LOBSTERS: BIOLOGY, MANAGEMENT, AQUACULTURE AND FISHERIES

Edited by

Bruce F. Phillips
Department of Environmental Biology, Muresk Institute, Curtin
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Preface

The stimulus for this book was the publication of the *Biology of Freshwater Crayfish*, edited by David M. Holdich (2002, Blackwell Science Ltd). Several other books on marine lobsters have also been published over the last 25 years, however, the Holdich book is different. Although it deals with topics such as growth, nutrition, reproduction and behaviour, the full material for the commercial species is presented under each separate genera, rather than under fisheries, countries or topics such as management, aquaculture or conservation. We have followed the same approach except for a few minor instances where it was appropriate to make comparisons for clarity.

The amount of material which has been published on marine lobsters is vast by comparison to the freshwater species. For this reason I have encouraged the authors to concentrate on publications which have appeared over approximately the last 10 years, particularly if the material has been reviewed.

Not all genera of marine lobsters are covered in this volume. In selecting the material, I have chosen those genera with the most commercially important populations. Readers will no doubt find gaps in the topics examined. Space limitations precluded the inclusion of additional material.

Readers will find some overlap between chapters in this book. This is not a bad thing and essentially impossible to prevent. For example, Chapter 3 (Behaviour), Chapter 1 (Growth) and Chapter 5 (Pathogens, parasites and commensals), all include aspects discussed in a number of other chapters, but their comments are different, usually dealing with aspects of impact on fisheries, fishing, populations, or their detection or measurement.

Many people contributed to the development and production of this book. We cannot acknowledge them individually because there isn't space, but all the authors wish to thank the many colleagues who assisted them with their contributions.

Bruce F. Phillips

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Chapter 1

Growth and Development: Understanding and Modelling Growth Variability in Lobsters

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1.1 Introduction

Lobsters are among the largest-bodied and longest-lived modern marine arthropods (Wolff, 1978; Sheehy, 2001). They are ecologically important as consumers in a variety of temperate and tropical marine ecosystems (Robles *et al.*, 1990; Mayfield *et al.*, 2000). In many parts of the world, lobsters also support commercially valuable fisheries, in some regions the most economically important one (FAO, 2004). Because demographic processes such as survival, reproduction and movements are body-size dependent, understanding growth processes is central to any understanding of population dynamics, ecological function and sustainable management.

This chapter builds upon several previous edited volumes with specific chapters on growth and development in the Crustacea (Wenner, 1985a, b; Lee & Wickins, 1992), and lobsters in particular (Cobb & Phillips, 1980a, b; Phillips *et al.*, 1994a; Factor, 1995; Phillips & Kittaka, 2000). These reviews cover aspects of growth, such as the physiology and endocrine control of moulting (Aiken, 1980; Hartnoll, 1982, 1985; Waddy *et al.*, 1995; Chang *et al.*, 2001; Hartnoll, 2001), intrinsic and external factors affecting growth (Waddy *et al.*, 1995; Booth & Kittaka, 2000; Hartnoll, 2001), and practical approaches to culturing lobsters (Lee & Wickins, 1992; Aiken & Waddy, 1995; Booth & Kittaka, 2000; Kittaka, 2000). Although these publications provide a wealth of information on growth, spanning a range of lobster taxa, we did not find a synthesis or critical evaluation of the modelling approaches employed in the study of lobster population dynamics. An especially challenging aspect of the study of crustacean populations is the determination of age. The absence of conspicuous age markers in crustaceans makes it all the more necessary to have a clear understanding of the age-to-body size relationship and the factors that contribute to its variability.

Lobster growth can be highly variable, reflecting the effect of quantum changes associated with moulting and in the probability distributions of moult increments (Fig. 1.1). Here we focus on recent developments in our understanding of the factors influencing growth and how to incorporate variability in population dynamics modelling to improve our ability to assess and forecast population trends. We primarily draw upon peer-reviewed literature and technical reports on the relatively well-studied genera of clawed (*Homarus, Nephrops*) and spiny (*Panulirus, Palinurus, Jasus*) lobsters. This chapter aims to provide an update of literature since 1980; however we frequently cite earlier literature where it is particularly relevant. First, we give a brief comparison of the different taxon-specific patterns of development, growth and the onset of maturity, as well as an overview of the stages of the moult cycle. The second section reviews the tools employed to measure growth or determine age in lobsters. Third, we survey the range of environmental influences on growth and sexual maturity, and in the final section we describe different modelling approaches that have been used

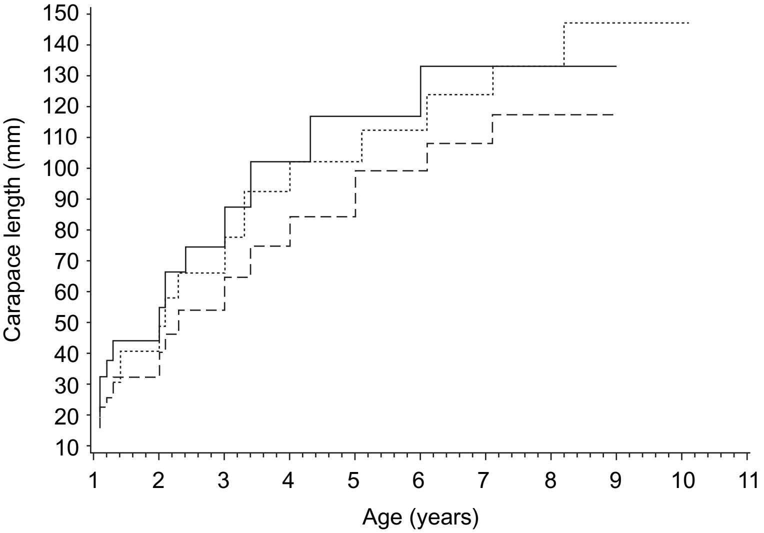

Fig. 1.1 Individual growth trajectories of American lobsters, *Homarus americanus*, reared in a culture facility illustrating variability in growth patterns (B. Estrella, personal communication).

to capture the influence of variability in size with age in population dynamics. This variability holds important implications for the development of demographic models for lobster populations.

