybrids. Carlberg et al. (1979) run individually and communally larvae and juvenile rearing experiments with *H. gammarus* and *H. americanus*, and found similar growth. *Homarus gammarus* suffered from much higher mortalities and it was suggested that this species was more aggressive. Audoiun and Leglise (1972) and Hedgecock et al. (1978) reported success when crossing *H. americanus* males with *H. gammarus* females. 1,300 one year old hybrid specimens were produced at the hatchery at I'Ile d'Yeu were released in 1975 in the Bay of Biscay, but no recaptured specimens were reported (Audouin 1981).

Talbot et al. (1984, 1986), Talbot (1991) and Waddy and Aiken (1985), studied egg-extrusion and egg loss in wild-captured and laboratory-hatched *H. americanus* and hybrid specimens (a cross between male American and female European lobster). Most laboratory-hatched females, including the hybrids, lost over 90% of the eggs prior to hatching due to malformation of the egg stalk and stunted pleopod setae. The spermatophore of the hybrid males, though normal-sized, were empty hence making the males sterile (Talbot et al. 1983).

Carlberg et al. (1978) also found that at high densities the hybrids, like *H. gammarus,* suffered higher cannibalism and higher rates of mortality. This could be an important aspect with respect to establishment of a permanent population of *H. americanus* in European waters. At present berried females have been caught, but a successful introduction of *H. americanus* must also be based on documentation of recruitment of juveniles in the wild, which so far has not been documented. There may also be differences between the two species with respect to early benthic juvenile recruitments. Juveniles of American lobster are found in the wild on a regular basis, and even used in recruitment indices (Ellis and Cowan 2001; Wahle et al. 2004), while European lobster juveniles smaller than 40 mm CL has never been found in the wild (Mercer et al. 2001). This indicates ontogenetic behavioural differences between the two species, possibly selection of different microhabitats that would counteract interaction between the two species at these early stages.

Moreover, young-of-year juveniles of American lobster are relatively easily found in a variety of habitats as e.g., cobble (e.g., Lawton and Lavalli 1995; Cowan et al. 2001). Despite intensive search using partly similar methodology and technology as in American lobster, suitable habitats of European lobster smaller 8–10 cm total length is still unknown (Linnane et al. 2001; Mercer et al. 2001). In European marine waters, habitats consisting of cobble are often dominated by a large number of species, which could represent a barrier for successful recruitment of *H. americanus* juveniles.

## 5 The Risk of Disease Introduction

Gaffkemia is a disease in *H. americanus* caused by the bacterium *Aerococcus viridans* (for review see Steward 1980). At high summer temperatures this infection often causes high mortalities in lobster- holding ponds. Infected individuals are also found, though at variable frequencies, in wild populations (Stewart et al. 1966). Egidius (1972) reported high mortalities (100%) in *H. gammarus* injected with the pathogen in controlled experiments.

The first reported outbreak of Gaffkemia in Norway occurred in 1976 when American lobsters, held in pond in Stavanger, died in the first week after arrival (Håstein et al. 1977; Egidius 1978). First believed to be due to polluted water, but

Gaffkemia was later diagnosed after high mortalities continued even following transfer to other areas (Egidius 1978). The outbreaks of the disease could imply further spread of the pathogen into the wild populations in the Rogaland region. A large-scale screening program of the European lobsters from this area was initiated in 1981, and in four years more than 3,000 specimens were analyzed (Wiik et al. 1987). Only one specimen, collected in 1981, was confirmed infected by the pathogen. From studies with DNA-DNA hybridization, Wiik et al. (1986) concluded that the lobster pathogenic strains isolated from *H. gammarus* from Norway and the U.K. is similar to strains isolated from *H. americanus* (80–100% homology), supporting the view that the disease is introduced.

The diminishing lobster populations in Norwegian waters prompted efforts of stock enhancement, and a large scale programme was initiated at the Kvitsøy Islands (Agnalt et al. 1999, 2004). Samples of the broodstock and the produced juveniles were all screened for Gaffkemia, and proved uninfected (Jørstad et al. 1999). All American lobsters identified in this study (Table 1) were also tested for Gafkemia, but none of the molecularly-identified *H. americanus* specimens proved infected.

Shell disease is a potential problem associated with introduction of *H. americanus* in European waters, and this disease so far has not been detected in European lobster populations. The causative agents are believed to consist of chitinoclastic bacteria of the *Cytophaga-Flavobacter* and Alpha proteobacteria groups (Chistoserdov et al. 2005; Becker et al. 2004). The disease has been causing severe problems in lobster holding facilities as well as in wild populations, especially in the southern part of the distribution range (Castro and Angell 2000; Castro et al. 2006). The prevalence of shell disease in northern regions such as the Gulf of St. Lawrence is low (Comeau and Benhalima 2009), so that the risk of introduction of shell disease into Scandinavian waters is unknown.

A few specimens of *H. americanus* captured in southern Norway have been suspected as being infected by shell disease (van der Meeren 2008). These were kept in aquarium for several years and shell deformities seem to develop over time. Pictures of carapace shell and claws have been evaluated for morphological similarities with sick specimens of lobsters in United States, but so far no bacteriological tests have been carried out (Karlsbakk and Sandlund, pers. comm. 2010).

## 6 Conclusion

During the last decade American lobsters have been identified in Norwegian waters by using diagnostic micro satellite DNA profiling. The first specimens were reported in an earlier report (Jørstad et al. 2007), while new and recent documented specimens are included in the overall situation presented in this contribution.

Commercial imports of live *H. americanus* from North America to the European market are presumably the vector of introduction and detection of the 24 specimens of *H. americanus* collected in the last decade in Scandinavian waters. So far, there is no indication of successful reproduction in the wild. The number of ovigerous American lobsters detected so far are small, which will possibly decrease the risk for successful hatching and thus producing viable offspring. Likewise, it also reduced the risk for interspecific hybridisation with native European lobster. This contrast with the full-scale release experiments of hatchery-reared lobsters (Agnalt et al. 2004) and the genetic aspects connected to stock enhancement experiments as discussed in Jørstad 2004. In some cases, however, several American lobsters have been caught in the same area, and considering the low density of native lobsters in many regions, hybridisation should be monitored in such areas.

The ongoing live trade of *H. americanus* is focused on the possibility of transmitting Gaffkemia and shell disease to the native population. The local lobster fishery should be carefully monitored to detect introduced *H. americanus*, and signs of Gaffkemia and shell disease in the native population. Tighter controls should be enforced on live imports to reduce the likelihood of escape and release.

In late autumn 2009 several new American lobsters were captured (not included in Table 1) and suspected for shell disease. These specimens are now kept at IMR in Bergen, and are investigated for shell disease as well as other lobster diseases (Karlsbakk and Sandlund, pers. comm. 2010). Thus the monitoring program on American lobster in Norway will continue, and focus on abundance and geographic distribution as well as lobster diseases and potential hybridisation.

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# Part VI
# *Carcinus* in the Wrong Place

# The Evolutionary Ecology of European Green Crab, *Carcinus maenas*, in North America

**Timothy C. Edgell and Johan Hollander**

**Abstract** Biological invasions offer fertile grounds for studying evolutionary ecology because species' contact histories are uncharacteristically well-defined. As a result, invasions can be used to gain glimpses of the earliest micro-evolutionary responses of natural populations to new species' interactions by studying changes in behaviour, physiology or morphology in space and time. Here, the known history of range expansion by the European green crab *Carcinus maenas* in North America is used to illustrate factors affecting invasion success and the resilience of native American prey.

We situate our discussion in the bourgeoning field of adaptive phenotypic plasticity. Phenotypic plasticity is the phenomenon where an individual's genotype interacts with its environment to produce better-fit behaviour, physiology, morphology, or life-history. Plasticity is considered adaptive when the environmentally-induced phenotype increases an individual's fitness.

Below, theory about phenotypic plasticity is reviewed as to why it may benefit invasive species in general and specifically *Carcinus maenas*. The plasticity-invasion hypothesis (i.e., biological invaders benefit from high levels of phenotypic plasticity) is then tested directly by comparing known levels in *C. maenas* and other invaders to plasticity in a diversity of non-invasive, marine invertebrates. This study also analyses whether phenotypic plasticity has helped North American prey species defend against escalated bouts of predation caused by the *C. maenas* invasion, and elucidates the role plasticity plays in an apparent case of predator-prey coevolution between *C. maenas* and at least one species of native gastropod, *Littorina obtusata*. Finally, knowledge gaps in the case studies presented are discussed along with suggestions for future research aimed at gaining a better appreciation for how plasticity guides phenotypic evolution after a biological invasion.

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# 1 Introduction

## *1.1 History of Range Expansion*

In 1817, *Carcinus maenas* was transported from its endemic range (north Africa to Scandinavia) to the vicinity of New York or New Jersey in North America (Audet et al. 2008). Prior to the advent of water as ships' ballast (ca. 1850), ballast consisted of a variety of heavy objects like stones, pig iron, and sand (Minchin et al. 2009); therefore, the first *C. maenas* to arrive in North America were likely juveniles or adults as either part of a hull-fouling community or clinging directly to ballast off-loaded at the New England coast.

By the early twentieth century, *Carcinus maenas* was established in New England and its range included the southerly parts of the Gulf of Maine (Fig. 1). Here, its voracious predatory habits and high population densities implicated it in the decline of wild softshell clam stocks (Scattergood 1952). It took another 50 years for *C. maenas* to reach the Canadian Maritimes; in 1955, a Canadian fisheries bulletin warned, "Watch for Green Crab; a new clam enemy" (Medcof and Dickie 1955).

By 2000, *Carcinus maenas* populations were found along New Brunswick, Nova Scotia, and Prince Edward Island (Audet et al. 2008), and finally along Newfoundland in 2007 (Klassen and Locke 2007). Thus, in about 100 years, *C. maenas* expanded its North American range by more than 1,800 km (i.e., over

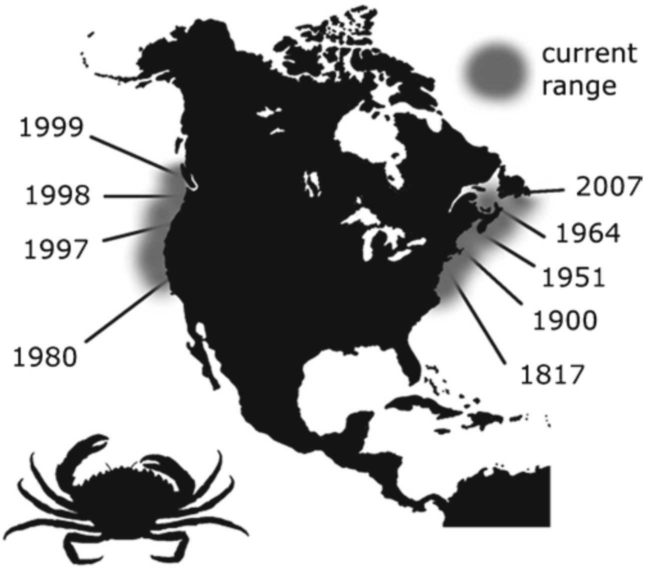

**Fig. 1** Timeline of invasion: European green crab, *Carcinus maenas*, in North America

18 km/year). The rate of range expansion was even faster along the west coast of North America (Gillespie et al. 2007); over 1,300 km in 18 years, from San Francisco Bay in 1980 to Vancouver Island in 1998 (i.e., about 72 km/year. These rates of range expansion were calculated by authors, and may be inflated under the special case of multiple invasions at different points along each coast e.g., see Roman 2006). Suffice to say, *C. maenas* is now widespread in North American coastal communities, and its interactions with native fauna exist along a well-documented latitudinal and temporal gradient; hundreds of years in southern New England, decades in the Bay of Fundy and California, and ten years or less in Newfoundland and British Columbia (Fig. 1).

## 2 Phenotypic Plasticity and Marine Biological Invasions

### *2.1 Phenotypic Plasticity and Invasion Success*

In the era of the Evolutionary Synthesis, genetic recombination and mutation were assumed to create the raw material for evolution by natural selection (Mayr 1942). More recently, however, the genetic versus environmental basis of new selectable traits, and how genotype × environment (G × E) interactions affect phenotypic evolution, has risen to the forefront of modern evolutionary biology (Schlichting and Pigliucci 1998; Agrawal 2001; West-Eberhard 2005).

Phenotypic plasticity (also known as the G × E interaction) is an individual's inherent ability to change behaviour, physiology, morphology, or life-history in response to environmental cues. Phenotypic plasticity in marine invertebrates is widespread taxonomically, and considered adaptive because induced phenotypes often increase individual fitness. For example, the burrowing bivalve *Macoma balthica* burrows deeper into sediments to escape predation when it senses water-borne cues from its predator (Griffiths and Richardson 2006). The pacific oyster *Crassostrea gigas* produces heat-shock proteins at high air temperatures, a physiological response to increase its thermal tolerance in summer intertidal zones (Hamdoun et al. 2003). Balanoid barnacles prevent appendage damage in high-flow environments by developing stunted feeding arms and, in at least one species, penises (Marchinko and Palmer 2003; Neufeld and Palmer 2008). Lastly, egg size, larvae size, and time to metamorphosis and settlement can vary from days to weeks within several species of benthic invertebrate as a function of food and substrate availability (reviewed by Hadfield and Strathmann 1996).

The evolution of phenotypic plasticity is predicted by grain-size theory (Hollander 2008). Grain size theory says long-lived species or those having extensive geographic ranges are likely to experience significant temporal or spatial heterogeneity, and thus live in a fine-grain environment (Levins 1968). Short-lived species and those with limited geographic ranges tend to experience little environmental flux, thus live in a coarse grain environment. Fine-grain environments favour the evolution of flexible phenotypes because plastic individuals will have greater fitness in a variety of selection regimes (i.e., generalists). Coarse-grain environments favour the evolution of stereotyped phenotypes by selecting highly specialized traits for constant and predictable selection pressures (Scheiner 1998; De Jong 1999; Berrigand and Scheiner 2004). For example, marine invertebrates with large-spatial-scale dispersals, such as species with planktotrophic larvae, have higher levels of phenotypic plasticity than species with low dispersal because spatial dispersal is inversely correlated to environmental grain size (Hollander 2008). Invasive species may also experience fine-grained environments because selection pressures in new environments are more likely to differ from those in native ranges; hence, grain size theory predicts invasions will favour species inheriting high levels of phenotypic plasticity.

It is new to consider phenotypic plasticity as a factor affecting biological invasion success (Smith 2009). In theory, moderate levels of plasticity may facilitate a population's expansion into novel environments by ensuring a match between an invader's traits and its new set of selection pressures (Donohue et al. 2001; Price et al. 2003; Parker et al. 2003). Alternatively, invasive species may thrive in novel environments irrespective of inherent plasticity, for reasons such as relaxed competition with members of the new community, release from natural enemies, or more favourable environmental conditions. Ultimately, the success of an introduced species in establishing a new population is contingent on its ability to overcome limits to self-sustained population growth (e.g., limits such as selective pressures imposed by new predators or competitors, novel prey with superior anti-predator defences, etc.). Therefore, self-sustaining growth requires phenotypic modification that can be driven either by plasticity or adaptation via natural selection on a standing pool of constitutive traits. For discussion about the rapid evolution of constitutive traits following an invasion (see Crawley 1987; Mack et al. 2000; Willis et al. 2000; Maron and Vila 2001; Keane and Crawley 2002; van Kleunen and Schmid 2003; Vila et al. 2003).

## 2.2 Phenotypic Plasticity and *Carcinus maenas*

The first *Carcinus maenas* to arrive in North America survived a plethora of selection pressures, including (1) physical and chemical pressures like wide-ranging temperatures and salinities, and (2) biological pressures imposed by novel enemies or prey. Therefore it is probable that phenotypic plasticity allowed *C. maenas* to rapidly adjust its physiology, behaviour and morphology to better match its new conditions, ultimately leading to widespread and ongoing invasion success. Below, known examples of phenotypic plasticity in *C. maenas* are reviewed, not to provide encyclopaedic coverage of the topic, but rather to give an appreciation of the different ways *C. maenas* can adjust its phenotype to match local selection pressures.

*Carcinus maenas* can tolerate large temperature and salinity fluctuations like those experienced between night and day, between low and high tide, between seasons, and between estuarine and fully marine habitats. Zoeae larvae tolerate temperature and salinity ranges from at least 10–25°C and 20–35 psu; metamorphic rate is delayed at lower temperatures and unaffected by different salinities, although whether slowed development at colder temperatures is adaptive is unclear (Nagaraj 1993). Adult crabs sense variations in salinity as low as 0.5 psu (McGaw and Naylor 1992), and tolerate brackish water by escalating urination rate; a four-fold increase in urination in 50% seawater (Binns 1969). Physiological acclimation to high and low salinities is surely adaptive since it gives crabs access to a wider range of marine habitats, from brackish estuaries and tide pools to sheltered bays along open coasts.

Physiology also responds to diet. Experimental evidence shows *Carcinus maenas* responds to starvation by drastically slowing its metabolic rate; a 40% reduction during the first week of starvation, increasing to 60% from control levels for another three months (Wallace 1973). The ability for adult crabs to survive without food for over three months would provide ample time for transport between coasts (e.g., the initial introduction to North America was probably adults), and time for invaders to learn and conquer novel prey. Muscle physiology is also affected by diet. After rearing crabs on either hard or soft diets (littorinid snails versus fish flesh, respectively), the claw muscles of hard-feeders produce stronger closing forces than those of soft-feeders, and the claw muscles of hard-feeders grow longer sarcomeres (good for producing strong closing forces) (Abby-Kalio and Warner 1984).