1.2 Development, growth patterns and the moult

1.2.1 Larvae and postlarvae

All lobsters have a complex life cycle with a long-lived adult phase, relatively late onset of maturity, fertilisation by stored sperm when the eggs are extruded by the female; external brooding of embryos for several months; larvae hatch and are planktonic for weeks to months and metamorphose to a postlarva that eventually settles, moults to a juvenile and takes up a benthic existence. In lobsters, the nauplius larva develops entirely within the embryonic membrane (Gore, 1985; Helluy & Beltz, 1991) and hatches as the developmental equivalent of the first zoea of brachyuran crabs. In clawed lobsters (nephropids) this is referred to as the stage I larva, and in spiny and slipper lobsters (palinurids and scyllarids) as the stage I phyllosoma. The larval forms of clawed and spiny lobsters are widely divergent in morphology, behaviour and duration. The size of larvae and postlarvae split quite clearly along taxonomic lines. The larvae and settling postlarvae of clawed lobsters tend to be substantially smaller than those of spiny and slipper lobsters. It is important to be aware of the distinction between stages and instars – the former relates to morphological changes, the latter to the number of moults (Kittaka, 1994). In clawed lobsters, there are just three morphologically distinct larval instars, stages I–III. In spiny lobsters, there are many more larval instars (Table 1.1) and the morphological stages of the phyllosoma can less dependably be linked to a particular instar. As a result, *Jasus edwardsii*, for example, will complete all phyllosoma stages in 13 to 17 instars (Kittaka, 1994). The larvae of both spiny and clawed lobsters are planktivorous and preferentially feed on zooplankton (McConaugha, 1985; Kittaka, 1994; Ennis, 1995; Kittaka, 2000). After the final larval instar, lobsters undergo metamorphosis to a postlarva which is developmentally equivalent to the megalopa in brachyuran crabs. In spiny lobsters this stage is called the puerulus. The postlarval stage more nearly resembles the adult and is the stage that starts its benthic existence. Unlike the postlarva of clawed lobsters, which continues to feed, the spiny lobster puerulus does not feed (Kittaka, 1994, 2000).

The daily energetic investment in growth during the larval stages is greater than during the first

Table 1.1 Comparison of selected lobster taxa by size and timing of larval, juvenile, and adult life history characteristics. CL = carapace length (mm). Numbers of larval instars for spiny lobsters were based on laboratory rearing studies and can vary; numbers in parentheses are presumed on the basis of observations of *J. verreauxi* (Kittaka, 2000).

	Number of larval instars	Larval duration (weeks)	Size at postlarval[a] settlement stage (CL)	Size at female maturity (CL)[b]	Age at female maturity (years)	Postlarval to adult growth factor[c]	Sources
Nephrops norvegicus	3	4–8	3.3–4.0	21–34	4.0–4.5	11.1	Morizur (1983), Pollock (1991),Tuck *et al.* (1997, 2000), Ulmestrand & Eggert (2001)
Homarus americanus	3	4–8	4.5	55–120	5–8	19.4	Aiken (1980), Pollock (1991), Estrella & MacKiernan (1989), Comeau & Savoie (2001)
Homarus gammarus	3	4–8	4.5	92–96	7–9[d]	20.9	Sheehy *et al.* (1999), Tully *et al.* (2000), Sheehy & Bannister (2002)
Jasus lalandii	(17)	44	10	56–74	7+	6.5	Annala (1991), Pollock (1991, 1997), Kittaka (1994, 2000)
Sagmariasus verreauxi	17	44	10.5	155–184	6–7	16.1	Annala (1991), Pollock (1991), Montgomery (1991) in Brown & Phillips (1994), Kittaka (1994, 2000)
Jasus edwardsii	(17)	43	11.4–12.3	<65–114	8	7.8	McKoy (1985), Annala & Bycroft (1988), MacDiarmid (1989a, b),Annala (1991), Pollock (1991), Brown & Phillips (1994), Kittaka (1994, 2000), Hobday & Ryan (1997), Phillips & Kittaka (2000)
Palinurus elephas	7–9	9–19	10	82–95	5–6	8.9	Kittaka (2000), Ceccaldi & Latrouite (2000)
Panulirus cygnus	9	39–47	7–8	90–100	6–7	11.3	Brown & Phillips (1994), Booth & Kittaka (2000), Phillips & Kittaka (2000)

Table 1.1 *continued*

	Number of larval instars	Larval duration (weeks)	Size at postlarval[a] settlement stage (CL)	Size at female maturity (CL)[b]	Age at female maturity (years)	Postlarval to adult growth factor[c]	Sources
Panulirus argus	11	26–34	6	75–91	2–3	13.8	Lewis (1951), Hunt & Lyons (1986), Baisre & Cruz (1994), Baisre (2000)
Panulirus guttatus	10	?	10	32	2–3	3.6	Pollock (1991), Sharp *et al.* (1997), Briones-Fourzán & McWilliam (1997), Robertson & Butler (2003)
Panulirus japonicus	27	49	6–8	38–42	1.5–2.0	5.7	Kittaka (1994), Nakamura (1994), Nonaka *et al.* (2000)

a. Postlarva = stage IV for *Nephrops* and *Homarus*; puerulus for *Jasus*, *Panulirus*, and *Palinurus.*
b. Size at 50% egg bearing.
c. Ratio of postlarval and adult carapace length using midpoints of size ranges where given.
d. Based on age pigment analysis.

benthic stages. For example, in the American lobster, growth rates were found to be almost twice as fast for planktonic postlarvae (0.46 mg per day) as they were for initial benthic stages (0.26 mg per day) (Juinio & Cobb, 1994; James-Pirri & Cobb, 1997). While clawed, spiny and slipper lobsters differ little with respect to the average growth factor between moults during larval development (Nephropidae: 127%, Palinuridae: 133%, Scyllaridae: 132%), the greater number of larval instars in spiny and slipper lobsters results in a dramatically greater overall length increase from first to last larval stage (Nephropidae: 185%, Palinuridae: 1258%, Scyllaridae: 926%; Gore, 1985). In contrast to the dramatic proportional size increase during larval development, intermoult growth factors during the juvenile and adult stages rarely amount to more than 15% in length, regardless of taxon (Table 1.1). There has been little speculation and virtually no research on the functional significance of the dramatic growth spiny and slipper lobsters undergo during their larval stages. For more detail on specific patterns of larval development, growth and allometry, readers are referred to Wenner (1985a).