The food-hardness experiment by Abby-Kalio and Warner (1984) was the first to show a manipulated diet could induce crab claw function to match prey defences, perhaps allowing *Carcinus maenas* to adjust rapidly to the defences of its new prey. Later studies supported the Abby-Kalio and Warner results compellingly, by showing both claw morphology and feeding behaviour also respond to diet by matching the relative robustness of prey defence. Baldridge and Smith (2008) reared *C. maenas* at 10°C and 16°C on diets of either thick or thin-shelled littorinid snails (i.e., different armament strengths, same nutritional value between diet treatments). At 10°C, diet appeared to have no affect on claw function; however, crabs fed thick-shelled snails at 16°C developed significantly larger claws than conspecifics fed thin shells. Edgell and Rochette (2009) studied the interactive effects of diet and feeding behaviour on *C. maenas* claw development. Shell-crushing behaviour dominated when crabs ate thin-shelled snails, whereas aperture-probing predation (i.e., extraction of snail flesh without damage to shell) dominated crabs eating shells too tough to break. Moreover, shell-crushing crabs grew larger claws than aperture-probing crabs, and crabs fed thick-shelled snails grew larger claws than those fed thin-shelled snails. In both the Baldridge and Smith, and Edgell and Rochette studies, inducible claw forms were only seen in the larger crushing claws of each individual, not the smaller pincer claw, evidence that morphological changes were caused by feeding habits, and a compelling mechanism for how *C. maenas* can adjust behaviour and morphology to exploit novel prey during an invasion.

*Carcinus maenas* has invaded many coasts other than North America; including Australia (late 1800s), Tasmania (1993), South Africa (1983), and Argentina

(2003), plus several other (apparently) un-successful introductions to the Red Sea, Brazil, Panama, Sri Lanka, Hawaii, Madagascar, Union of Myanmar, Pakistan and, maybe, Japan (reviewed by Klassen and Locke 2007). Each of these regions has unique physical and biological attributes that will challenge foreign invaders. The connection between phenotypic plasticity and invasion success can be explored further by comparing levels in *C. maenas* to a variety of non-invasive marine invertebrates through meta-analysis.

## *2.3 Testing the Plasticity-Invasion Hypothesis: Meta-Analysis*

Whether phenotypic plasticity makes some marine invertebrates better invaders than others is not known, largely because effort to reconcile invasion biology with plasticity theory is in its infancy (Smith 2009). However, a general pattern in terrestrial plants suggests plasticity is indeed a good predictor of invasion success (Parker et al. 2003; Geng et al. 2007). The hypothesis that *Carcinus maenas* is a good invader because of inherently high levels of phenotypic plasticity (hereafter called the plasticity-invasion hypothesis) can be tested by comparing it to other marine invertebrates.

The plasticity-invasion hypothesis is tested by meta-analysis. Meta-analysis allows us to compare plasticity across a diversity of species by transforming experimental effect sizes from different studies into a single, standardized response variable: Hedge's d (i.e., a statistic weighted by differences in the number of studies per group and their deviation from each other) (Gurevitch and Hedges 1993; Rosenberg et al. 2000). Therefore, the mean Hedge's d (±95% confidence intervals) was calculated from 56 published plasticity experiments since 1974 that reported trait means, sample sizes, and standard deviation of the means for both experimental treatments and controls. Using Hedge's d, we can (1) evaluate whether a species shows significant levels of plasticity (i.e., when it's 95% confidence interval does not intersect d = 0), and (2) compare the amount of morphological plasticity in *C. maenas* and other invasive species to a diversity of other marine invertebrates. [Invasive species status was assigned according to the Invasive Species Specialist Group database (IUCN, http://www.issg.org/database), the Mediterranean Science Commission (http://www.ciesm.org), plus other published reports.]

The strength of a meta-analysis is it allows us to synthesize results from multiple independent studies into one coherent, comparative analysis (Rosenthal 1984; Gurevitch et al. 1992; Gurevitch and Hedges 1993; Arnqvist and Wooster 1995). A limitation to meta-analysis, however, is its ability to detect true effects is reduced when (1) few experiments have been conducted for a particular species or group, (2) the experimental effect size is small, or (3) inter-study variances are large. For example, in Fig. 2, the error bar for *Nucella lapillus* intercepts d = 0, suggesting this species is not plastic despite experimental results to the contrary (Palmer 1990).

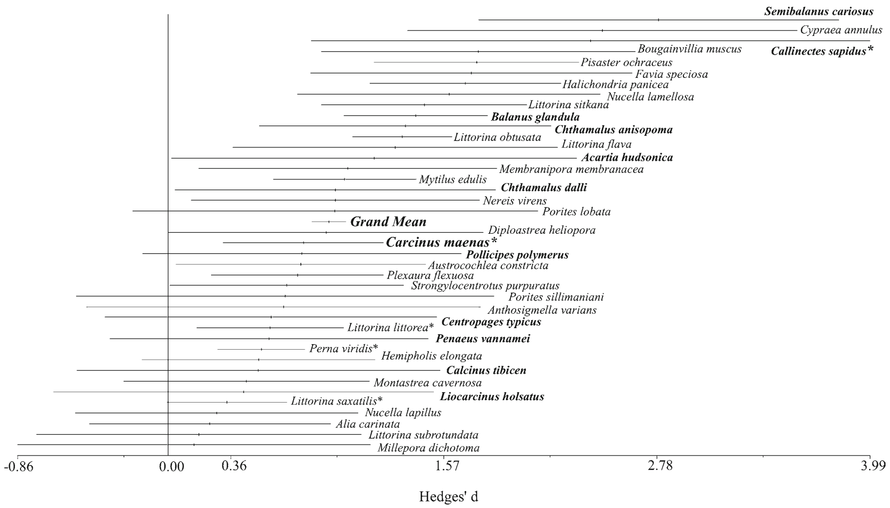

**Fig. 2** Meta-analysis of phenotypic plasticity experiments involving 44 species of marine invertebrate. Figure describes the mean effect size and the 95% confidence interval for each species. Confidence intervals (CI) that overlap with zero (*the vertical line*) suggest non-significant levels of phenotypic plasticity. Species in bold font are marine crustaceans. Asterisks indicate species known to be biological invaders. Importantly, this meta-analysis summarizes phenotypic plasticity at juvenile and adult stages in ontogeny only, although plasticity in larval invertebrates is undoubtedly important for marine biological invaders, especially those translocated as larvae by ballast water. For each species, the citations for data origins, experimental response variables and induction cues can be found in the appendix of Hollander 2008

This particular conflicting result involving *N. lapillus* stems from (1) too few independent experiments involving this species, (2) small experimental effect sizes (cf. mean Hedge's d of *N. lapillus* to other species in Fig. 2), and (3) variance in one of the experiments used for calculating Hedge's d was relatively large compared to its effect size. Nevertheless, meta-analysis is an easily accessible tool that is useful for testing or generating hypotheses via an empirical review of the literature. Refer to Hollander (2008) for further discussion about meta-analysis, including tests for publication and taxonomic biases in the results of a pre-cursor to the analysis presented in this chapter.

The meta-analysis illustrated by Fig. 2 showed marine invertebrates to possess significant phenotypic plasticity in different experimental environments, such as enhanced defensive structures in the presence of predatory cues (Appleton and Palmer 1988), larger or more robust feeding appendages in response to a manipulated diet (Baldridge and Smith 2008), and changes to body allometry due to faster, resource-induced, growth rates (Kemp and Bertness 1984). Furthermore, results showed *C. maenas* to possess significant levels of plasticity, as did three of the other four marine invasive species (cf. 23 of the 37 non-invaders also had significant plasticity). What is surprising, however, is that mean plasticity in *C. maenas* and all except one of the other invaders (*Littorina littorea*, *Littorina saxatilis*, *Perna viridis*) was lower than average for marine invertebrates (Fig. 2). The only invasive species to apparently support the plasticity-invasion hypothesis is the blue crab *Callinectes sapidus*, which hails from North America and colonized the coast of France in 1900 and the Mediterranean Sea in 1949 (The Mediterranean Science Commission, www.ciesm.org); *C. sapidus* was ranked by our meta-analysis to be one of the most plastic marine invertebrates studied. The unexpectedly low plasticity in *C. maenas* compared to other species does not appear to result from a taxonomic bias in our meta-analysis, since plasticity in *C. maenas* also ranked low among other crustaceans, and far below the other portunid crab *Callinectes sapidus* (Fig. 2, crustaceans denoted by bold font).

Low levels of plasticity among invasive species (Fig. 2, known invaders denoted by asterisks) seem to negate the plasticity-invasion hypothesis predicted by grain size theory (cf. Sect. 2.1). Nevertheless, plasticity may improve invasion success by optimizing phenotypes in concert with other adaptive strategies such as bet-hedging (Leimar 2005; Ripa et al. 2010) or genetic polymorphism (Parker et al. 2003). Bet-hedging is a strategy where arbitrarily alternative phenotypes are produced to match phenotypes to predictably variable environments. The theory has been tested few times in the framework of invasive species, with conflicting results (e.g., Mandak 2003; Mandak and Holmanova 2004; Hotchkiss et al. 2008). Genetic polymorphisms evolve when a reproductive barrier develops within a population spanning environments with contrasting selection pressures, creating ecotypes that are locally specialized. For example, the marine gastropod *Littorina saxatilis* has two ecotypes that can live within meters of each other; in Sweden, one ecotype lives in boulder habitats (i.e., crab habitat) and has shell forms adapted for shell-crushing predators like *C. maenas*, whereas the other ecotype lives in cliff habitats and has shells adapted for hydrodynamic forces. Finally, the evolution of polymorphisms (i.e., ecotypes) and phenotypic plasticity are usually treated as two opposite developmental strategies among species, and when partial plasticity is observed among distinct ecotypes the plasticity has often been considered as secondary or residual of previous evolutionary history (Pigliucci 2001). Hollander and Butlin (2010) studied two true ecotypes of *Littorina saxatilis* and demonstrated partial phenotypic plasticity in each ecotype increased individual survival rate. Small amounts of plasticity could thus benefit invaders by fine-tuning selectable traits around genetically-determinate mean phenotypes, to ultimately increase fitness under the new selection regime (Hollander et al. 2006).

Other reasons why low levels of phenotypic plasticity may benefit invasive species: If there is a high degree of environmental matching between native and invaded habitats, a phenotypic specialist (i.e., species with low inherent plasticity) may be better suited for competing with natives for shared and limiting resources. Native-invaded habitat matching may have contributed to the initial success of *Carcinus* in America because the rocky intertidal shores along New England and the U.K. have comparable sea surface temperatures, an abundance of sheltered and semi-sheltered shores, similar assemblages of fucoid macroalgae serving as habitat, and both share an abundance of common prey items that are favoured by *C. maenas* like littorinid snails, muricid whelks, and a variety of small bivalves (Ebling et al. 1964; Elner 1981; Tyrrell and Harris 2000; Edgell et al. 2009). Such native-invaded habitat matching may futher explain the renewed range expansion of *C. maenas* towards colder-water habitats in Atlantic Canada, insomuch that molecular evidence suggests these pioneering crabs derive from a secondary, cryptic invasion of cold-water adapted *C. maenas* from Scandinavia (Roman 2006). Finally, the meta-analysis presented here may have detected low levels of plasticity in extant populations of *C. maenas* if plasticity in itself was evolving towards an optimal character state (i.e., canalization), a hypothesis that assumes high plasticity to be the ancestral condition that may have promoted the initial invasion success. Future work can test the canalization hypothesis by comparing levels of plasticity between long-established populations to those currently undergoing range expansions, predicting that populations undergoing range expansion will be relatively more plastic.

Only five published studies were found with available data about plasticity in invasive marine invertebrates, reminding us the link between phenotypic plasticity and invasion success is a vastly under-studied possibility. A potentially fruitful avenue for future work in this area is to study plasticity in either newly invasive populations or in long-established populations undergoing range expansions. Such efforts will enlighten our understanding of how invaders cope with new environmental stressors like novel prey, and, as we will see in the following section, how native species react and adapt quickly to introduced enemies.

## 3 History and Geography of Predator-Prey Phenotypes

### *3.1 Phenotypic Response of Native Gastropod Prey*

When *Carcinus maenas* invaded Newfoundland, Canada, its foraging habits were likened (gratuitously) to "… the sea-based equivalent of a scorched earth policy, with few survivors left after an infestation takes hold" (Fisheries and Oceans Canada 2008). Although local authorities may have overplayed the veracity of green crab's appetite, there is little doubt *C. maenas* escalated the predatory environment of North American molluscs: the invasion history correlates to measurable declines in commercially-important bivalve stocks (Scattergood 1952) and to an escalation of anti-predator defences in wild gastropods (e.g., Seeley 1986).

The impact of *Carcinus maenas* on the phenotype of native molluscs has been described using five principal approaches: (1) by comparing phenotypes of known prey collected from single locations pre- to post invasion (e.g., Vermeij 1982a, b; Seeley 1986; Fisher et al. 2009), (2) by comparing phenotypes of known prey along a time-since-invasion gradient (e.g., Trussell 1996; Freeman and Byers 2006), (3) by comparing anti-crab defences between coexisting species of prey, whereby one species is naturally favoured by *C. maenas* and the other is not (e.g., Vermeij 1982b; Edgell and Rochette 2008), (4) comparing distributions of *C. maenas* phenotypes to prey phenotypes (e.g., Smith 2004; Edgell and Rochette 2008), and (5) exploring the proximate causes of trait development in both *C. maenas* and its prey (e.g., Trussell and Smith 2000; Baldridge and Smith 2008).

The shells of *Nucella lapillus*, a common intertidal whelk along the Atlantic coast of North America and prey to *C. maenas*, are more frequently scarred in post- than pre-*Carcinus* museum collections (Vermeij 1982a, b). Shell scars develop when chips and minor breaks, like those resulting from an unsuccessful crab attack, are repaired by the surviving snail; consequently, the frequency of scars in a population can estimate natural selection for thicker shells, whether the shells belong to an extant population or a museum shelf (Vermeij et al. 1981; Vermeij 1987). Hence, the higher rate of shell scarring after arrival of *C. maenas* reflects an escalation in natural selection for stronger shells. In the Gulf of Maine, the increasing incidence of shell-scarring in *Nucella lapillus* was met by a suite of new shell forms, each correlating positively to shell strength: increased mass, thickness, and overall size (Vermeij 1982a; Fisher et al. 2009). Similarly, the intertidal snail *Littorina obtusata*, which coexists with *Nucella lapillus* and is another preferred prey of *C. maenas*, increased shell thickness by about 50% after arrival of *C. maenas* in the Gulf of Maine (Seeley 1986).

Historic patterns of shell-breaking, shell defences, and the concurrent introduction of *Carcinus maenas* may also explain current spatial patterns of crab and snail phenotypes. In the southern Gulf of Maine, where *C. maenas* invaded about 100 years ago, native *Littorina obtusata* shells are thick and heavy, making them well-defended against *C. maenas* attacks (Trussell 2000; Rochette et al. 2007). In contrast, northern Gulf conspecifics have coexisted with *C. maenas* for substantially less time (ca. 60 years), have relatively thin and light-weight shells, and are less likely to survive an attack. Furthermore, in regions where *Littorina obtusata* snails have relatively thick shells, *C. maenas* have relatively large claws (Smith 2004), evidence of a strong ecological interaction between predator and prey. Significantly, this shell-claw covariance, which occurs in at least twenty six populations in the Gulf of Maine and lower Bay of Fundy, (1) involves only the larger crushing claw of *C. maenas*, used for chipping, peeling, and breaking shells, and not the smaller pincer claw used for grasping and handling, and (2) does not exist between *C. maenas* and the equally-available yet less-favoured prey item *Littorina littorea* (Tyrrell and Harris 2000; Edgell and Rochette 2007, 2008). Incidentally, *Littorina littorea* shells did not become thicker after the arrival of *C. maenas* unlike *L. obtusata* shells (Vermeij 1982b; Seeley 1986), *L. littorea* shells in extant populations have fewer scars than coexisting *L. obtusata*, and both field and lab experiments suggest *L. obtusata* suffers significantly higher predation than *L. littorea* to *C. maenas* (Edgell and Rochette 2008). Of course, other factors could drive geographic differences in shell form like sea surface temperature (Trussell and Smith 2000); however, environmental variables are likely to have similar affects on both coexisting *Littorina* spp., hence the phenotypic covariance between crab claws and *Littorina obtusata* (but not *L. littorea*) points to *C. meanas* as the case of historic and geographic changes in *L. obtusata* phenotype. The apparent resilience of *Littorina littorea* to *C. maenas* predation has received little attention, but may be related the evolutionary history of this species pair: *Littorina littorea* is also a European invader of North America, hence its ancestors would have co-existed with *C. maenas* for millennia in Europe prior to being re-acquainted on America shores. Therefore, it is plausible that *Littorina littorea* in North America were pre-adapted to *C. maenas* predation, which explains why historically there was not a change in shell form from before to after *C. maenas* invaded the Gulf of Maine (re. Vermeij 1982b).

## *3.2 Anti-Predator Adaptation or Inducible Defence in Gastropods?*

Initially, the combination of increased shell scarring and thicker shells was considered evidence of evolution by natural selection, which assumed thickness to be a constitutive shell trait in littorinid snails (Vermeij 1982a, b; Seeley 1986). However, it was becoming clear that dramatic changes in shell form could occur within the lifetime of individual snails via phenotypic plasticity, inducible by contact with the waterborne scent of predation (Appleton and Palmer 1988). After discovering plasticity in shells of the whelk *Nucella lapillus*, induced by the scent of a native predatory crab *Cancer pagurus* (Palmer 1990), it came into question whether the historic increase of shell thickening in North American was caused by (1) evolution by natural selection, the leading hypothesis, or (2) an inducible defence caused by elevated concentrations of predation smell (i.e., dying conspecific snails) in *Carcinus maenas*-rich environments.

Significantly, the intertidal snail *Littorina obtusata*, whose shell thickness co-varies with claw size of *C. maenas*, responds to the scent of *C. maenas* by increasing shell thickness by a magnitude comparable to the natural changes observed over the past 100 years (Trussell 1996, 2000; Trussell and Smith 2000). Moreover, *C. maenas* scent also induces defensive behaviour in *Littorina obtusata*, causing them to withdraw more deeply into their shells when perturbed, and bettering their chance of surviving a shell-entry attack by *C. maenas* (Edgell et al. 2008, 2009). Incidentally, both anti-crushing and anti-entry defences co-vary among natural populations of *Littorina obtusata*, an expected result in prey populations defending against predators with complex attack strategies (DeWitt et al. 2000; such as *C. maenas*: Ebling et al. 1964; Kitching et al. 1966; Rochette et al. 2007; Edgell and Rochette 2008).

### 3.3 Evolving Reaction Norms and Latent Plasticity

Reaction norms are defined by the range of phenotypes produced by a single genotype in different environments. Because reaction norms are under genetic control, they can be targeted by natural selection and evolve (Schlichting and Pigliucci 1998; DeWitt and Scheiner 2004). A key question in the study of phenotypic plasticity, therefore, asks under what conditions do reaction norms evolve to become either canalized (stereotyped) or more plastic (flexible)? Here, experimental evidence is reviewed suggesting the reaction norm of *Littorina obtusata* snails and *Mytilus edulis* blue mussels have evolved based on population-level differences in their response to the scent of invasive *Carcinus maenas*.

The scent of crushed conspecifics is a general warning of predation threat and induces *Littorina obtusata* snails to rapidly develop thicker shells (Trussell and Smith 2000). However, the non-induced state of snails from the southern Gulf of Maine is more heavily armoured than that of conspecifics in the north, rendering the reaction norm of southerners (i.e., the mean difference between non-induced and *Carcinus*-induced individuals) significantly smaller than the reaction norm of northerners. Similarly, both northern and southern Gulf of Maine snails respond to *C. maenas* scent by retracting more deeply into their shells when perturbed, however, the significantly shallower retraction depth of non-induced snails from the north renders their reaction norm significantly larger than southern conspecifics (Edgell et al. 2009). In other words, snails from populations having coexisted with *C. maenas* for longer have better morphological and behavioural defences in the absence of predation threat, unlike the highly susceptible phenotypes of predator-naïve snails from northern populations where contact with *C. maenas* is relatively recent. Moreover, *Littorina obtusata* from the U.K., where the *Carcinus-Littorina* interaction is ancient, show little or no plasticity (i.e., they have canalized anti-predator behaviour), such that predator-naïve snails are equally defended as those exposed to predator cues. Therefore, the 50-year difference in interaction with *C. maenas* between north and south New England appears to have caused the reaction norm controlling the phenotype of *Littorina obtusata* to evolve rapidly towards canalization. Such stereotyped defences make snails perpetually well-protected against *C. maenas* predation with or without continual chemical contact, an adaptive state in environments where intense predation threat varies (e.g., between seasons) but is predictably present over the lifetime of the prey (Hollander 2008).

The blue mussel *Mytilus edulis*, also an inhabitant of New England, has overlapping distribution with two invasive and molluscivorous crabs: *Carcinus maenas* and the more recent invader, Asian shore crab *Hemigrapsus sanguineus*. The range of *C. maenas* extends farther north than that of *H. sanguineus*, resulting in northerly areas where blue mussels coexist with the former but not the latter crab species, and southerly areas where all three species coexist. In southern regions where the three species coexist, blue mussels respond to the scent of both crabs by increasing shell thickness (Freeman and Byers 2006); however, in regions yet to be invaded by *H. sanguineus* (i.e., a region long-since invaded by *C. maenas*), enhanced shell strength is only inducible by the scent of the known predator, *C. maenas*. Freeman and Byers (2006) argue the unresponsive phenotype of northern blue mussels to be ancestral, versus the derived condition of responding adaptively to the scent of *H. sanguineus* (the new invader); an adaptation that would have evolved in less than 15 years in southerly populations. This argument for explaining regional difference in the blue mussel reaction norm is consistent with classical evolutionary thinking, whereby genetically-determinate traits (in this case, cue recognition) arise via mutation and rapidly become fixed in the gene pool because of natural selection.

Freeman and Byers's (2006) evolution by natural selection explanation is open to debate, however, since population geneticists cast doubt whether the responsive and unresponsive phenotypes of *Mytilus edulis* blue mussels are a single species, and whether the minor changes in shell thickness induced in the lab had functional significance against shell-crushing crabs like *Carcinus maenas* and *Hemigrapsus sanguineus* (Rawson et al. 2007; but see Freeman and Byers 2007 for rebuttal). Moreover, the unresponsive phenotype of blue mussels is analogous to that seen in the Pacific whelk *Nucella lamellosa*, for which the unresponsive condition was given a wholly different explanation. *Nucella lamellosa* produce thicker shells when exposed to the scent of a known molluscivore, the red rock crab *Cancer productus*, but appear unresponsive to the unknown scent of a recent invader *Carcinus maenas* (Edgell and Neufeld 2008). Adaptive phenotypic plasticity was therefore inherent (i.e., whelks responded appropriately to the scent of a known predatory crab), however, there was yet to be a functional link between shell plasticity and the machinery to perceive and properly interpret the scent of the unknown predator (i.e., the invader, *C. maenas*). In the presence of *C. maenas*, therefore, adaptive phenotypic plasticity in *Nucella lamellosa* shell form was said to be latent, and it was posited that adaptive plasticity would appear in natural whelk populations that were exposed to *C. maenas* either (1) slowly, if the link between threat recognition and shell plasticity was under genetic control (e.g., the Freeman and Byers hypothesis), or (2) quickly and pervasively, if threat recognition developed via associative learning (i.e., associating novel *C. maenas* smell with the waterborne scent of conspecific death). Associative learning offers a powerful explanation for how entire populations may respond rapidly to the introduction of a new enemy, like *Mytilus edulis* blue mussels within 15 years of the *H. sanguineus* invasion, without needing time for adaptive genes to emerge via mutation and become distributed throughout the population by natural selection (Neufeld and Palmer 2010).

Because antagonistic traits of both *Carcinus maenas* and its prey are plastic and respond adaptively to each other's character state (reviewed above), it is unclear how much of the broad temporal or spatial trends (such as the geographic shell-claw covariance between *Littorina obtusata* and *Carcinus maenas*) results from evolution versus phenotypic plasticity. Future work should strive to understand the genetic underpinnings to regional differences in reaction norms. To date, studies of phenotypic plasticity and the evolution of reaction norms in *Carcinus maenas* and its prey, including those reviewed in this chapter, have based experiments on wild-caught, juvenile animals; thus, any putative maternal or early-life environmental effects incurred in the wild are confounded with experimental origin effects. For example, prey collected from predator-rich environments may be more responsive to predator scent in subsequent plasticity experiments (Edgell 2010). Proper multi-generational, common-garden experiments are needed to properly detect genetically-based differences in the reaction norm between populations. Moreover, multigenerational studies will increase the number of species available for experimentation, especially those in groups that are difficult to identify at larval or juvenile stages, and those belonging to intricate and naturally-hybridizing species complexes like the Atlantic mussels *Mytilus* spp.

## 4 Summary and Future Study

*Carcinus maenas* is established along both east and west coasts of North America, with northerly range limits thought to be governed by cold, Canadian coastal waters (Roman 2006). Its interactions with native fauna exist along a well-documented latitudinal and temporal gradient; hundreds of years in southern New England, decades in the Canadian Maritimes and California, and less than 10 years in Newfoundland and British Columbia (Fig. 1). Documented range expansions are characteristic of many biological invasions, making them ideal systems for studies of ecology and evolutionary biology in natural populations because interactions with native enemies (predators, prey, competitors) are uncharacteristically well-defined.

The ongoing invasion success of *Carcinus maenas* is in part owed to its ability to tolerate a wide range of environmental conditions. The mechanism underlying this tolerance is in part phenotypic plasticity, whereby *C. maenas* can alter its physiology, behaviour and morphology to better match local biotic and abiotic conditions. For example, *C. maenas* responds to more heavily defended prey by altering muscle physiology, foraging behaviour, and skeletal morphology, and it withstands extended bouts of starvation by slowing its metabolism. However, results of our meta-analysis suggest *C. maenas* is less plastic than other crustaceans and, in general, invasive species have lower than average levels of plasticity compared to other marine invertebrates. Although there does not appear to be a one-to-one relationship between levels of inherent phenotypic plasticity and invasion success, even moderate levels of plasticity can contribute to colonization success if it promotes the initial stages of genetic adaptation by fine-tuning phenotypes to new selection pressures (Price et al. 2003), or if plasticity works in concert with other adaptive life history traits (Ren and Zhang 2009). Moreover, invasive species may benefit from phenotypic plasticity if it allows them to initially thrive in a wider range of environmental conditions than they could having non-plastic traits specialized for conditions unique to their native range. For example, if a specialist phenotype incurs greatest fitness in the newly invaded environment, trait plasticity may allow an invader to survive long enough for natural selection to canalize the fittest portion of its reaction norm (Waddington 1942; Rollo 1994; Braendle and Flatt 2006). Future studies should explore life history and developmental strategies among a larger set of invasive species to elucidate the role of plasticity in augmenting invasion success.

Studying temporal and geographic patterns in predator and prey phenotype has offered insight into the impact of *Carcinus maenas* on native American coastal communities. Results include evidence that the introduction of *C. maenas* to North America caused an escalation in the predatory environment for several native molluscs, followed by an historic increase in anti-predator defences, geographic structuring of prey phenotypes related to their time of interaction with *C. maenas*, and widespread covariance between *C. maenas* claw size and the defensive strength of at least one of its preferred prey. There is also beginning to be an understanding of how plasticity itself is evolving based on experimental comparisons of developmental reaction norms in prey species along time-gradients of interaction with *C. maenas*, and also comparisons between populations recently invaded to those not yet invaded. Future work needs to shed light on the genetic structuring of population level differences in plasticity using multigenerational common-garden experiments; to date, all of the population-level comparisons have been based on experiments using juveniles collected from the wild, thus, in each case, the experimental origin effect is potentially confounded by maternal effects or early-life experiences gained prior to experimentation.

Although invasive species conjure negative thoughts about human interference and a biodiversity crisis, they have instrumental value for studies in ecology and evolution in natural populations. The European green crab system in North America is no exception: its invasion history is well defined, allowing us to study the mechanisms of phenotypic evolution that have contributed to this crab's invasion success and also the resilience of its novel prey to escalating predation pressure. In this chapter, the focus has been mostly on the role of inducible offences and defences to illustrate mechanisms underlying phenotypic change, and how such mechanisms can structure historic and geographic patterns in phenotypic evolution. The *C. maenas* system is also shedding considerable light on how inducible phenotypes in native prey can have cascading effects through higher levels of biological organization, altering energy flow through food webs and potentially structuring entire intertidal communities (reviewed by Hay 2009; Kishida et al. 2010). Indeed, the European green crab is now inseparable from the ecological function of many North American coastal communities and, as its range continues to expand northward on both east and west coasts, there has never been a better foundation for understanding how and how fast coastal communities will adapt.

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# More than One Way to Invade: Lessons from Genetic Studies of *Carcinus* Shore Crabs

**John A. Darling**

**Abstract** The European green crab *Carcinus maenas* is one of the world's most widely recognized marine invaders. The success of this species has provided opportunities to explore genetic patterns associated with establishment and population expansion following independent introduction events to widely different recipient ecosystems. Recent studies have revealed an extraordinary diversity of such patterns. Globally, genetic reconstruction of invasion histories suggests complicated scenarios comprising multiple introductions to some regions as well as secondary introductions deriving from previously established invasive populations. In addition, detailed genetic analyses of several introduced populations indicate that successful invasion may involve rapid expansion from single low diversity founder populations, multiple introductions from genetically distinct sources with subsequent intraspecific admixture, or even interspecific hybridization between *C. maenas* and its sibling species *C. aestuarii*. The complexity of this global picture highlights the contingent nature of individual biological invasion events. Nevertheless, genetic study of non-native *Carcinus* populations provides crucial insights into invasion dynamics relevant to green crab management and control, and offers an unusually rich system within which to explore the genetic consequences of colonizations and range expansions in coastal marine ecosystems.

## 1 Introduction

When the International Union for the Conservation of Nature (IUCN) published its list of "100 of the World's Worst Invasive Alien Species" a decade ago (Browne and Boudjelas 2000), fewer than ten marine species were listed. The European green crab *Carcinus maenas* was among them. At the time, established non-native populations of *C. maenas* (or *C. maenas* hybrids) were already known from Australia,

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South Africa, Japan and both coasts of North America (Carlton and Cohen 2003), and the species had been widely recognized for its potential to negatively impact recipient ecosystems (Cohen et al. 1995; Grosholz and Ruiz 1995; Leroux et al. 1990). In the years since publication of IUCN's list, evidence justifying the inclusion of *C. maenas* has continued to surface at a rapid pace. Reports have emerged of additional *C. maenas* range expansions, with newly established populations recognized in the Canadian Maritimes in the northwest Atlantic (Roman 2006) and Argentina (Hidalgo et al. 2005). Further, recent studies have convincingly demonstrated the ability of invasive *C. maenas* populations to dramatically alter native benthic coastal communities (Grosholz et al. 2000; Kimbro et al. 2009), and negatively impact human economies (Lovell et al. 2007).

One result of this growing notoriety has been a rapidly expanding scientific literature describing the organismal biology, ecology, and population dynamics of invasive *Carcinus*; an ISI Web of Science search for the topic "*Carcinus*" returned 1,393 articles published in the first decade of the new millenium, 270 of which included the search term in the article title. That this literature includes a number of studies utilizing molecular genetic approaches should come as no surprise, as the adoption of such methods has recently become a common and often indispensable component of research on biological invasions. Genetic analyses have proven extremely effective in a variety of systems for elucidating the likely sources of species introductions (Muirhead et al. 2008), clarifying the identity of invaders and recognizing previously undescribed cryptic diversity among invasive populations (Geller et al. 2010; Miura 2007), and reconstructing demographic scenarios associated with rapid post-establishment spread (Estoup et al. 2004). The insights gained through these studies have not only informed risk assessments and management strategies associated with particular invasive taxa (Stepien et al. 2005), they have substantially advanced our basic understanding of the mechanisms driving the spread of invasive species (Dlugosch and Parker 2008; Hanfling 2007).

The global success of *C. maenas* has provided ample opportunity to explore the utility of molecular genetic approaches for reconstructing patterns of green crab introduction and post-establishment range expansion. The aim of this present study is to review this body of research and comment on its importance for scientifically informed management strategies as well as its potential contribution to a broader appreciation of the population dynamics of coastal marine biological invasions. In many ways, genetic study of *Carcinus* appears to support the notion that the contingent nature of invasion events (events involving unique populations, unique recipient habitats, and unique circumstances of propagule release and environmental conditions) presents potentially insuperable hurdles to broad predictive generalizations regarding the likely outcome of introductions (Colautti et al. 2007; Darling et al. 2008). The purpose of this study is nonetheless to illustrate that the dramatic variation exhibited among green crab invasions has been instrumental to the value of this system for illuminating various mechanisms driving invasion success in coastal marine habitats. At the same time, I hope that review of the multiple roles that genetic study has played in deciphering patterns of *Carcinus* invasions will, for those unfamiliar with genetic analysis, serve as a valuable introduction to the remarkable utility of such analysis in furthering the study of biological invasions.

## 2 The Invader at Home: *Carcinus* in Its Native Range

Thorough understanding of the native biogeography of invasive species is critical for accurate reconstruction of invasion history and effective future risk assessments, and numerous studies have now demonstrated the value of comprehensive investigation of native populations (e.g., Hierro et al. 2005; Muirhead et al. 2008). Given two centuries of invasion history and global recognition as a nuisance taxon, it may come as something of a surprise that the native biogeography of *Carcinus* remains incompletely understood. The native range of the genus is known to extend throughout Atlantic and Mediterranean Europe and as far south as Mauritania in North Africa, spanning approximately 50° of north latitude (see Carlton and Cohen 2003; Clark et al. 2001, and citations therein). Although recognized as a distinct genus in the early Nineteenth century (Leach 1814), it was not until the 1950s that researchers acknowledged the possibility of distinct Atlantic and Mediterranean species (Holthuis and Gottlieb 1958). However, despite subsequent general consensus regarding the taxonomic separation of *C. maenas* and *C. aestuarii* (sometimes *C. mediterraneus*), even recent morphometric analyses have failed to uncover quantitative morphological evidence in support of the species level distinction (Clark et al. 2001).