1.2.2 *Juveniles and adults*

Hartnoll (1982, 2001) refers to a range of growth patterns exhibited by the Crustacea, spanning taxa with indeterminate growth and reproduction at every instar after maturity to those with a terminal, or maturation moult that reproduce only once. Lobsters fall at one end of the continuum by uniformly exhibiting indeterminate growth and being capable of reproducing at every instar after the onset of maturity. The intermoult period increases with size from a few days in the larval and early juvenile stages to a few years in large, older adults. On the other hand, the percent increment of growth per moult typically diminishes with body size (e.g. Aiken, 1980). Although the intermoult growth factor during the benthic stages is small by comparison to the planktonic larvae, overall growth during benthic life is far greater, the difference between the settling postlarva and sexually mature adult often being many times in carapace length and several orders of magnitude in body mass (Table 1.1).

The early benthic phase of lobsters is typically cryptic, sedentary and solitary, rarely leaving shelter, the nursery habitat being a complex substratum – rocks, coral rubble, macroalgae or sea grass – providing protection to the young lobster (e.g. Pollock, 1997). Most lobsters are omnivorous, consuming molluscs, other crustaceans and algae, although different levels of trophic specialisation are documented (*J. lalandii* – Mayfield *et al.*, 2000). Suspension feeding has been documented in juvenile *N. norvegicus* and *H. gammarus* (Loo *et al.*, 1993). Juveniles undergo an ontogenetic shift in behaviour in which they either become wider ranging in their movements or change habitats altogether. While clawed lobsters remain largely solitary in their shelter use, spiny lobsters become more social and gregarious, and are often found sharing shelters or migrating in groups (Chapter 8).

The growth rate and onset of maturity varies widely among spiny and clawed lobsters, and in general the taxa from warmer environments grow faster and mature sooner than those in cooler regions (Table 1.1). Males of all taxa mature physiologically at a smaller size than females, however, it is likely that males need to be as large as or larger than females to successfully mate. There is more than one mature instar and all female instars after maturity are capable of being ovigerous. The age and size at maturity varies from species to species (Table 1.1). Maturation, in turn, has a retarding effect on growth and the effect is usually greater on females than males because of the greater energetic allocation to reproduction. Taxonomically or ecologically similar groups can vary widely in size at maturity (Table 1.1). Growth rates and the onset of maturity within taxa are strongly under the influence of the environment, and the nature of the proximate, environmentally induced variability is discussed in Section 1.4. The ultimate cause of this variability among taxa has been difficult to identify, although Hartnoll (1985) proposed the idea that early survivorship will be an important determinant of lifetime egg production, and therefore a significant force in the evolution of the size and age of maturity in Crustacea.

Maturation also brings on sex-specific allometric growth patterns. The onset of maturity is typically earlier and at a smaller size in male than in female lobsters and the instars over which it occurs depends on the environment. When females begin to mature, their intermoult period begins to increase relative to males in the same instar. Sexual differences in allometry can be a useful indicator of the size at onset of sexual maturity (Aiken & Waddy, 1989; Megumi & Satoru, 1997; Robertson & Butler, 2003). For example, in *H. americanus* claws become relatively larger in males while the abdomen becomes relatively larger in females (Aiken & Waddy, 1989; Conan *et al.*, 2001; MacCormack & DeMont, 2003). In spiny lobsters, the first and second pereiopods become relatively longer, but the surface area of pleopods becomes relatively smaller in males than in females (*P. argus* – Aiken, 1980; Hartnoll, 1985; Mykles & Skinner, 1985; Skinner *et al.*, 1985; Waddy *et al.*, 1995; *Panulirus japonicus* – Megumi & Satoru, 1997; Chang *et al.*, 2001; Robertson & Butler, 2003).

1.2.3 Moult stages and endocrine control

The mechanism and physiology of moulting has been reviewed in some detail by Aiken (1980), Hartnoll (1985), Skinner *et al.* (1985), and Waddy *et al.* (1995). The key events of the moult cycle are summarised here. The moulting process undergoes a sequence of stages in which the old skeleton separates from the underlying epidermal cells and a new cuticle is formed, which, after the old skeleton is shed, thickens and hardens to form the new one. As the old exoskeleton is decalcified from underneath, calcium carbonate is temporarily conserved in crystalline form as a pair of gastroliths on the lateral walls of the foregut. Given the opportunity, as another means of conserving calcium, lobsters will consume their cast-off exoskeleton after their mouthparts have hardened.

The externally-conspicuous characteristics of the five stages (A–E) of the moult cycle are outlined here, modified somewhat from an earlier scheme developed by Drach (1939). The stages have been particularly well illustrated for *H. americanus* by Waddy *et al.* (1995). Starting immediately after ecdysis, stage A occupies the brief time – usually 24–48 hours – it takes for the soft and wrinkled newly-exposed integument to stretch out to its now larger form and deposit the first of several inner layers of the new exoskeleton, the endocuticle. The endocuticle lies below the exocuticle and epicuticle already laid down just prior to the moult. Stage B is completed when the final layers of the endocuticle have been deposited. During stage C, the exoskeleton achieves maximum rigidity by virtue of chemical changes that harden the already deposited endocuticle; and at this point intermoult has been reached, the protracted period lasting until the onset of physiological changes that prepare the integument for another moult. Stage D, premoult or proecdysis, involves the separation of the endocuticle of the old skeleton from the underlying epidermis, followed by the deposition of what will be the outer layers of the new exoskeleton, first the epicuticle and then the exocuticle. Through demineralisation, a conspicuous softening in parts of the old skeleton and the ecdysial sutures occurs during this stage, that facilitates ecdysis. During ecdysis, stage E, water is ingested and absorbed with the effect of increasing hydrostatic pressure within the body which causes the ecdysial sutures, such as the one along the dorsal midline of the carapace, to break. In 10–20 minutes of immobility, the animal rolls on its side, the exoskeletal membrane between the thorax and abdomen ruptures, and the animal withdraws, thereby completing the cycle.

Most growth and regeneration occurs during intermoult and early premoult periods. Muscle tissue, for example, grows in size by elongation; the number and arrangement of muscle fibres (cells) remain constant while the number of thick and thin myofibrils (myosin and actin) increases (Skinner *et al.*, 1985). The control of form and morphogenesis was reviewed by Mittenthal (1985). During proecdysis, just prior to the moult, the muscles atrophy temporarily by an enzyme-mediated degradation of actin myofibrils (Mykles & Skinner, 1985) presumably aiding the animal in withdrawing from the old exoskeleton, although it is likely to be accompanied by partial and temporary loss of mobility.

While the hormonal regulation of moulting is often presented as a simple system of two antagonistic hormones, as so aptly put by Waddy *et al.* (1995), crustacean moulting physiology 'is a profoundly complex process about which much is known, but little is understood'. Hormonal biochemistry and physiology has been intensively studied in *H. americanus* (Waddy *et al.*, 1995; Chang *et al.*, 2001). Three families of hormones come into play: (1) moulting hormones (ecdysteroids), (2) moult inhibiting hormone (MIH) and related crustacean hyperglycemic hormone (CHH) neuropeptides, and (3) terpenoid methyl farnesoate (MF). Each of these hormone groups serves a diversity of functions, in some cases changing at different stages of development. Their role in lobster growth is briefly summarised below. Greater detail may be found in useful reviews by Waddy *et al.* (1995) and Chang *et al.* (2001).

Moulting hormones (ecdysteroids) induce the physiological changes that lead to the moult. This family of hormones is produced by the Y organ, a pair of hypodermal glands to either side of the thorax. Haemolymph titres of ecdysteroids peak at premoult sub-stage D_1 and D_2 when pre-exuvial cuticle is being formed. At sub-stage D_3, levels drop dramatically when the old exoskeleton is being resorbed and remain low after ecdysis from stage A to D_0 when premoult begins.

The moult inhibiting hormone (MIH) is considered the main regulator of moulting. It is structurally similar to crustacean hypoglycemic hormone, which may also play a role in moult regulation. The X organ–sinus gland complex, a specialised neural tissue located in the eyestalks, produces this family of neuropeptides. Heightened levels of MIH typically present during intermoult, suppress the synthesis of moulting hormones in the Y organs. As the location of the X organ suggests, environmental factors, particularly light levels, photoperiod and temperature can influence the synthesis of MIH, explaining the responsiveness of the moult cycle to changes in the environment. The peptide sequence of MIH is very similar to CHH, however one derivative, CHHa, has both a hypoglycemic and moult inhibiting effect, while the other, CHHb, has only a hypoglycemic effect (Chang *et al.*, 2001). Levels of CHH appear to increase in the haemolymph in the latter part of the moult, apparently play-ing a role in increasing water retention during exuviation.

Methyl farnesoate (MF), a sesquiterpene, is a precursor of juvenile hormone and can also play a role in the regulation of the moult cycle by retarding the moult in larvae (Borst *et al.*, 1987). MF is secreted by the mandibular organ. In adult lobsters it is also thought to play a role in reproduction; larger mandibular organs and higher haemolymph concentrations of MF in adult females suggest it has a sex-specific function and may be important in sexual differentiation (Chang *et al.*, 2001).

1.3 Measuring growth

Growth in crustaceans has been measured by both direct and indirect methods. Direct measures of growth per moult or per unit time have been provided by rearing studies of captive animals or tag–recapture studies in the wild. Indirect measures of growth and size at age are provided by the analysis of size frequency distributions of samples of wild lobster populations. The quantification of so-called ‘age pigments,’ metabolic by-products that accumulate with age, have been used with varying degrees of success in lobsters and crayfish as a proxy for age. Additional methods such as RNA : DNA ratios can provide further information on the nutritional status of the animal and therefore its growth potential.

A large number of laboratory and hatchery-based studies of lobster growth have accumulated over the decades. A comprehensive review of rearing techniques for larval and postlarval stages of lobsters is provided by Lee and Wickins (1992). Virtually all growth studies of larvae and a large number of post-settlement stage studies have been conducted in the laboratory. One of the great advantages of conducting laboratory growth studies is that it has provided a valuable setting in which to conduct factorial experiments to evaluate heritable and environmental effects (Van Olst *et al.*, 1976; Jong, 1993; Rahman *et al.*, 1997; Crear *et al.*, 2000, 2003) as well as for detailed descriptive studies of the moult cycle (Aiken, 1980; Dupre, 2000). Experiments have been conducted to evaluate the effect of temperature, photoperiod, space, substrate, feeding regimes, and stocking density among other factors. Many of these studies report valuable information on growth increment, intermoult duration and factors affecting growth, and have demonstrated the potential for widely divergent growth patterns of individual lobsters (Fig. 1.1).