Interestingly, early genetic evidence similarly failed to support the taxonomic division of *C. maenas* and *C. aestuarii*. Based on 19 mostly monomorphic allozyme loci, Bulnheim and Bahns (1996) concluded that genetic differentiation was insufficient to warrant independent species status, and recommended designation of two subspecies of *C. maenas* (Bulnheim and Bahns 1996). However, in the following year Geller et al. (1997) recognized species-diagnostic differences in partial sequences of the 16S small subunit rRNA gene, again supporting sibling species status for *C. maenas* and *C. aestuarii* (Geller et al. 1997). A later more comprehensive study based on the mitochondrial cytochrome c oxidase subunit I (COI) gene revealed considerable divergence between Atlantic populations and a single Mediterranean population, further cementing a species-level taxonomic distinction (Roman and Palumbi 2004). That study utilized published estimates of mutation rates at the COI locus to approximate the split between *C. maenas* and *C. aestuarii* at 5–8 million years ago, though it should be noted that application of such estimates requires a number of assumptions (including selective neutrality of the mitochondrial genome and constancy of mutation rates over evolutionary time) that have been challenged in recent years (Ho et al. 2005; Bazin et al. 2006).

In addition to providing further evidence for two sibling species within the genus, Roman and Palumbi (2004) described significant geographic structuring of genetic variation within *C. maenas* in Europe. The most substantial genetic differentiation was observed between populations inhabiting shorelines on the continental shelf (including those in Great Britain) and two populations located off the continental shelf along the shores of Iceland and the Faroe Islands, suggesting a deep water barrier to dispersal. A second, less dramatic genetic break was also recorded between Germany and Holland, indicating some restrictions to gene flow even along the contiguous European coastline. This pattern appears to be generally consistent with previously described faunal breaks in the region (Roman and Palumbi 2004), suggesting that despite considerable anthropogenic influence on its contemporary distribution *Carcinus* has preserved genetic signatures of its evolutionary history in Europe. The phylogeography of *Carcinus* in its home range was subsequently supported by analysis of nuclear microsatellite loci, although levels of differentiation proved much less striking at these loci than at the COI locus (Tepolt et al. 2006; Darling et al. 2008). This reduced phylogeographic signal may reflect the greater sensitivity of uni-parentally inherited mitochondrial loci to the effects of genetic drift. Alternatively, it is possible that the accumulation of homoplasies (alleles identical by state but with different evolutionary histories) at microsatellite loci obscures divergence at the interspecific level (Darling et al. 2008). While homoplasies should be rare for sequence-based markers, their presence in microsatellite datasets could mask phylogenetic signals, thus seriously limiting the utility of these markers for drawing inferences of genetic structure above the population level.

Notwithstanding these advances, questions remain regarding the native biogeography of *Carcinus*, associated primarily with poor sampling of the Mediterranean and regions potentially harboring naturally occurring hybrid zones between *C. maenas* and *C. aestuarii*. Genetic study of native *C. aestuarii* has to this point been restricted to two populations at Banyuls-sur-Mer, France and Naples, Italy, although results of even that limited analysis suggest that there may be substantial intraspecific genetic structure in the region (Darling et al. 2008). Still, inadequate sampling has constrained some efforts to infer invasion histories for non-native *C. aestuarii* mitochondrial lineages. Even more troubling is the near complete absence of genetic data from regions of likely overlap in the distributions of *C. maenas* and *C. aestuarii*. The possibility of successful crosses between these sibling species is suggested by both early experimental studies (Demeusy and Veillet 1953), and the presence of apparent hybrid populations outside of the native range (see Sect. 5). In addition, Clark et al. (2001) reported morphometric evidence for incomplete reproductive isolation of the two species at sites in southern Spain, although subsequent genetic analysis of crabs sampled from one of these sites (the Palmones estuary) identified all individuals unambiguously as *C. maenas* (Darling et al. 2008). More thorough genetic investigation of the Mediterranean region, aided by recently developed molecular markers for *C. aestuarii* (Marino et al. 2008), is clearly required to better understand the evolutionary history and contemporary phylogeography of *Carcinus* in its home range and to help clarify the relative roles of reproductive isolation, geographic distribution, ecology, and possible interspecific hybridization in maintaining species boundaries between *C. maenas* and *C. aestuarii*.

## 3 Global Genetic Patterns: Sourcing Introduced Populations

Determining the most likely sources of introduced individuals may be the single most widely adopted application of genetic data among invasion biologists, with critically important relevance to risk assessment, management, and policy-making (Rollins et al. 2006).

The development and application of methods ranging from phylogeography to assignment testing based on multilocus genotype data (Davies et al. 1999; Manel et al. 2005) has enabled source tracking of invasive populations in a wide variety of systems (Muirhead et al. 2008). Unfortunately, the geographic resolution of these approaches is limited not only by logistical constraints on sampling intensity, but on contemporary native range genetic structure (Muirhead et al. 2008).

Recent attempts to reconstruct introduction histories for invasive *Carcinus* populations illustrate both the benefits and limitations of these methods. Darling et al. (2008) conducted comprehensive analysis of genetic relationships between *Carcinus* populations on a global scale using both mitochondrial COI sequence data and highly polymorphic nuclear microsatellites. Figure 1 shows that both population level distance-based analysis (Fig. 1a) and individual-based Bayesian assignment methods (Fig. 1b) based on microsatellite data reveal similar patterns and are consistent with certain hypotheses regarding the origins of invasive populations. For example, clustering of crabs from western North America with those from the eastern US substantiate early claims of an eastern US origin for the Pacific coast invasion based on both preliminary genetic data (Bagley and Geller 2000), and observations of crabs in live seafood shipments arriving to California and Oregon from New England (Cohen et al. 1995). Similarly, the close genetic relationship between crabs in Tasmania (FAL in Fig. 1a) and mainland Australia (COR) is consistent with the proposed southward range expansion of *C. maenas* across the Bass Strait (Thresher et al. 2003). These analyses also suggest at least one novel hypothesis regarding *C. maenas* invasion history, as genetic affinities imply the possibility of an Australian origin for the recently established population in Argentina (Hidalgo et al. 2005). Thus, not only can genetic data support hypothetical reconstructions of invasion pathways based on the timing of introduction events and availability of effective dispersal vectors, they can raise the possibility of previously unrecognized pathways deserving consideration in future management strategies. Satisfactory assessment of the putative connection between Australia and Argentina will likely require not only additional genetic analysis, but also investigation of patterns of potential anthropogenic vectors connecting these locales.

Note that the clearest successes of source tracking for *Carcinus* invasions involve secondary introductions; invasions that derive from populations that are themselves introduced. In fact, all three of the above examples involve the introduction of *C. maenas* populations from regions invaded in the Nineteenth century (green crabs were first recorded in Australia in 1890, and in the eastern US in 1817). This is not to suggest that previously established invasive populations are more likely to serve as sources for new introductions (although the hypothesis deserves consideration), but rather to indicate the dependence of accurate source assignment on genetic differentiation among potential sources. Invasive populations established more than 100 years ago reveal a striking degree of genetic differentiation from native populations (Fig. 1), almost certainly due to both genetic bottlenecks associated with initial founding cohorts and long periods of genetic drift in the absence of connectivity with the native range. The result is that individuals derived from either of these sources are readily identifiable, allowing clear inference

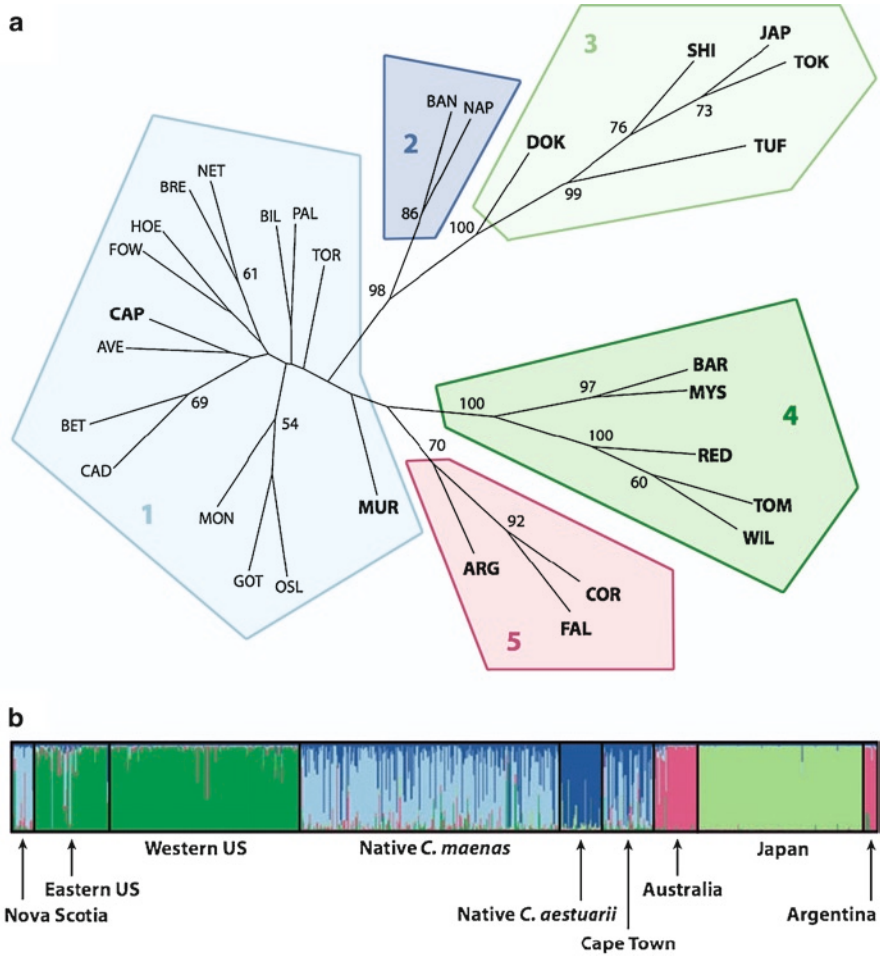
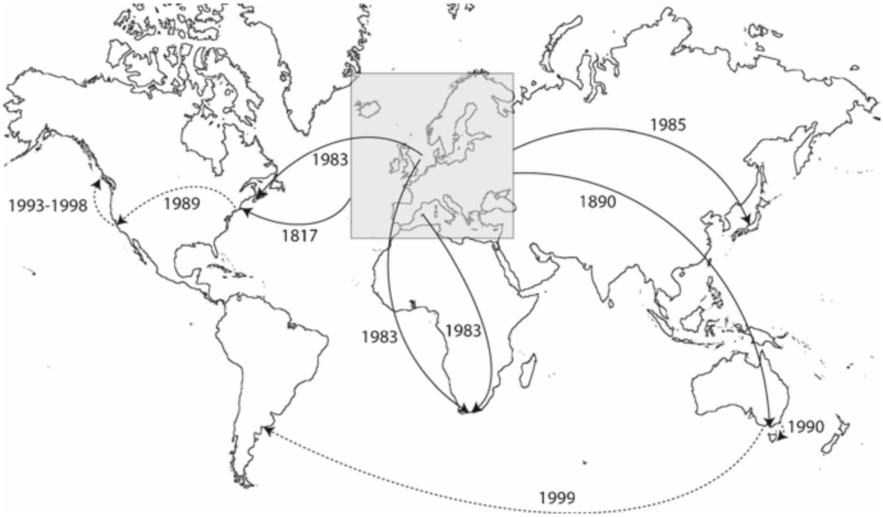


**Fig. 1** Determining sources for global *Carcinus* invasions (Geller et al. 2010, modified from Darling et al. 2008). (**a**) Neighbor joining (NJ) tree based on microsatellite genetic distances between populations. Non-native populations are indicated in bold type, and shaded polygons indicate clustering based on Bayesian inference as illustrated in panel B. Cluster 1 consists of all native *C. maenas* along with two introduced populations in Cape Town (CAP) and Nova Scotia (MUR). Other well supported groups in the NJ tree include native *C. aestuarii* (2) and introduced populations in Japan (3), eastern and western United States (4), and Australia and Argentina (5). Groupings suggest that the both the western US invasion (RED, TOM, WIL) and the Argentine invasion (ARG) source to earlier invasive populations in the eastern US (MYS, BAR) and Australia (COR, FAL), respectively. (**b**) Assignment of individual multilocus microsatellite genotypes based on the Bayesian clustering method implemented in the program STRUCTURE. Individual genotypes are represented by narrow vertical lines; proportional ancestry in five predicted clusters (corresponding to numbers 1 through 5 in (**a**) is indicated by color. Note that the western US populations cluster with the eastern US, and the Argentine population clusters with Australia. Also clear is the fact that the Nova Scotia population, though geographically proximate to the eastern US, does not belong to the US cluster. Earlier analysis of this population indicated that it derives from an independent introduction to North America (see text for details)

of secondary introductions. This high confidence in source determination enables more detailed exploration of the demographic parameters associated with some introductions. For instance, given strong evidence supporting an eastern US origin for the western North American invasion, Tepolt et al. (2009) directly assessed changes in microsatellite allele frequencies between the more recently colonizing population and its presumed source in order to estimate that the effective size of the cohort establishing the secondary invasion in the northeast Pacific may have been as few as 30 crabs (95% confidence interval ranging from 20 to 48 individuals). It is important to note, however, that effective size may be weakly correlated with the actual number of crabs initially invading the region, and represents only the minimum cohort size necessary to convey the observed contemporary genetic diversity.

Unfortunately, *Carcinus* is typical of many invasive taxa in that the native phylogeography is insufficiently resolved to allow accurate source assignment at high geographic resolution in most cases. For example, Roman (2006) employed mitochondrial sequence data to determine that the arrival of *C. maenas* in the Canadian Maritimes represents not a natural expansion from the eastern US population, but rather a novel introduction from native European sources (for a more detailed discussion, see Sect. 4). This is illustrated in Fig. 1, where crabs from Nova Scotia cluster independently of crabs from the eastern US. However, the lack of native range population genetic structure at microsatellite loci precludes assignment of the Nova Scotia crabs to any particular native locale. At best, we can say that the recent invasion appears to be poorly differentiated from native *C. maenas* at nuclear loci, a symptom of recent gene flow and possibly high propagule pressure associated with ballast water transport (Roman 2006). Interestingly, it turns out that mitochondrial data may be more informative in this case. COI haplotypes common among the recently introduced Canadian crabs belong to a strongly supported clade represented in the native range only north of the Netherlands, and occurring most frequently in Scandinavian populations (Darling et al. 2008; Roman 2006). Hence moderate native genetic structure at mitochondrial loci does allow source tracking, but with resolution limited to the regional level. Roman (2006) inferred a likely Norwegian origin for this particular *C. maenas* invasion based both on consistency with the genetic data and the frequent passage of oil tankers between Norway and the recently opened Strait of Canso Superport in Nova Scotia. The importance of both mitochondrial and nuclear markers in reconstructing invasion pathways for *Carcinus* serves as a valuable illustration of the utility of multiple genetic markers and multiple analytical methods in genetic studies of biological invasions. Accuracy and precision of source tracking depends on native range genetic structure, and the geographic resolution of that structure is in turn a function of how the locus used in its assessment tracks the evolutionary history of the taxon being investigated (Geller et al. 2010). Different genetic loci may thus yield very different levels of resolution when inferring invasion histories.

For *Carcinus*, the combination of mitochondrial and nuclear genetic data have provided a compelling, though still incomplete, picture of global patterns of anthropogenic dispersal (Fig. 2). This includes a number of secondary introductions,



| ***Introduced population*** | ***Date of introduction*** | ***Most likely vector(s) of introduction*** | ***Most likely source region*** | ***Loss of diversity relative to source?*** | ***Loss of diversity relative to native range?*** | ***Evidence for multiple introductions?*** |
|---|---|---|---|---|---|---|
| Eastern United States | 1817 | solid ballast, hull fouling | Atlantic Europe | yes | yes | no |
| Australia | 1890 | solid ballast, hull fouling | Atlantic Europe | no | no | no |
| Cape Town | 1983 | ballast water, equipment fouling | Northern Europe and Mediterranean | no | no | yes* |
| Japan | 1984 | ballast water | Atlantic Europe and Mediterranean | yes | yes | yes* |
| Western United States | 1989† | shellfish transport | *Eastern North America* | no | yes | no |
| Nova Scotia | 1980s | ballast water | Northern Europe/Scandinavia | no | no | yes‡ |
| Tasmania | 1993 | natural dispersal | *Australia* | yes | yes | no |
| Argentina | 1999 | ballast water | *Australia* | yes | yes | no |

**Fig. 2** (*Top*) Most likely pathways of *Carcinus* invasions inferred from combined genetic studies of both mitochondrial COI sequence data and nuclear microsatellites. The *gray square* indicates the present native range of the genus. A number of introductions (Atlantic United States, Japan, Australia) cannot be sourced precisely to any particular native region (although see text Sect. 5 for details on the Japanese invasion). *Dotted arrows* indicate secondary introductions from previously invasive sources. (*Bottom*) Summary of global *Carcinus* introductions modified from Darling et al. (2008). Non-native sources for secondary introduction are indicated in italics. *, see text for details regarding inference of multiple introductions for Cape Town and Japan. †, expansion of this population northward (shown above) is not considered a separate invasion here. ‡, diversity comparisons for Nova Scotia refer to the later (1980s) invasion to the Strait of Canso, although some populations in Nova Scotia possess haplotypes derived from both this introduction and the earlier (1817) introduction to the eastern US (see text and Fig. 3)

suggesting that regions harbouring invasive populations effectively serve to broaden the range of potential sources for future introductions. In addition, it appears that multiple introductions may have occurred to some regions. Clearly the Atlantic coast of North America has experienced two independent invasion events separated by nearly 200 years. Genetic data also reveal that mitochondrial lineages of both *C. maenas* and its sibling *C. aestuarii* have been introduced to South Africa and Japan (Darling et al. 2008; Geller et al. 1997), although it is difficult to ascertain whether this is the result of independent introductions of the two species, simultaneous introduction of both species from a native region where they co-occur, or introduction of a native population with hybrid origins (see Sect. 5). Genetic analyses of *Carcinus* and other invasive taxa (e.g., Voisin et al. 2005) thus continue to demonstrate the likelihood of complex global expansion patterns for species with long histories of anthropogenic translocation.