Exact estimates of intermoult duration (or alternatively, the number of moults per unit time) are particularly difficult to obtain in the field. Laboratory observations have proven to be extremely valuable in this regard although caution is always necessary in extrapolating their results to wild populations. An illustration of the variability in the number of moults for different age classes of American lobster in a culture facility is provided in Fig. 1.2. The variation in the number of moults

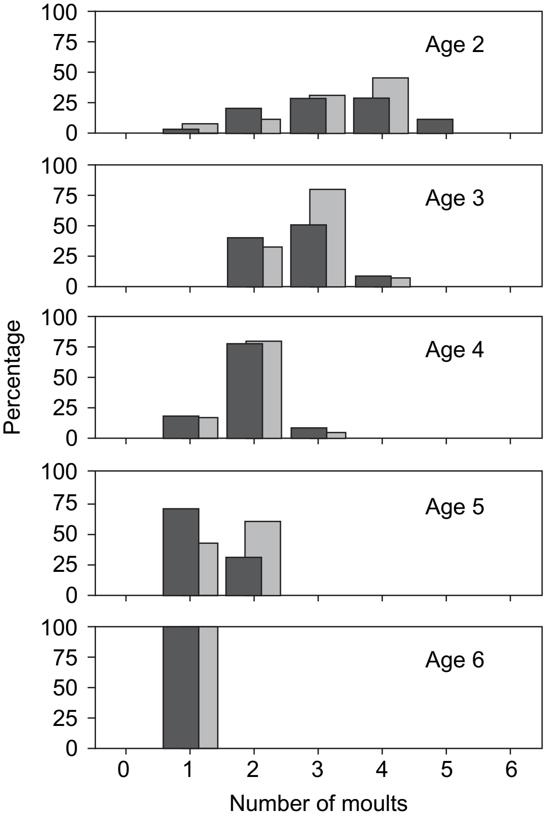

Fig. 1.2 Number of moults per age (age groups 2–6) of American lobsters, *Homarus americanus*, reared in a culture facility (B. Estrella, personal communication).

at younger age classes sets the stage for wide variation in length at age throughout the lifespan.

It is important to state at the outset that while carapace length is used almost universally as the measure of lobster body size, it cannot be assumed to vary isometrically with body mass. It is therefore important to determine the carapace-length-to-body-mass relationship by sex for each species, and preferably by region within a species. Because body mass varies approximately as the cube of body length, some workers have used the cube root of body mass, the so called 'nominal length,' as a linear proxy for body mass, providing a way to study allometric deviations of actual linear dimensions of the body from an isometric slope of 1.0. For example, in a study of regional differences in allometry of the American lobster, MacCormack and DeMont (2003) found that relative to nominal length, carapace length became proportionally larger in males and smaller in females by scaling factors of 1.05 and 0.86, respectively. To our knowledge, a similar analysis of carapace length against nominal length has not been done for other lobster taxa. In practice, carapace length remains the conventional index of body size, and it is understood that the carapace-length-to-body-mass relationship is one of the first morphometrics to assess in any study of growth, so that size-dependent processes, whether physiological or ecological, may easily be expressed as a function of body mass.

1.3.1 First moult in captivity

A common approach to obtaining measures of growth increment that are likely to be free of laboratory artefacts and representative of growth in the wild is to hold newly-captured premoult lobsters in captivity only long enough for them to moult and allow their new skeletons to harden (e.g. *J. lalandii* – Hazell *et al.*, 1998; *N. norvegicus* – Castro *et al.*, 2003). This provides a valuable measure of moult increment as a function of size before the moult (see the Hiatt model, Section 1.5.1). The assumption is that the effects of laboratory artefacts on the growth increment are minimal because the factors affecting growth up to that moult would already have acted.

1.3.2 Tagging

Tag–recapture methods have been widely employed to assess growth of lobsters in the wild. This is probably the most widely used method of obtaining growth data that is in most cases unbiased by artefacts associated with handling or captivity (but see Brown & Caputi, 1985; Phillips *et al.*, 1992). In the 1960s, the development of internal spherion tags that are anchored in the musculature and not lost during the moult was a methodological breakthrough for the study of growth in wild populations of crustaceans (e.g. Wilder, 1963). Since then a number of innovative tags have been invented for different applications ranging from internally anchored, but externally visible t-bar and streamer tags (e.g. Campbell, 1983a; Comeau & Savoie, 2001) to entirely internal microwire tags that are detected magnetically (Walker, 1986; Bannister *et al.*, 1994; Incze *et al.*, 1997; Cowan, 1999) and internal coloured latex tags (Robertson & Butler, 2003).

Internal tagging is not without risks, however. Of most concern is the mortality associated with tagging, either from the trauma of the tagging process itself or secondary infection. Also of concern is the loss of tags either from natural wear and tear, contact with other lobsters especially in traps, or during the moulting process itself. This is why it is highly recommended that any tagging study includes an assessment of tag-loss rates and lethal and sublethal effects (e.g. Brown & Caputi, 1985). Double tagging is one way to assess tag losses in the field.

A particularly innovative tagging approach developed by Shelton and Belchier (1995) has been to embed a small section of cuticle and underlying dermal tissue within a large muscle. The embedded tissue continues to go through the normal moult cycle, but since the cast-off cuticles are trapped within the musculature, they accumulate in layers, thereby giving a record of the number of moults occurring over the time elapsed. However, this living tag method has yet to be used widely.

Aside from trauma-related effects of tagging or handling, it is important to be aware of more subtle biases that may occur in mark–recapture sampling. In developing size-transition probabilities from tag–recapture data, one must be aware of tag loss, tag-related mortality, and size selectivity in the sampling process. For example, as pointed out by Punt and Kennedy (1997) and Punt *et al.* (1997), if the probability of recapture increases with size, the probability of recapturing an animal that has grown will exceed that of an animal of the same original size that has not grown. In a similar vein, multiple recaptures can also bias growth estimates, especially in the case where lobsters may be prone to multiple recapture while they are sublegal, but then are retained by the harvester after they have recruited to the legal size; it is recommended only to use first recaptures in these cases.

1.3.3 Analysis of size-frequency distributions

The analysis of size-frequency distributions has been the most common indirect way to assess growth in lobsters, probably due to the widespread availability of size data from population surveys. This method is most successful when age classes already form fairly discrete modes in the size distribution, or one has some prior knowledge of the age–size relationship and associated individual variability (e.g. Sainte-Marie *et al.*, 1996; Tuck *et al.*, 1997; Castro *et al.*, 1998; Ulmestrand & Eggert, 2001). With long-lived crustaceans such as lobsters, it is more the rule than the exception that age classes overlap in size so that age-specific modes in the distribution are obscured. However, it is often the case that the younger age classes at least are represented as one or a few conspicuous modes in the distribution (e.g. MacDonald & Pitcher, 1979; Sainte-Marie *et al.*, 1996). While it may be possible simply by visual inspection of the distribution to infer the likely distributions of the separate age classes, methods are also available that provide a more statistically objective approach. Statistical software such as MIX (MacDonald & Pitcher, 1979), ELEFAN (Pauly & Neal, 1984) and MULTIFAN (Tuck *et al.*, 1997) are good examples. Even these approaches require the user to make some initial assumptions about the number of age classes in the population, the constancy of recruitment, as well as the mean, standard deviation, and skewness of the size distributions for each age class, depending on which program is used. These educated guesses are then the starting point for an iterative series of goodness-of-fit tests to fine tune the estimates. Clearly, the quality of the analysis largely depends on the validity of these assumptions. MIX treats a single length distribution while the other programs permit evaluation of a time sequence of length composition estimates (Fig. 1.3).

Prior to conducting an analysis of size-frequency distributions, it is important to be wary of how sensitive the distributions can be to the sampling method; the investigator should be especially cognisant of the size-selectivity of the sampling gear and how it might bias any representation of the size distribution. For example, trapping surveys are notoriously size selective and may entirely miss the early juvenile segments of the population that are otherwise well documented by other methods at the same location. ELEFAN, for example, can account for the effects of selectivity in the sampling method.

1.3.4 Physiological age markers

The absence of anatomical age markers in crustaceans has posed a major challenge to an assessment of growth in wild populations. The so-called ‘age pigment’, lipofuscin, accumulates in the brains of crustaceans and has been shown to be a useful proxy for age in a variety of Crustacea, including lobsters (Nicol, 1987; Berman *et al.*, 1989; Sheehy, 1990, 1992; Belchier *et al.*, 1994; Sheehy *et al.*, 1996, 1998, 1999; Wahle *et al.*, 1996). A brief overview of the development of the method and its prospects for the future is worthwhile here.

Lipofuscin fluoresces under ultraviolet light enabling quantification by optical methods. Fluorescence microscopy and image analysis of histological preparations of brain tissue became the preferred method over solvent extraction of the pigment because density, sizes and shapes of pigment granules can be distinguished from any background fluorescence (Sheehy & Ettershank, 1988; Berman *et al.*, 1989). Initially, image analysis was performed on paraffin-embedded sections of the olfactory lobe. During the early 1990s, analyses of known-age specimens of lobster and crayfish produced promising regressions between

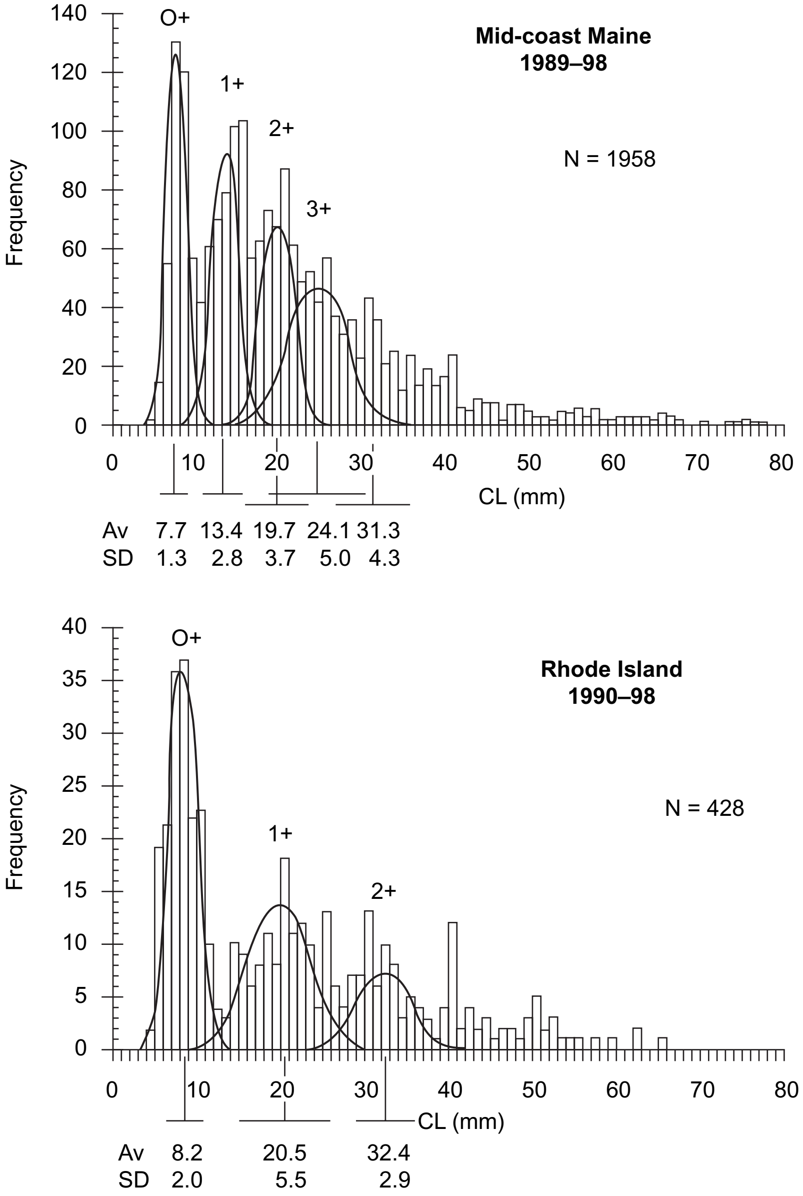

Fig. 1.3 Decomposition of American lobster, *Homarus americanus*, length-frequency distributions into estimated age classes for early age groups in Maine and Rhode Island (R. Wahle, unpublished).