## 4 Patterns of Regional Spread

The oldest extant non-native population of *C. maenas* was first recorded in 1817 in New York, whence it began a slow and episodic expansion along the Atlantic coast of North America (Carlton and Cohen 2003; Yamada 2000). By the 1950s green crabs were present as far north as southern Nova Scotia, although population abundances appeared to be limited at the species' northernmost invasion front (Audet et al. 2003). However, in the 1980s *C. maenas* rapidly became prevalent throughout Nova Scotia and the species has subsequently spread as far north as Newfoundland (Audet et al. 2003; Klassen and Locke 2007; Roman 2006). The most prominent explanation for this rather sudden range expansion invoked relaxation of the previous thermal limits to northward spread of *C. maenas*. Either sea temperature warming trends had opened up new northern habitats suited to the physiological tolerances of existing green crab populations or those populations had adapted to the cold temperature regimes of the Canadian Maritimes (Audet et al. 2003). However, the discovery in Canadian *C. maenas* populations of novel mitochondrial haplotypes absent from New England, along with observations suggesting that those haplotypes derived from native Scandinavian sources (Roman 2006), presented a compelling case for an independent invasion event masquerading as northward population expansion (Fig. 3).

The study of Roman (2006) demonstrates the value of genetic analysis for understanding regional spread of an invasive species by refocusing the set of appropriate hypotheses addressing invasiveness of *C. maenas* in the northwest Atlantic. While previous hypotheses focused primarily on *in situ* adaptation to the temperature regime experienced in the Canadian Maritimes (Audet et al. 2003), genetic analysis has shifted attention instead to possible pre-adaptation of Scandinavian *C. maenas* populations to cold water habitats (Roman 2006), or postulation of an important role for anthropogenic assistance in overcoming the prevailing southwesterly advective currents in the region.

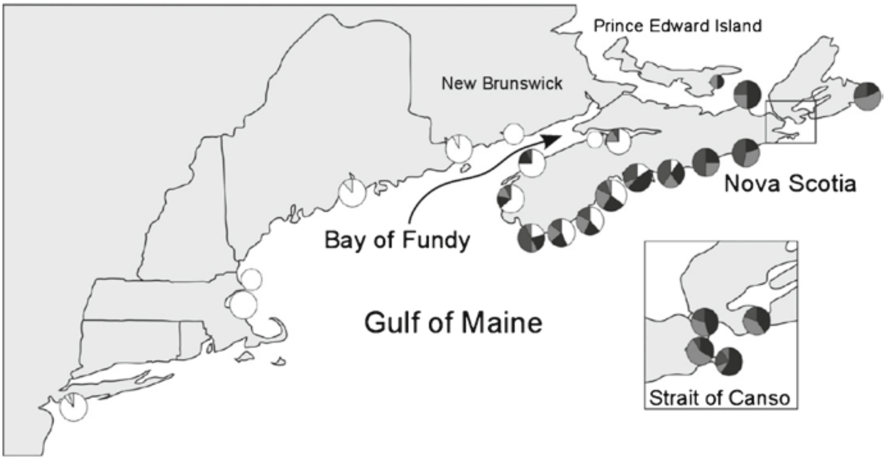


**Fig. 3** Multiple *C. maenas* invasions to the northwest Atlantic (modified from Roman 2006). Pie charts indicate haplotype frequencies, with the size of charts scaled to sample size. White and light gray shades represent haplotypes present in the earlier invasion (first reported in 1817); black and dark gray shades represent haplotypes from the later invasion (established in the 1980s). The Strait of Canso region, presumably the site of introduction for the latter invasion, is shown in detail inset. A genetic cline between the two haplotype groups extends from the northern end of the Bay of Fundy around the southern end of Nova Scotia to just north of Halifax. This cline has shifted southward and broadened over time, consistent with predictions based on larval dispersal dynamics (see Sect. 4 for details)

This latter course of inquiry has proven particularly intriguing. Byers and Pringle (2006) recently demonstrated that range limits of coastal marine species with benthic adults and planktonic larvae are not determined solely or even primarily by environmental suitability of habitat. Rather, upstream range limits in advective environments may occur where the reproductive rate of a population achieves balance between larval retention and the loss of larvae to downstream currents. This finding holds critical implications for predicting expansions of established non-native coastal taxa, as it argues that habitat suitability models may overestimate potential range limits in some cases. It also suggests that the success of coastal invasions may be mediated in part by availability of upstream retention zones such as inlets and estuaries shielded from alongshore advective currents. Genetic evidence for anthropogenic upstream advancement of the western Atlantic *C. maenas* invasion is clearly consistent with this model. Northward expansion of the original invasive population was apparently limited to the southern portion of the Scotian Shelf, possibly because reproductive output of the northernmost *C. maenas* populations was insufficient to overcome advective currents driving larvae southward. However, an independent introduction of *C. maenas* may have overcome this limitation through establishment of populations in northern retention zones associated with saltwater lakes in the Strait of Canso region, providing persistent sources of larvae for seeding downstream sites. One clear prediction of this scenario is that upstream (northern) *C maenas* populations should have a substantial competitive advantage over downstream (southern) populations due to the dynamics of larval dispersal, an advantage that should manifest in the replacement of southern haplotypes by the unique haplotypes associated with the more recent introduction (Byers and Pringle 2008). In fact, genetic analysis of *C. maenas* in the region has borne out this prediction. Comparison of the distribution of COI haplotypes in 2000, 2002 and 2007 reveals a significant southward shift in the centre of the genetic cline between southern and northern haplotypes first observed by Roman (2006) and illustrated in Fig. 3 (J. Pringle, pers. comm. 2009; Blakeslee et al. 2010). The magnitude of this shift is consistent with expectations based on physical models of larval drift in the region.

A different expansion scenario is revealed by genetic analysis of *C. maenas* in the eastern Pacific. This is not unexpected, given the dramatic dissimilarity in historical patterns of spread observed on the Atlantic and Pacific coasts of North America. While *C. maenas* in the western Atlantic advanced ponderously northward from the initial site of introduction, the same species spread at a rather menacing rate in the northeast Pacific. Initially introduced to San Francisco Bay in the late 1980s (Cohen et al. 1995), the *C. maenas* population expanded well over 1,500 km northward within 25 years, and green crabs were abundant at the northern end of Vancouver Island by 2006 (Gillespie et al. 2007). Again, advancement of the invasion front was episodic, sometimes extraordinarily so: during the summer of 1998 green crabs were first discovered in estuaries ranging from Humboldt Bay in central California to Vancouver Island (Yamada and Hunt 2000). This rapid but discontinuous expansion was commonly attributed to larval dispersal driven by northward-moving currents occasionally enhanced by El Niño events, including the strongest such event on record beginning in the fall of 1997 and extending through the spring of 1998 (Huyer et al. 1998; Yamada and Hunt 2000).

A recent study by Tepolt et al. (2009) reveals geographic patterns of genetic variation consistent with this hypothesis. Those authors divided 21 collection sites into three regions associated with different phases of the invasion: "primary" invasion sites within the San Francisco Bay region, "secondary" sites extending from northern California through Washington, and "tertiary" sites throughout Vancouver Island in British Columbia. Figure 4 graphically illustrates the loss of microsatellite allelic diversity as the invasion front progressed northward. Most alleles (64.6%) were shared across the entire invasive range. However, a small percentage (15.4%) of the alleles present in the primary invasive cohort were lost during expansion into the secondary range, and an additional 15.4% were lost from the tertiary range in Vancouver Island. This sequential loss of allelic diversity is consistent with the expectation of decreasing genetic diversity at the periphery of expanding populations, driven in particular by the stochastic removal of rare alleles (Austerlitz et al. 1997; Ibrahim et al. 1996). Further, the lack of any substantial influx of novel alleles strongly suggests that no secondary independent introduction has contributed to the episodic spread of *C. maenas* along the Pacific coast. In fact, consistent with previous genetic studies (Bagley and Geller 2000; Darling et al. 2008), Tepolt et al. (2009) demonstrate that the eastern US is the only plausible source for the west

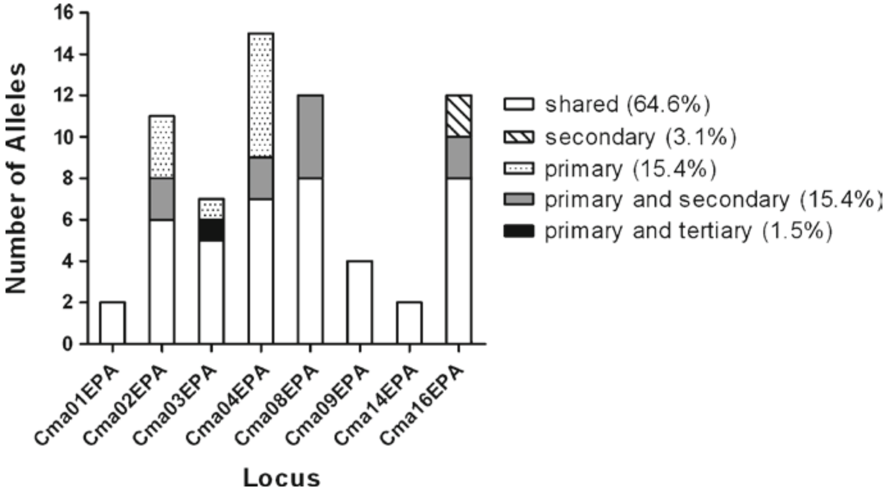


**Fig. 4** Regional distribution of *C. maenas* microsatellite alleles in the northeast Pacific (from Tepolt et al. 2009). Eight different microsatellite loci were surveyed (indicated on the x-axis), and the number of alleles observed at each locus is indicated on the y-axis. The primary invasion region comprised populations within the San Francisco Bay area; the secondary invasion region included sites from northern California to Washington; and the tertiary invasion region included sites on Vancouver Island. Most alleles (64.6%) were shared throughout the entire invasive range (indicated in white). A high frequency (15.4%) of alleles were observed only in the primary region, indicating loss of alleles during spread to the secondary region (dotted); similarly, 15.4% of alleles were shared between primary and secondary regions but lost during spread to the tertiary region (shaded gray). Only two alleles were observed in the secondary invasion region but absent from the primary region (hatched, Cma16EPA), and only one allele was observed in the tertiary region but absent from the secondary region (this allele was shared with the primary invasion; black, Cma03EPA)

coast invasion, and that the loss of nuclear genetic diversity observed during the west coast expansion occurred subsequent to a much more significant loss of diversity associated with the initial secondary introduction event (Fig. 5).

Remarkably, despite the measurable reduction in microsatellite diversity during the course of the North American west coast invasion, genetic differentiation across the region has remained extremely low (Tepolt et al. 2009). Significant pairwise differentiation between collection sites (as measured by $F_{ST}$) was observed in only a few cases, including a single site near the northern periphery of the current range and a site at Elkhorn Slough, which represents the only established population to the south of San Francisco. These sites were exceptions to a general pattern of apparent genetic connectivity implying sufficient gene flow throughout the broad regional *C. maenas* population to mitigate development of significant genetic structure, which in turn, suggests substantial connectivity via larval dispersal between sites. Thus, not only has the current-driven dispersal of larval crabs contributed to rapid range expansion, but propagule pressure to new recipient sites must be adequate in most cases to prevent strong founder events and subsequent genetic drift. Ongoing migration between sites is further indicated by direct estimates of gene

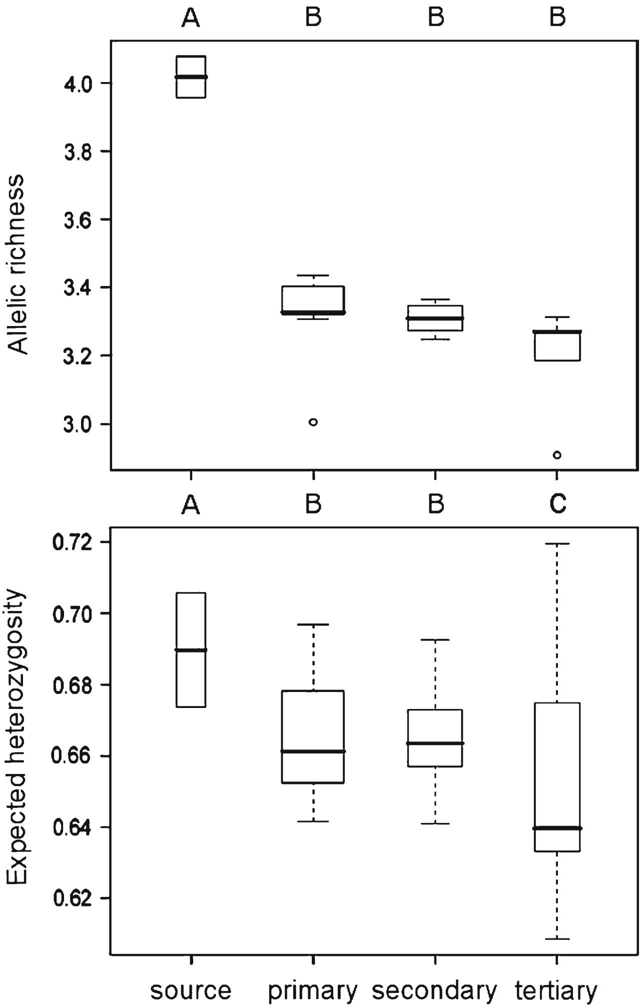


**Fig. 5** Box plots illustrating microsatellite allelic richness and expected heterozygosity for primary, secondary, and tertiary *C. maenas* invasions in the northeast Pacific, and for the putative Atlantic source population (from Tepolt et al. 2009). Mean (heavy bar), upper and lower quartile (upper and lower bounds of box), minimum and maximum values (upper and lower whiskers), and outliers (*open circles*) are shown. Letters above boxplots indicate pairwise significance; groups with the same letter do not differ significantly. Two-tailed P values for significance of difference between regions in the eastern Pacific: for $A$, $P = 0.087$; for $H_E$, $P = 0.018$

flow based on temporal shifts in allele frequency in several populations monitored over multiple years (Tepolt et al. 2009). For three *C. maenas* populations in the San Francisco Bay region (Bodega Bay, Bolinas Lagoon, and Tomales Bay) and one in Willapa Bay, Oregon, a significant fraction of allelic diversity was found to derive from sources outside each population over the time periods examined, indicating a strong contribution of gene flow between sites to population genetic structure.

Unfortunately, the inference of high propagule pressure associated with natural dispersal mechanisms has somewhat sobering implications for the management of invasive green crabs in the Northeastern Pacific. In particular, it suggests that efforts at targeted local eradication of crab populations are likely to be thwarted by new inoculations of larvae from other populations in the region. This reflects a general lesson that has already been learned in marine systems, where the expected efficacy of control efforts directed at widely established pest species is overwhelmingly perceived to be very low (Thresher and Kuris 2004). In fact, successful eradications in such systems have generally been limited to locally established populations with negligible (or manageable) connectivity to external sources of new colonizers (Anderson 2005; Bax et al. 2002; Culver and Kuris 2000). In the case of *C. maenas* in the northeast Pacific, high gene flow via larval dispersal, particularly the directional dispersal implied by both genetic data and invasion history, indicates the necessity of regionally coordinated control efforts sensitive to the likelihood of continued larval recruitment to northern sites from established southern populations. More generally, combined genetic evidence from both the Atlantic and Pacific coasts of North America now plainly demonstrates the significance of advective currents in determining expansion dynamics of *C. maenas* and confirms the general importance of upstream retention zones to the persistence of regional populations.

Yet these lessons may still offer a glimpse of silver lining. For instance, on the west coast of North America potential for spread of green crabs to the south from existing populations seems to be very limited, particularly given evidence for significant genetic bottlenecks associated with even the modest geographic expansion from San Francisco Bay to Elkhorn Slough (Tepolt et al. 2009). Further southward expansion of the species' range along the North American Pacific coast may thus depend on rare human-mediated intracoastal translocations of crabs or independent introductions from external sources. Similarly, substantial northward movement beyond retention zones in the northwest Atlantic will likely depend on human-mediated dispersal, a prediction already supported by genetic evidence suggesting that green crabs recently introduced to Newfoundland arrived by shipping traffic from sites south of the Strait of Canso (Blakeslee et al. 2010). It remains to be seen whether or not *C. maenas* will be capable of establishing additional retention zones in the northern extent of its eastern Pacific range. The observation of strong recruitment among *C. maenas* populations established in highly sheltered inlets on Vancouver Island (Yamada and Kosro in press) strikes an ominous tone, as these sites may be providing retention zones for seeding downstream sites in British Columbia and southeast Alaska.