pigment concentration and age in the freshwater crayfish, *Cherax* (Sheehy, 1990, 1992) and the lobsters *N. norvegicus* (Tully, 1993), *H. gammarus* (Sheehy & Wickens, 1994) and *H. americanus* (de Kerros *et al.*, 1995; Wahle *et al.*, 1996). Later, confocal microscopy streamlined the methodology considerably by permitting the analysis of fresh specimens (Belchier *et al.*, 1994; Sheehy *et al.*, 1999), thereby sidestepping concerns that tissue fluorescence of preserved specimens tends to increase over time (Nicol, 1987). Moreover, eyestalk ganglia provided a more convenient source of neural material than the olfactory lobe, which required more involved dissection. Subsequent field tests, one with *P. cygnus* (Sheehy *et al.*, 1998), and one with *H. gammarus* (Sheehy *et al.*, 1999; Uglem *et al.*, 2005), in which tagged known-age lobsters were at liberty in the wild for most of their lives, provide clear evidence that age pigments resolved age classes better than did size-based methods. In the case of *H. gammarus*, the dramatic variability in age at recruitment to the fishery and the inferred extreme ages of some of the wild lobsters provided new insight into how protracted the recruitment process can be for some species (Sheehy *et al*., 1999).

Lipofuscin accumulation is not independent of environmental effects, however. Its rate of accumulation demonstrably increases with temperature and therefore may be a better indication of physiological age – the accumulated aerobic respiration with age – than of chronological age (Tully *et al*., 2000; Sheehy & Bannister, 2002). Thus, corrections for regional, seasonal and annual differences in thermal regime have been incorporated in the assessment of age (Tully *et al*., 2000; Sheehy & Bannister, 2002). While this may be possible where the thermal history of a wild lobster can be determined, it will become problematic for lobsters whose patterns of movements result in dramatically different thermal regimes being experienced over the lifespan. Thus, expectations for the use of age pigments as a new standard for chronological age have yet to be realised in most cases. The method remains costly and time consuming. Nonetheless, these promising research developments warrant a continued effort to pursue an independent measure of age.

1.3.5 Radionucleotide ratios to determine intermoult periods

Originally applied as an aging tool in molluscs (e.g. Turekian & Cochran, 1981 in Hartnoll, 2001), this radiometric method evaluates ^{228}Thorium to ^{228}Radium ratios in calcified skeletons. In crustaceans it can be useful as a means to determine the time since the last moult, and was first applied to the lobster *H. gammarus* by Le Foll (1989). We are aware of no more recent application of this method in lobsters.

1.3.6 Indicators of growth potential

Several indicators of the nutritional status of lobsters can be useful in assessing the prospects for future growth. For example, high tissue RNA : DNA ratios indicate high rates of protein synthesis and can serve as a proxy for nutritional status. This method has been applied in larvae and early benthic *H. americanus* to project future growth potential (Cobb *et al*., 1991; Juinio & Cobb, 1994; James-Pirri & Cobb, 1997). Similarly, premoult concentrations of lipids in the haemolymph are in the exploratory stages as a possible predictor of moult increment in *J. edwardsii* and warrant further investigation in the field (Musgrove & Babidge, 2003).

1.4 Environmental influences on growth and maturity

Regional and temporal variability in growth, development and the size at sexual maturity in lobsters are largely attributed to environmental heterogeneity. But even when reared under identical conditions there is often substantial individual variability in growth, even within offspring from the same mother (Aiken & Waddy, 1988). In communal rearing studies with the American lobster, small differences in initial size have been shown to be an important factor in determining individual growth trajectories (Waddy *et al*., 1995). Differences in thermal regime are among the most often cited environmental factors to play a role, but others may enter in as well, such as food limitation or intraspecific interactions. Stressful environmental conditions often result in delaying the moult or reduced growth increment, and even shrinkage (Cockcroft & Goosen, 1995). Such sensitivity of growth to environmental conditions can have important implications for population dynamics and management. In the lobster literature we found no rigorous analysis of the degree to which regional differences in growth rate or maturity may be explained by heritable variation as a result of population differentiation. Following the lead of similar reviews for spiny and clawed lobster (Phillips *et al*., 1994a, b; Waddy *et al*., 1995), we provide an overview of key environmental factors occurring naturally – both abiotic and biotic – that cause geographic and temporal differences in growth in both pelagic larvae and the postlarva as well as in benthic juveniles and adults.

1.4.1 Temperature

Larvae and postlarvae

The larval and postlarval development of nephropid lobsters is particularly temperature sensitive and despite an ability to control position in the water column, pelagic stages are largely at the mercy of the thermal regime in which they drift during their first weeks or months of life. It is perhaps not surprising that the greatest volume of literature on thermal effects on nephropid lobster growth comes from the part of the world where sea surface temperatures exhibit dramatic latitudinal and seasonal extremes.

In the American lobster, larval development will occur over a relatively large temperature range. However, it is inhibited at temperatures below 10°C. Development time from hatching to the postlarva, ranges from two months at 10°C to only ten days at 22–24°C (e.g. MacKenzie, 1988). Larval size can also vary with temperature: larval American lobsters reared at 15–18°C were larger than those reared at either higher or lower temperatures (MacKenzie, 1988). Recent studies conducted in the Gulf of St Lawrence (Ouellet & Allard, 2002) are consistent with early hypotheses that larval and postlarval sizes tend to be smaller at warmer temperatures, because of smaller growth increments that accompany accelerated development (Templeman, 1936). However, geographic differences in the size of wild larvae do not always correlate with temperature (Waddy *et al.*, 1995; Incze *et al.*, 1997), and it is difficult to determine whether spatial or temporal differences in size are the result of size-dependent mortality or earlier settlement of larger individuals from the plankton.

Less growth information is available for larval spiny lobsters, probably because of the difficulty of rearing them and the protracted larval duration of many months (Kittaka, 1994, 2000). In general, successful rearing of larvae of the cool water species, such as *Jasus* and *Palinurus* has been done at 20°C, and of the warm water species of *Panulirus* at 25°C (Kittaka, 2000). Rearing experiments with phyllosoma larvae of the subtropical Japanese spiny lobster, *P. japonicus*, suggest that the optimum temperature for growth is 26°C, but that it shifts downward to 24°C in more advanced larval stages (Kittaka, 1994).