## 5 Admixture and Hybridization

Invasion events, by their very nature, force encounters between biological entities that would be highly unlikely in the absence of human disturbance. Typically, such encounters are thought of at the organismal level and above: invasive populations must integrate into novel ecological communities, for example, and native taxa must contend with invasive predators. But important interactions occur at lower levels of the biological hierarchy, as well. In particular, a large number of recent studies have shown that the convergence of previously separated genotypes at either the intra- or interspecific level can dramatically influence the course of biological invasions (Ellstrand and Schierenbeck 2000; Roman and Darling 2007; Vellend et al. 2007). Empirical examples abound of interspecific hybridization (either between invasive and native taxa or between previously allopatric invasive species) leading to the formation of novel genetic complexes with uniquely invasive characteristics (Ellstrand and Schierenbeck 2000; Hanfling 2007; Rieseberg et al. 2007). And evidence is growing that similar genetic admixture at the intraspecific level has the potential to increase genetic and phenotypic variance among introduced populations, with implications for the capacity of those populations to respond to selection pressures in their recipient environments (Facon et al. 2008; Kolbe et al. 2007).

Although there exists no evidence for hybridization of green crabs with native crab species, in several non-native *Carcinus* populations there clearly has been opportunity for admixture and hybridization between invasive lineages. We have already considered one such case in the northwestern Atlantic, where two independent introductions of *C. maenas* have resulted in the admixture of genetically distinct populations (Roman 2006; Blakeslee et al. 2010). The COI haplotype distribution of *C. maenas* sampled from 1999 to 2001 (Fig. 3) reveals populations comprised exclusively of the older southern haplotypes throughout New England, while these haplotypes are absent from populations near the Strait of Canso in northern Nova Scotia. However, a conspicuous genetic cline between southern and northern haplotypes exists in the southern half of Nova Scotia, indicating admixture between these divergent genetic lineages. Later (2002 and 2007) investigations of these same populations have revealed a broadening of this admixture zone accompanied by a prominent southward shift (see section 4) above), suggesting that the system continues to evolve as haplotypes equilibrate between populations. Recent analysis of nuclear loci reveal individuals in the admixture zone possessing partial genetic coancestry in both the northern and southern populations, thus clearly indicating that this pattern results not only from dispersal of individual crabs, but from interbreeding between individuals derived from the two distinct introduction events (Blakeslee et al. 2010). In addition, although the overall movement of the admixture zone is clearly toward the south, southern haplotypes have also extended their range northward beyond their range limit prior to the Strait of Canso introduction (Jamie Pringle, pers. comm. 2009). In other words, the presence of established populations in northern Nova Scotia has enabled southern alleles to migrate against the prevailing advective currents. This pattern may result from demographic and genetic mechanisms facilitating the rapid introgression of selectively neutral alleles from established populations to newly invading ones (Currat et al. 2008; Excoffier et al. 2009). Ongoing exploration of genetic admixture in these populations based on both mitochondrial and nuclear loci may provide additional insights into the complex dynamics of gene flow in this system.

*Carcinus* also provides a striking example of interspecific hybridization between invasive sibling taxa. Ever since mitochondrial DNA studies revealed the presence of both *C. maenas* and *C. aestuarii* haplotypes in Japan (Geller et al. 1997), there has been speculation regarding the possible hybrid origin of green crabs in that region. While Geller et al. (1997) argued for independent invasions of both sibling species, Bagley and Geller (2001) suggested instead that the population derived from a single source possessing haplotypes of both species. Both studies noted hybridization as a possible explanation for the observed patterns of genetic diversity, but the absence of direct comparisons of mitochondrial and nuclear markers precluded definitive assessment of hybrid status. That limitation has more recently been overcome, leading to explicit confirmation of hybrid origin for Japanese green crabs (Darling et al. 2008). This conclusion is bolstered by the observation of complete cytonuclear equilibrium within Japanese *Carcinus* populations (Darling, in press). The two COI haplotypes present among Japanese green crabs unequivocally belong to different species, with 10.1% sequence distance (Kimura 2-parameter) between the two and unambiguous membership within the two well supported clades representing *C. maenas* and *C. aestuarii* in phylogenetic reconstructions (Darling et al. 2008; Roman and Palumbi 2004). Nevertheless, there appears to be no significant genetic differentiation at nuclear loci. Regardless of which species haplotype they possess, Japanese green crabs cluster within a single panmictic population in factorial correspondence analysis of nuclear microsatellite data (Fig. 6). In addition, Fig. 6 shows that Japanese green crabs are strongly differentiated from all studied native populations of both *C. maenas* and *C. aestuarii*.

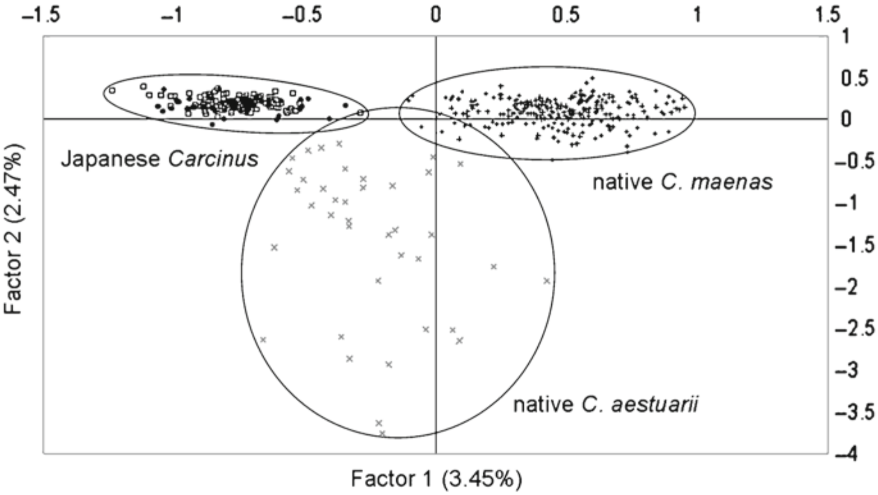


**Fig. 6** Factorial correspondence analysis of nuclear microsatellite data. Clusters comprising individual multilocus genotypes from native *C. maenas*, native *C. aestuarii*, and Japanese *Carcinus* populations are indicated with ovals. Among Japanese individuals, crabs possessing the *C. maenas* mitochondrial COI haplotype are depicted with closed symbols, those with the *C. aestuarii* haplotype are shown with open symbols

These results render the conclusion of hybrid origin for Japanese *Carcinus* difficult if not impossible to avoid, and raise questions regarding continued reference to Japanese crabs as *C. aestuarii* in recent literature (Chen et al. 2004; Yamada and Hauck 2001). Morphometric analysis of Japanese crabs does appear to support the notion that they belong to *C. aestuarii*, although there have been suggestions that even morphological criteria indicate mixed parentage for at least some crabs (Yamada and Hauck 2001). Still, the genetic evidence seems incontrovertible, and future integration of genetic and morphometric analysis will likely be required to adequately assess the inheritance of phenotypic characters currently employed as species-specific diagnostic markers. The genetic data also raise additional questions regarding the origin of Japanese *Carcinus*. In particular, the question remains whether the hybridization event giving rise to this population occurred pre- or post-invasion. A recent analysis argues that, given the known invasion history of *Carcinus* in Japan, the most parsimonious explanation for the observed distribution of genetic variation at both mitochondrial and nuclear loci is introduction from a single hybrid source population (Darling, in press). In fact, examination of admixture patterns indicates that hybridization between the sister species resulted in introgression of the *C. maenas* mitochondrial genome into a nuclear background characteristic of *C. aestuarii*. Given certain demographic considerations, this observation suggests that initial hybridization may have resulted from the rare incursion of *C. maenas* individuals into a predominantly *C. aestuarii* population (Darling, in press). Future exploration of *Carcinus* in regions of potential sympatry between the two congeners may provide additional insight into the evolutionary and biogeographical history of the Japanese invasion.

## 6 Genetic Diversity and Invasion Success

Conventional wisdom has long considered the success of invasive populations to be something of a “genetic paradox” (Frankham 2005). Colonizing populations introduced to new recipient habitats should represent only a small sample of native genetic diversity, and thus should experience, at least in some cases, severe genetic bottlenecks. Given the known negative influences of such bottlenecks on population viability and capacity to respond to selective pressures (Allendorf and Luikart 2007), how can introduced populations be so spectacularly successful? A number of recent reviews have addressed this issue, and have generally found a complex relationship between modes of anthropogenic introduction, diversity of colonizing populations, and invasive success as judged by establishment and spread in non-native ranges (Dlugosch and Parker 2008; Roman and Darling 2007; Wares et al. 2005). Although some introduced populations clearly do experience genetic founder effects, this is not necessarily the rule (Roman and Darling 2007). And while high genetic diversity of introduced populations may in fact contribute directly to invasiveness (Facon et al. 2008; Kolbe et al. 2007), some of the most astonishing examples of post-establishment spread involve populations with little or no genetic diversity (Mergeay et al. 2006).

This complexity is clearly reflected in the genetics of *Carcinus*. Globally, invasive *Carcinus* populations exhibit an extremely broad range of genetic diversity, especially at mitochondrial loci (Darling et al. 2008). Bottlenecks have been particularly severe in the Americas and Japan. In North America, with the exception of the more recent invasion to the Canadian Maritimes, a single mitochondrial COI haplotype was observed in all but two individuals out of hundreds surveyed; that haplotype was also found in all 15 individuals collected from Argentina. The situation is similar in Japan, where the only diversity at the COI locus results from the presence of a single *C. aestuarii* haplotype alongside the same common *C. maenas* haplotype found in the Americas. Other populations, in stark contrast, appear to be at least as diverse as native populations; sites in Nova Scotia (NW Atlantic) and Cape Town (South Africa) harbor especially high genetic diversity.

Several patterns do emerge from this data, although they are not generally the patterns that might be expected. For instance, Fig. 7 illustrates the relationship between both mitochondrial (a) and microsatellite (b) genetic diversity and time since establishment (relative to time of sampling) for all non-native *Carcinus* populations. *Carcinus* has likely been conveyed by different vectors in different episodes of its anthropogenic global expansion (Carlton and Cohen 2003). Given that more recent vectors (e.g., ballast water) should be associated with higher propagule pressures than many older vectors (e.g., solid ballast and hull fouling), and assuming that propagule pressure should be positively correlated with the genetic diversity of colonizing populations, one might expect more recently established populations to exhibit higher genetic diversity (Roman 2006; Roman and Darling 2007). This generally proves not to be the case. Certain recent introductions (e.g., to Nova Scotia and Cape Town, likely conveyed by ballast water) do exhibit relatively high levels of diversity, and the oldest invasion to the Atlantic US (probably introduced by solid ballast) ranks among the lowest diversity populations. But the invasion to Australia (despite arriving over 100 years ago, likely by solid ballast) appears to be rather highly diverse. Even more noticeably, a number of very recent invasions (e.g., Tasmania, Argentina, and Pacific North America) are surprisingly low in diversity. However, it is important to note that observed deviations from expectation reveal much about how complicated invasion histories might violate our assumptions. For instance, the three most recently established populations in Tasmania, western North America and Argentina also happen to be those three populations designated as likely secondary introductions by genetic methods (see Sect. 3). These populations have almost certainly experienced not just one, but two population bottlenecks associated with anthropogenic introductions, as indicated by their significantly lower diversity relative to their presumed non-native sources (Figs. 2 and 7). Thus, the playing field is markedly uneven in terms of retaining native genetic diversity, and some recent introductions exhibit low levels of diversity in large part because they derive from non-native sources.

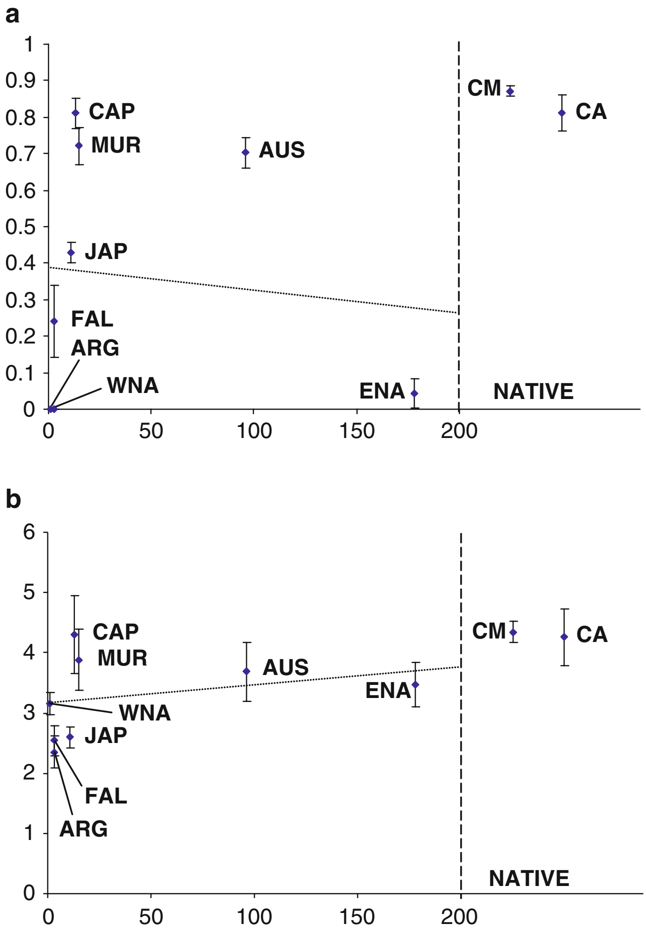


**Fig. 7** Mitochondrial gene diversity (**a**) and microsatellite allelic richness (**b**) of invasive *Carcinus* populations (y axis) as a function of time elapsed between initial establishment and sampling (x axis, in years). Values for native *C. maenas* and *C. aestuarii* are shown for comparison. Regression lines are shown, but no significant correlation was found in either case. ARG, Argentina; FAL, Tasmania; JAP, Japan; WNA, west coast North America; ENA, east coast US (New England); MUR, Nova Scotia (Canadian Maritimes); CAP, Cape Town; AUS, Australia; CM, native *C. maenas*; CA, native *C. aestuarii*

Multiple introductions may also play an important role in determining the diversity of invasive populations. This is now a widely recognized general phenomenon among invasive taxa (Dlugosch and Parker 2008), and may hold true for *Carcinus*, as well. Unfortunately, in most cases the lack of strong phylogeographic structure in the native range makes recognizing multiple introductions difficult. Genetic evidence for two introductions to the Atlantic coast of North America is a special exception illustrating this rule. The conclusion in this instance is supported not by the presence of particular haplotypes, but rather by a regional pattern of haplotype distribution that appears to be temporally unstable (see Sect. 4). Although the common haplotypes observed among crabs recently introduced to the Canadian Maritimes likely derive from northern European sources (Roman 2006), the predominant haplotype in the earlier *C. maenas* invasion is also the most common and widely distributed haplotype in the native range, observed in nearly every population surveyed (Darling et al. 2008). Thus the particular combination of haplotypes observed in the western Atlantic is alone insufficient evidence for multiple introductions, as some northern European populations exhibit very similar haplotype compositions. For *Carcinus*, inference of multiple introductions is therefore exceedingly difficult with temporal "snapshots" of genetic variation at particular sites. This may in fact be true of many invasive taxa with slight to moderate native genetic structure and highlights both the importance of regional patterns of non-native genetic diversity as well as the potential value of including a temporal sampling component in genetic studies of biological invasions.

The most convincing evidence of multiple *Carcinus* introductions involves those populations that harbour haplotypes of both *C. maenas* and its sibling species *C. aestuarii*. We have already seen that in Japan the presence of *C. maenas* haplotypes alongside *C. aestuarii* haplotypes possibly derived from eastern Mediterranean sources suggests that multiple introductions may have been involved in the establishment of these invasive populations (Sect. 5), although we have also noted that this conclusion is based on limited sampling of *C. aestuarii* genetic diversity and so must be considered highly tentative. Interestingly, if there have been multiple introductions it has hardly resulted in high genetic diversity for the Japanese populations, which rank among the least diverse populations globally at both mitochondrial and nuclear loci (Fig. 7). Similar inferences can be made in the case of Cape Town, South Africa. *C. aestuarii* haplotypes have been reported there at considerably lower frequency than in Japan (Darling et al. 2008; Geller et al. 1997), but their co-occurrence with *C. maenas* haplotypes of probable northern European origin strongly argues for multiple introductions to this region (Darling et al. 2008).

Perhaps a more interesting issue is the relationship between genetic diversity and invasiveness. Much discussion has focused on this relationship and the possibility that knowledge of genetic diversity may provide some predictive power in assessing the risks associated with particular introduced populations (Dlugosch and Parker 2008; Roman and Darling 2007). Here the example of *Carcinus* is particularly revealing, as there appears to be no correlation whatsoever between genetic diversity and invasiveness if the latter is judged as the capacity for post-establishment expansion and ecological impact. Perhaps the best illustration of this is the fact that the extraordinarily rapid spread of a single *C. maenas* population from San Francisco Bay to Vancouver Island (a geographic range that in all likelihood will continue to expand northward) has occurred despite remarkably low genetic diversity resulting from two separate bottlenecks, the second of which may have involved an effective founding population of as few as several dozen crabs (see Sect. 4). In contrast, the highly diverse mixed *Carcinus* population in Cape Town has remained virtually static. The comparison highlights the relative importance of biophysical context over genetic diversity, a relationship that is certain to hold true for many introduction events. While the combination of available estuarine habitats and advective currents conducive to long-distance larval dispersal have enabled the prodigious expansion of *C. maenas* in the eastern Pacific, South African green crabs seem to be constrained both by a preponderance of inhospitable rocky shores with heavy wave action (Hampton and Griffiths 2007), and by strong coastal upwelling driving larvae offshore and limiting recruitment to novel sites (Yamada and Kosro 2010). The validity of these comparisons depends in part on the degree to which the presence of *C. aestuarii* in South Africa may affect the ecology and population dynamics of *Carcinus* in the region, though the rarity of *C. aestuarii* COI haplotypes and the absence of substantial introgression of *C. aestuarii* nuclear microsatellite alleles suggests that comparisons with other *C. maenas* populations may well be appropriate.

## 7 Conclusions

The case of *Carcinus* provides a wealth of evidence for the diverse and valuable roles that genetic data can play in the study of biological invasions. Exploratory analyses of genetic data can prompt novel hypotheses regarding the most likely pathways of introduction for invasive populations. Predicted distributions of genetic variation can serve as explicit tests of hypotheses based on prior knowledge of the history and ecology of particular invasion events. And genetic analyses may even allow tests of generalized theoretical models explaining patterns of colonization and range expansion. The insights yielded by these analyses have the potential both to inform management of particular invasive taxa and to advance general understanding of the processes driving the successful establishment and spread of introduced populations.

There is every reason to believe that future genetic investigations of green crabs will continue to demonstrate their value in both domains. For instance, ongoing research aimed at better understanding the native phylogeography of *Carcinus* and the potential for interspecific hybridization in Europe (F. Palero, pers. comm. 2009) may yield insights not only into invasion history but also into the dynamics of interspecific admixture and their genetic consequences. Additional exploration of the western Atlantic *C. maenas* invasion will also likely enhance our appreciation for the complicated relationships between advective currents, larval dispersal, gene flow and genetic introgression between established and invading populations. Unfortunately, *C. maenas* shows every indication of increasing its global range, and will certainly provide further opportunities to examine expansion dynamics in different recipient environments and test hypotheses regarding the contributions of both life history and biophysical context in determining ultimate limits of invasive spread in places like the northeast Pacific and Argentina. All available evidence thus suggests that study of *Carcinus* will continue to inform our understanding of biological invasions in coastal marine systems and to provide a compelling case for the utility of genetic analysis in diverse facets of invasion biology.

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# Ecological Impacts of Replacing One Invasive Species with Another in Rocky Intertidal Areas

**Blaine D. Griffen**

**Abstract** As humans continue to move about the globe with ever-increasing frequency, they carry (intentionally and unintentionally) a host of species that are being introduced to new habitats. Consequently, there is now growing concern about the impacts of these numerous invasions for native communities. Determining the implications of species invasion requires comparing the impacts of invaders to those of species that are already present within invaded communities. As species invasion becomes more common, these comparisons are increasingly required between new invasive species and previously established invasive species. Here a case study is presented of the implications of replacing one invader with a new invader. The European green crab *Carcinus maenas* invaded the east coast of North America in the early 1800s. As an omnivorous predator, this invader has had widespread consumptive and nonconsumptive impacts on the native community. Two decades ago, a second predatory crab, the Asian shore crab *Hemigrapsus sanguineus* invaded this same region. In some parts of the invaded range, *H. sanguineus* has now replaced *C. maenas* as the dominant intertidal predator. The interactions between these two species that have likely contributed to this species replacement are reviewed. Then the implications of this species replacement for the native community are examined, specifically with regards to the differences in consumptive and nonconsumptive effects of these two predators, including both direct and indirect effects. Finally, population density and differences in habitat use by these two species are incorporated to predict how their impacts vary spatially along a latitudinal gradient throughout the invaded range.

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# 1 Multiple Invasions

With increasing globalization, species are being moved to new locations at increasing rates (Ruiz et al. 1997). Species transport is particularly prevalent in coastal marine habitats because of large volumes of water used as shipping ballast that carries stow-a-ways (Ruiz et al. 1997). The result is that most habitats are host to multiple nonindigenous species. When multiple invaders co-occur and interact, they may either influence each other positively, resulting in an invasion meltdown (when one invader facilitates subsequent invaders), or they may interact negatively, inhibiting each other's success (Simberloff and Von Holle 1999). Because of the alarming prospects of invasion meltdowns, positive interactions between invaders have received considerable attention, though few examples have been confirmed (Simberloff 2006). In fact, previous work suggests that interactions where at least one of the species of an interacting pair is negatively affected may be more common than facilitative interactions (Simberloff and Von Holle 1999). When negative interactions between invaders become sufficiently intense, agonistic exclusion of one of the species may occur. The result is potentially the replacement of one invader by another. The impacts of replacing one invader with another depend on the impacts of the individual species involved. The aim of the present study is therefore to provide a single case study of such a replacement in order to illustrate the range of factors involved in both the mechanisms and the implications for the native community.

# 2 A Case Study of Species Replacement

Two invasive crabs are currently found on the Northeast coasts of the United States. The European green crab *Carcinus maenas* (Linnaeus, 1758) was first noted on the Atlantic coast of North America in New York and New Jersey in 1817 (Say 1817), and spread into the Gulf of Maine by the early 1900s (Rathbun 1905). *Carcinus maenas* has invaded many areas globally, and is therefore found on each continent except the Antarctic (reviewed in Grosholz and Ruiz 1995, 1996; Audet et al. 2003). Recently, the Asian shore crab *Hemigrapsus sanguineus* (de Haan, 1835) has invaded much of the same region in Atlantic North America. First documented in New Jersey in 1988 (Williams and Mcdermott 1990), *H. sanguineus* rapidly spread into the Gulf of Maine within less than a decade (McDermott 1998a).

Though *C. maenas* is also found in subtidal and in soft sediment habitats, there is extensive overlap of these species in the preferred habitat of *H. sanguineus* - rocky intertidal areas (Tyrrell and Harris 1999; Lohrer et al. 2000; Jensen et al. 2002). Rapid increases in *H. sanguineus* densities in rocky intertidal sites throughout the southern portion of its invaded range have been correlated with simultaneous decreases in *C. maenas* densities at the same sites, so that just 2–3 years after the arrival of *H. sanguineus* in Connecticut and New York, *C. maenas* had almost entirely disappeared from rocky shores (Lohrer and Whitlatch 2002a; Kraemer et al. 2007).

North of Cape Cod, the shift appears to have occurred somewhat more slowly; still, throughout much of Massachusetts, *H. sanguineus* is now the numerically dominant species. Overall, a mere 20 years after it first arrived on the North American Atlantic coast, *H. sanguineus* was 20 times more abundant than *C. maenas* in sites south of Boston, Massachusetts (Fig. 1), while the density of the two species were similar at sites that *H. sanguineus* had invaded north of Boston (Griffen and Delaney 2007).

This pattern of expansion and species replacement is striking; however, *H. sanguineus* is unlikely to continue to spread northwards unchecked. Given larval development times and the mean southward flow of prevailing currents, a limit to the northern expansion of *H. sanguineus* is predicted along the central Maine coast (in fact, around its current northernmost extent), and populations at this northern limit may be ephemeral (Byers and Pringle 2006). Despite this prediction, the northern boundary of *H. sanguineus* does not appear to have finished expanding, as its northern extent was discovered to have pushed further northward as recently as 2008 (Delaney et al. 2008).

## 3 Why Is *Hemigrapsus* Replacing *Carcinus*?

While *H. sanguineus* has replaced *C. maenas* as the dominant intertidal consumer in many areas (Fig. 1), the reason for this is not entirely clear. Lohrer and Whitlatch (2002a) suggested that predation on postlarval *C. maenas* during or shortly after settlement is responsible for the observed replacement. This conclusion was based

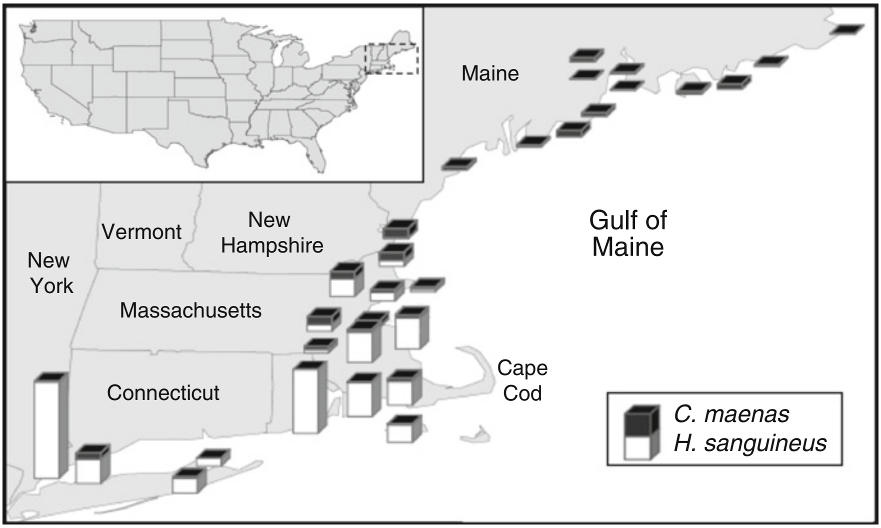

**Fig. 1** Relative densities (height of bars) of *C. maenas* and *H. sanguineus* at several rocky intertidal sites in New England in the summer of 2006 (Adapted from Griffen and Delaney (2007))

on results of caging experiments where *C. maenas* recruits were found in cages without *H. sanguineus*, but were not found in cages with *H. sanguineus*. However, several pieces of evidence suggest that the interaction between the two species may be more complex than this initial suggestion.

First, *C. maenas* is highly cannibalistic (Moksnes 2002). Cannibalism is especially strong among postlarvae and small juveniles (Moksnes et al. 1998), which are the very size classes that Lohrer and Whitlatch (2002a) proposed were being consumed by *H. sanguineus*. Further, this cannibalism is density-dependent, leading to self regulation of *C. maenas* populations (Moksnes 2004). Therefore, any mortality of *C. maenas* as a result of predation by *H. sanguineus* should simply serve to decrease *C. maenas* densities, thereby decreasing the strength of density-dependent cannibalism. Mortality from *H. sanguineus* predation should therefore simply represent compensatory mortality, and would need to be nearly 100% efficient to be solely responsible for locally eliminating *C. maenas*. But in fact, Lohrer and Whitlatch (2002a) found that *C. maenas* recruitment was depressed to similar levels inside cages with either *C. maenas* (from cannibalism) or *H. sanguineus* (from predation), supporting the supposition that predation should be compensatory. Moreover, *C. maenas* is highly efficient at selecting habitat that limits predation risk (Moksnes 2002; Moksnes et al. 2003). The absence of *C. maenas* in cages that housed larger (predatory) crabs during the experiment by Lohrer and Whitlatch (2002a) may reflect avoidance of settlement in these sites by postlarvae rather than solely post-settlement consumption. Predation between these species certainly occurs (Lohrer and Whitlatch 2002a; Griffen and Byers 2009), and may in fact be stronger than cannibalism given that cannibalism has a built in negative feedback that is not present in predation. However, the arguments above suggest that predation may not be solely responsible for the observed shift.

Second, in addition to direct predation, *H. sanguineus* is responsible for several other negative impacts on *C. maenas*, including reduced use of refuge habitat by juveniles (Jensen et al. 2002; Griffen pers. obs.), and diet shifts in adults from consuming primarily mussels to consuming primarily red algae (Griffen et al. 2008). Either of these two impacts could potentially contribute to the observed species replacement. Reduced refuge use by juvenile *C. maenas* may increase exposure to predatory birds or other predators. The diet shift by adult *C. maenas* in the presence of the new invader may reduce *C. maenas* population size by two mechanisms. First, the observed diet shift decreases individual growth rates (Griffen et al. 2008), potentially increasing the length of time that individuals are susceptible to size-dependent predation. Nitrogen is important for *C. maenas* growth (Mente 2003), and the induced reduction in individual growth rates may occur predominantly through nitrogen limitation. Mussels (*Mytilus edulis*: the predominant food when *C. maenas* forages alone) and the red alga *Chondrus crispus* (the predominant food item when *C. maenas* forages in the presence of *H. sanguineus*) differ greatly in their nitrogen composition. Percent nitrogen (%N) for both of these food sources varies seasonally, ranging from 0.4%N to 1.4%N for *Chondrus crispus* with highest values in the winter and lowest in the summer (Chopin and Floch 1992), and ranging from 7.7%N to 9.6%N for *Mytilus edulis* with the highest values in the spring and lowest values in the late summer and fall (Smaal and Vonck 1997). As a result, crabs that consume mussel tissue gain one to two orders of magnitude more nitrogen than crabs that consumed the same mass of algae. This difference may be further exacerbated by differences in assimilation of nitrogen from plant and animal foods, as the assimilation of nitrogen by crabs may also be up to 30% less efficient from plant food than from animal food (Wolcott and Wolcott 1984). The importance of this diet shift for *C. maenas* growth likely depends on how completely mussel consumption is eliminated and therefore likely differs across individuals. Second, the observed diet shift may limit reproductive capacity. For example, reproductive failure occurs in the herbivorous crab *Grapsus albolineatus* when nitrogen intake drops below 7% of the diet (Kennish 1996). The propensity for a molluscan diet in *C. maenas* (Ropes 1968) suggests that nitrogen intake is important. However, the specific nitrogen requirements for *C. maenas* reproduction are at this point unknown.

The precise mechanism underlying the replacement of *C. maenas* by *H. sanguineus* is therefore not certain, and may actually be the result of a combination of the mechanism posited previously (Lohrer and Whitlatch 2002a) and those described above. If this is the case, the relative importance of each mechanism is unclear. But despite the mechanism behind the replacement, it has occurred in southern regions of the invaded range, and may be progressing in northern regions (Fig. 1), though recent evidence suggests that the relative abundance of the two species has changed slowly in coastal New Hampshire sites over the last several years (Griffen et al. in review). An important question, therefore, is: what are the impacts of these two invaders and what are the impacts of replacing one with the other?

## 4 What Are the Impacts of These Species?

*Carcinus maenas* is a global invader (reviewed in Grosholz and Ruiz 1996; Audet et al. 2003) and consequently its impacts have been extensively studied. *Hemigrapsus sanguineus* has been less studied; however, since its introduction to the mid-Atlantic, it too has received considerable attention. Despite numerous excellent studies that substantiate the impacts of *C. maenas* in both native and invaded areas around the globe, comments here are restricted to studies conducted on the North American east coast where both crabs have invaded (i.e., New England and Long Island Sound, and primarily rocky shore studies) in order to facilitate direct comparison of their invasive impacts. Throughout this region are places where one species is overwhelmingly predominant (*C. maenas* in northern New England and *H. sanguineus* south of Cape Cod, Fig. 1) and there are areas where both species are found in similar abundances (New Hampshire and southern Maine, Fig. 1). In areas where both species are abundant, considerable attention has been devoted to understanding competitive interference between these two species that alters foraging behavior. The general conclusion is that these interactions greatly alter foraging behavior of *C. maenas*, and thus its diet, both qualitatively and quantitatively, while these interactions seem to have little influence on *H. sanguineus* foraging (Jensen et al. 2002; Griffen 2006; Griffen and Byers 2006a, b; Griffen et al. 2008; Griffen and Williamson 2008). However, changes in *C. maenas* foraging as a result of interactions with *H. sanguineus* appear to differ little from changes that result from interactions with conspecifics (Griffen and Williamson 2008). Therefore it is appropriate to focus primarily on the individual impacts of these species.

*Carcinus maenas* was introduced to the western Atlantic in the mid 1800s and now ranges from Nova Scotia to Maryland (deRivera et al. 2005), where it affects the native community as a voracious consumer. This European invader is omnivorous, and is responsible for a suite of consumptive and nonconsumptive effects that include direct and indirect effects on focal organisms, as well as broad effects that are manifest across the entire invaded community. While diet studies indicate that *C. maenas* is omnivorous, it preferentially consumes bivalves (Ropes 1968). As a result, it often has large direct predatory impacts on bivalves (Glude 1955; Richards et al. 1999; Lohrer and Whitlatch 2002b; Whitlow et al. 2003). For example, in the mid 1950s, *C. maenas* density increased dramatically throughout New England and it subsequently decimated the soft shell clam industry (Glude 1955). A recent study estimates that the impact of *C. maenas* on the United States Atlantic coast currently cost $22.6 million annually in loss to the shellfishery industry (Lovell et al. 2007).

*Carcinus maenas* also strongly impacts species with important ecological significance. For example, the native blue mussel *Mytilus edulis* is an important species ecologically on open coast shores of New England (Menge 1976), and is a major diet component of *C. maenas* (Elner 1981). Devastating impacts of *C. maenas* on mussel populations in the crab's native range have been documented (Ebling et al. 1964), and due to its high feeding rate on mussels in the invaded range (Lohrer and Whitlatch 2002b; DeGraaf and Tyrrell 2004; Griffen 2006), its effects on invaded mussel populations are also strong (Lohrer and Whitlatch 2002b). In addition to bivalves, *C. maenas* in New England also readily consumes snails <10 mm in shell height (Perez et al. 2009), and may have substantial direct predatory impacts on both herbivorous (*Littorina* spp.) and carnivorous (*Nucella lapillus*) snails (Griffen and Byers 2009). Thus, not only does *C. maenas* predation cause substantial economic impacts, but it also causes substantial ecological impacts on the native community by reducing the density of important filter feeders, micrograzers, and predators.

*Carcinus maenas* is also responsible for numerous nonconsumptive effects on prey throughout the invaded region, including both behavioural and morphological prey changes. For example, *Littorina littorea* is more likely to utilize crevices and other spatial refuges in the presence of *C. maenas* to avoid predation (Hadlock 1980). Additionally, herbivorous and carnivorous snails have experienced changes in shell morphology due to both selective consumption by *C. maenas* (Seeley 1986) and as a plastic response to the mere presence of *C. maenas* (Trussell 1996, 2000; Trussell and Smith 2000). Similarly, the bivalve *M. edulis* increases its shell thickness in the presence of *C. maenas* (Freeman and Byers 2006). Presumably these inducible defenses reduce the efficiency with which *C. maenas* consumes snail and bivalve prey.

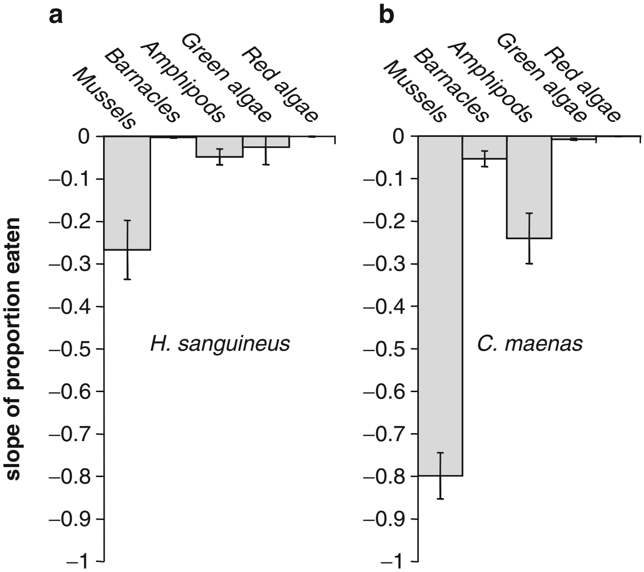

**Fig. 2** Prey preference of *H. sanguineus* (**a**) and *C. maenas* (**b**) during 30 h laboratory prey preference trials. Crabs were provided with animals and algae simultaneously to determine which was consumed more readily. Because different units were used for different food types (i.e., number of individuals for animals and mass for algae), food consumption was standardized by looking at the proportion remaining over time. This was done by using least squares to draw a line from the initial proportion available (i.e., 1.0) through the proportion remaining at the 5 time points examined for each individual crab. The mean ± std. error of the slopes of these regression lines are plotted here ($n = 10$ for each species). Slopes that are more negative indicate prey that were consumed more rapidly. The overall higher (more negative) slopes for *C. maenas* than for *H. sanguineus* indicate that *C. maenas* had higher overall consumption rates. For both species, mussels were preferred most, then amphipods, then barnacles (for *C. maenas*) and green algae (for *H. sanguineus*). Red algae were least preferred for both species

*Hemigrapsus sanguineus* is also a generalist predator, but is frequently found with large amounts of plant material in its gut (McDermott 1998b; Tyrrell and Harris 1999; Lohrer et al. 2000). However, *H. sanguineus* readily consumes animal tissues in laboratory feeding preference trials (McDermott 1998a; Tyrrell and Harris 1999; Brousseau et al. 2001; Bourdeau and O'Connor 2003; Brousseau and Baglivo 2005), and in fact appears to prefer animal prey over plants (Fig. 2). It therefore appears that *H. sanguineus* is highly opportunistic, and that the proportion of prey consumed under natural conditions likely reflects availability and ease of consumption.

Direct consumptive effects of *H. sanguineus* on the invaded community are predicted to be quite large given its incredibly high density and reasonably large per capita impacts (Lohrer and Whitlatch 2002b). Although animal tissues comprise a minority of *H. sanguineus*' diet, mussels are consistently found in gut examinations (McDermott 1998a; Tyrrell and Harris 1999; Lohrer et al. 2000), and *H. sanguineus* is capable of consuming large quantities of mussel prey (Ledesma and O’Connor 2001; Bourdeau and O’Connor 2003; DeGraaf and Tyrrell 2004; Brousseau and Baglivo 2005). For this reason, *H. sanguineus* has been implicated in drastic reductions in mussel populations within Long Island Sound (Lohrer and Whitlatch 2002b). Recent findings suggest that this could be due as much to removal of important mussel settlement sites with the consumption of barnacles (i.e., an indirect consumptive effect) as to direct mussel consumption (Griffen and Byers 2009). However, other studies question the impact of *H. sanguineus* on intertidal barnacles in Long Island Sound (Brousseau and Goldberg 2007), despite strong impacts of both crab species on barnacles in the Gulf of Maine (Tyrrell et al. 2006; Griffen and Byers 2009).

Several studies have directly compared the diet, consumption rates, or community impacts of *C. maenas* and *H. sanguineus* with the goal of understanding the implications of this species shift. These are each reviewed here.

## *4.1 Diet*

Studies that have directly compared the diets of *C. maenas* and *H. sanguineus* have found conflicting results. Laboratory studies that have compared the preference of these two species find little difference, suggesting that both prefer to consume animal rather than plant tissues (Fig. 2; Tyrrell and Harris 1999). Conversely, studies that examine the natural diet using gut contents have found that *H. sanguineus* consumed more plant material than *C. maenas* (for a single site in Connecticut: Lohrer et al. 2000). This may likely be due to dietary shifts by *H. sanguineus* to consuming more animal tissues under laboratory conditions where these foods are readily offered.

In an unpublished study conducted at the Isle of Shoals, Maine in 2005, an undergraduate student (Travis Guy from Albertson College) and I examined the diet of both *C. maenas* ($n$ = 25 adults, 35–50 mm carapace width, CW) and *H. sanguineus* ($n$ = 30 adult male, 22–28 mm CW), and then related this back to prey availability in the surrounding habitat (as determined from low tide sampling of ten 0.25 $m^2$ quadrats) using the foraging ratio (Krebs 1999) to determine which food types were preferentially selected for or against. We found that *C. maenas* overwhelmingly selected mussels (>70% of overall diet) and amphipods, while avoiding barnacles, and red, brown, and green algae (forage ratio, $\chi^2 = 231.42$, $p < 0.001$). Conversely, we found that *H. sanguineus* consumed mainly red algae (approx. 75% of diet) and that *H. sanguineus* preferentially selected red and green algae, while avoiding mussels, barnacles, amphipods, and brown algae (forage ratio, $\chi^2 = 48.43$, $p < 0.001$). Snails were not included in this study, but can also comprise an important part of the diet of *C. maenas*. Thus, available evidence suggests that under natural conditions, both species are omnivorous, but *H. sanguineus* is generally more herbivorous than *C. maenas.*

## *4.2 Consumption Rates*

Comparisons of mussel prey consumption have been made in both the laboratory and the field, again with conflicting results. In laboratory assays, consumption rates of *H. sanguineus* appear to be slightly higher than those of similarly sized *C. maenas* (DeGraaf and Tyrrell, 2004). In contrast, in field caging trials, consumption rates on mussels were much higher for *C. maenas* than for *H. sanguineus*, and this was true whether comparing similar sized individuals of the two species, both when foraging singly and in conspecific groups (Lohrer and Whitlatch 2002b), or when comparing different-sized individuals of the two species (i.e., large adult males), both when foraging singly and in conspecific groups (Griffen 2006; Griffen and Williamson 2008). The difference in consumption rates of these two species in the field is somewhat reduced when each species is offered its preferred size of mussel prey (*C. maenas*: 14–17 mm shell length; *H. sanguineus*: 7–10 mm shell length); yet even under these conditions, consumption rates of *C. maenas* are substantially higher (Griffen and Delaney 2007). This discrepancy between laboratory comparisons and field comparisons, again, may reflect a strategy where *H. sanguineus* readily consumes animal tissue under benign (laboratory) conditions, but less so under more stressful (field) conditions.

## *4.3 Community Impacts*

Experiments comparing the community impacts of these species have spanned a wide range of methods, from simplified 2-day laboratory and field experiments (Tyrrell et al. 2006), to 14-day field experiments (Tyrrell et al. 2006), to 5-month field experiments (Griffen and Byers 2009). Similarly these studies have differed in crab treatments from experiments with low densities of crabs designed to examine qualitative impacts of the two species (Tyrrell et al. 2006), to experiments that mimicked field densities and population structure in an effort to quantitatively define population-level impacts (Griffen and Byers 2009).

Under all of these conditions (field and lab, short and long term), both crab species drastically reduced the number of barnacles (Tyrrell et al. 2006; Griffen and Byers 2009), and over longer time scales, this indirectly reduced mussel density by eliminating favorable settlement sites as compared to control treatments that had no crabs of either species (Griffen and Byers 2009). In general, while there were some prey-specific differences in the population level impacts of these species over an entire foraging season, *C. maenas* and *H. sanguineus* depressed the levels of most animal (herbivorous and carnivorous snails, barnacles, mussels) and plant (red and brown algae) prey types to similarly low levels (Griffen and Byers 2009). This despite the much higher population sizes of *H. sanguineus*.

In long term field experiments, the two species also caused qualitatively similar indirect effects (Griffen and Byers 2009). Specifically, predation by both species of crab reduced the number of carnivorous snails (*Nucella lapillus*), though *C. maenas* consumed more than *H. sanguineus*. Additionally, both crab species caused *N. lapillus* to reduce its consumption rates on barnacles, while only *C. maenas* caused a reduction in *N. lapillus* predation on mussels. Thus, though both crabs directly consumed barnacles and mussels, consumption was somewhat offset by these positive indirect effects elicited via changes in the density and behaviour of *N. lapillus*. All of these impacts, both direct and indirect, were highly dependent on the abundance of prey, which differed across years with annual variation in prey recruitment. Indirect effects also depended on the size structure of *N. lapillus* populations, as only small snails were consumed by crabs or changed their foraging behaviour in response to crabs (Griffen and Byers 2009).

In addition to these positive indirect effects, both species also had negative indirect effects caused by barnacle consumption (Griffen and Byers 2009). Barnacles provide settlement sites for both mussels and macroalgae. Reductions in barnacle density therefore indirectly reduced the numbers of mussels and macroalgae that successfully recruited. These negative indirect effects were stronger for *H. sanguineus* than for *C. maenas* because *H. sanguineus* reduced barnacles to lower densities. Further, these indirect effects were consistent across years, suggesting that over longer time scales, these effects may accumulate resulting in stronger impacts than were observed in these relatively short (5 month) experiments.

These two crab species differ somewhat in their nonconsumptive effects, though these differences may be fleeting. *Mytilus edulis* from regions where *H. sanguineus* has been present for approximately 20 years, respond morphologically to the presence of either species by developing thicker shells, presumably to reduce mortality to crab predation. Yet mussels found in northern regions where *H. sanguineus* has been present for much shorter periods of time respond to *C. maenas* (which has been present in the region for many decades), but not to *H. sanguineus* (Freeman and Byers 2006). This suggests that prey are capable of developing plastic responses to the threat of crab predation fairly quickly, and that within decades and without other mitigating circumstances, these two species may elicit similar responses throughout their ranges. As with mussels, the presence of *C. maenas* causes nonconsumptive morphological changes in other prey, including carnivorous and herbivorous snails (Trussell 1996, 2000; Trussell and Smith 2000). To date, studies have not yet demonstrated whether *H. sanguineus* elicits similar morphological changes in non-mussel prey.

## 5 Ecological Impacts of Replacing *C. maenas* with *H. sanguineus*

If replacing *C. maenas* with *H. sanguineus* were a simple one-for-one substitute, the impacts on the invaded region would likely be minimal given the similarity in diet and consumption rates of these species and the fact that native species appear to be “learning” to respond similarly to the two invaders. However, this species replacement does not appear to be on a one-for-one basis. Rather, densities of *H. sanguineus* throughout the invaded range are on average approximately six times higher than those of *C. maenas*, and this difference is much more pronounced in southern areas (Fig. 1) (Griffen and Delaney 2007). Several factors may contribute to this difference in species abundance, including stronger conspecific aggression among *C. maenas* than among *H. sanguineus* (Griffen and Delaney 2007), higher reproductive output for *H. sanguineus* (McDermott 1998c), and lower mortality of young-of-the-year for *H. sanguineus*, which appears to represent a bottleneck for *C. maenas* populations (Moksnes 2004). However, even with drastic differences in population densities, community impacts of the two species do not differ greatly for many prey species (Griffen and Byers 2009). Yet, some important differences do occur. For instance, *H. sanguineus* had larger impacts over a single foraging season on brown algae. Further, these differences, as well as many smaller, non-statistically significant differences in effects across the rest of the community over a single foraging season could accumulate across foraging seasons (i.e., longer than the duration of any experimental investigations to date) to ultimately yield different community structures.

Aside from small differences that derive from differential consumption of these two species, important differences may also occur as a result of the spatial distribution of these invaders. To understand this point, three pieces of information are important. First, strong conspecific interference among *C. maenas* causes individual crabs to spread out spatially, thus limiting the local density of these consumers (Griffen 2009). In contrast, *H. sanguineus* is much less aggressive towards conspecifics (Griffen and Williamson 2008), and tends to aggregate much more readily. Second, there is a latitudinal shift in the abundance of intertidal boulders utilized by both *H. sanguineus* and *C. maenas* as refuge habitat. Large intertidal boulder fields are common in the Gulf of Maine, but are much less frequent, for example, throughout Long Island Sound. Third, interference from high densities of conspecifics has different influences on predation by these two species. Conspecific interference strongly reduces predation rates of *C. maenas*, but has little influence on predation rates by *H. sanguineus* (Griffen and Delaney 2007; Griffen and Williamson 2008).

Putting these three pieces of information together, the following may be predicted. In southern areas (e.g., Long Island Sound), where intertidal refuge is limited, *H. sanguineus* will aggregate into areas with available intertidal refuge (boulders). Because this refuge is less abundant, local densities in these areas will be high and impacts on prey in the immediate area will be large. Whereas in northern areas (e.g., central to southern Gulf of Maine), where intertidal refuge is abundant, *H. sanguineus* are likely to be spread more evenly across intertidal areas and their impacts will therefore not be as concentrated, and thus not as strong. This hypothesis is consistent with both the incredibly high densities in southern areas that have previously been reported (Lohrer and Whitlatch 2002b; Brousseau et al. 2003), and the strong impacts on sessile prey in these areas (Lohrer and Whitlatch 2002b), as well as with the much lower *H. sanguineus* densities within the Gulf of Maine (Griffen and Delaney 2007; Griffen et al. 2008) and their relatively modest impacts (Griffen and Byers 2009). These patterns may further be strengthened by spatial differences in larval supply that may inhibit *H. sanguineus* population growth in northern regions (Byers and Pringle 2006).

These same differences in refuge habitat and concentration of *H. sanguineus* may also contribute to the spatial difference in replacement of *C. maenas*. In southern intertidal sites, *C. maenas* was essentially eliminated from rocky shores less than a decade after the arrival of *H. sanguineus* (Lohrer and Whitlatch 2002a; Kraemer et al. 2007), while in Gulf of Maine intertidal areas *C. maenas* remains at similar abundances nearly two decades after *H. sanguineus*' arrival (Tyrrell et al. 2006; Griffen and Delaney 2007; Griffen et al. 2008; Griffen in prep.). The high concentration of *H. sanguineus* in southern areas and the subsequent intense levels of interactions between these species (both competitive and predatory), is likely responsible for the disappearance of *C. maenas* from these limited intertidal refuge habitats. Whereas in northern areas where refuge is much more abundant and *H. sanguineus* is much less dense, interactions between the species are likely much less detrimental and therefore do not elicit the pressure necessary to eliminate *C. maenas* from these regions.

Existing studies documenting this species replacement have focused solely on rocky intertidal habitats (Lohrer and Whitlatch 2002a; Kraemer et al. 2007). *Carcinus maenas* is a habitat generalist, and its elimination from rocky intertidal sites may not reflect its total elimination from the region, but may potentially reflect a habitat shift towards greater use of soft bottom habitats. To date, no data have been presented to examine this possibility.

In conclusion, replacing *C. maenas* with *H. sanguineus* may potentially have large impacts on the invaded area. However, these impacts are unlikely to stem from minor differences in diet. Rather, impacts are likely to result from increased crab biomass following this shift, as *H. sanguineus* appears capable of reaching much higher densities and biomass than *C. maenas* (Griffen and Delaney 2007). Thus, the arrival of *H. sanguineus* in Long Island Sound resulted in the elimination of *C. maenas*, the proliferation of extremely high *H. sanguineus* densities, and the subsequent decline of important prey species (Lohrer and Whitlatch 2002a, b). However, these same drastic changes are unlikely to be seen throughout the range of *H. sanguineus* within the Gulf of Maine. Rather, limited recruitment due to prevailing currents (Byers and Pringle 2006) and the high abundance of intertidal refuge in northern areas suggest that in New Hampshire and Maine, *H. sanguineus* numbers may remain more diffuse and its impacts may prove to be less dramatic. This highlights the importance of understanding the influence of environmental factors when examining the influence of invasive crustaceans and other invasive species (Griffen and Byers 2009).

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