Juveniles and adults

Regional differences in the growth rate of juvenile and adult benthic stages are well documented and are readily attributable to temperature, especially in clawed lobsters. In the American lobster, thermal enhancement of growth is proportional to temperature increase from 8–25°C (Carlberg & Van Olst, 1976). Below 5°C, metabolism is slowed to a point where the moult does not occur, and temperatures above 25°C are physiologically stressful or lethal (Waddy *et al.*, 1995). The southern Gulf of St Lawrence and southern New England where summer temperatures rise above 20°C, boast some of the fastest growing *H. americanus*, whereas in the colder waters of the northern Gulf of St Lawrence and the Bay of Fundy, lobsters grow more slowly. Under constant 20°C temperatures, *H. americanus* in captivity has been reared to marketable size (83 mm carapace length (CL)) in two years (Hughes, 1972), but this species is not likely to ever experience that level of growth in the wild. To a lobster within the legal size range, regional or year-to-year differences in temperature can substantially alter the timing and frequency of the moult (Templeman, 1936; Munro & Therriault, 1983; Comeau & Savoie, 2001, 2002) – a factor having significant consequences for annual recruitment to the fishery.

Similar, but less dramatic thermal effects on growth have been observed for microwire-tagged European lobsters released at the age of one year in different thermal regimes in England, Scotland and Norway (Sheehy & Bannister, 2002; Uglem *et al.*, 2005). Even under these less extreme thermal conditions compared to the north-west Atlantic, Sheehy and Bannister (2002) demonstrated that lobsters recruit to the fishery over a broad range of sizes, suggesting that other factors also influenced variability in growth.

For *N. norvegicus*, a deep-water lobster that, unlike *Homarus* does not migrate to warmer shoal waters during the summer, Hillis and Tully (1993) found vertical mixing had a positive effect on growth. That is, at locations in the Irish Sea where *Nephrops* grew more slowly, the water column became thermally stratified during the summer, and bottom temperatures were as much as 3–4°C colder than locations that were vertically mixed.

Temperature also strongly influences growth of spiny lobster juveniles and adults, although these species do not tolerate as great a range of temperatures as clawed lobsters do. Growth rates tend to vary more strongly among species, with warm-water forms growing faster than cooler-water forms (Booth & Kittaka, 1994). Generally, within limits most species grow faster if held at slightly warmer than ambient temperatures in captivity. Optimal temperatures for growth in culture is reported to be 29–30°C for *P. argus* and 18–20°C for *J. edwardsii*, for example (Booth & Kittaka, 1994). However, rearing at these temperatures may incur adverse effects such as lower food conversion efficiency and higher incidence of disease. Despite regional differences in temperature, growth rates of *J. edwardsii* are similar over hundreds of km of coast encompassing a large portion of this species' range (Annala & Bycroft, 1988). This may be explained in part by the fact that changes in temperature oppositely affect increment and moult frequency. For example, in a growth experiment with juvenile *J. edwardsii* reared under different temperature regimes between 18 and 22°C, the overall growth response did not change. However, this disguises the fact that as moults became more frequent, the moult increment diminished. In contrast, at 24°C, growth slowed because of longer intermoult periods, possibly reflecting physiologically stressful conditions.

Warm temperatures also hasten the onset of maturity in lobsters. Lobsters in warmer regions not only grow faster, but they mature at a smaller size than the conspecifics living in cooler water. For example, in the American lobster, *H. americanus*, females mature between 68 and 76 mm CL in the warmer parts of their range, but between 87 and 97 mm in the cooler parts (Estrella & McKiernan, 1989; Comeau & Savoie, 2001). Similarly, size at maturity of female *J. edwardsii* in New Zealand shifts from 72 mm to 122 mm CL with declining gradient in temperature (Annala, 1991). In turn, thermally-mediated differences in the onset of maturity affect the degree of claw and abdomen allometry in the American lobster (MacCormack & DeMont, 2003).

Laboratory manipulation of the seasonal temperature cycle can dramatically alter the moult cycle. For example, if American lobsters are held at 10°C or higher in the spring they quickly enter premoult and advance to ecdysis. But if they are artificially held at the same temperatures into the autumn, the moult is inhibited even into the next summer (Waddy *et al.*, 1995). Moreover, Waddy *et al.* (1995) reported that warmer than normal temperatures of 15–20°C experienced during the winter override seasonal moult inhibition so that the moult may occur at any time of year. Still, lobsters reared under constant temperature will retain some seasonality in their growth cycle. American lobsters reared from hatching at a constant 20°C in the absence of a seasonal temperature cycle nonetheless exhibited a seasonal pattern of moulting with the highest frequency in the spring and autumn, and lowest in mid-summer and winter (Aiken & Waddy, 1989) suggesting factors other than temperature may affect seasonal patterns of growth. Waddy and Aiken (1999) suggest this may be an effect of photoperiod or the presence of an endogenous rhythm.

1.4.2 Light and photoperiod

Larvae and postlarvae

Light intensity and day length can significantly affect growth and development and determine the seasonality of the moult cycle. Bright lights inhibit the moult in American lobster larvae, and larvae grown in complete darkness take on more weight (Hadley, 1906; Templeman, 1936; Eagles *et al.*, 1984). The response of larval growth to day length varies with the season; laboratory experiments have demonstrated that in spring and summer, short day lengths are most favourable for growth, whereas in early autumn, long day lengths favour growth (Waddy *et al.*, 1995). In *Homarus*, the metamorphic moult from larval stage 3 to the post-larva has been shown to occur with highest frequency during the dark phase of a photoperiod, but with continuous illumination it occurs randomly throughout the day (Aiken & Waddy, 1995). Waddy and Aiken (1999) expanded on this work; they found that the metamorphic moult occurs in the form of a population-based daily rhythm. Moulting is arrhythmic in larvae reared in constant illumination, but in cyclic photoperiods moulting occurs predominantly in the dark phase, even when the light and dark phases of the cycle are reversed. The results suggest that the moulting rhythm is under the influence of an endogenous pacemaker that is entrained by the photoperiod.

Juveniles and adults

Juvenile and adult American lobsters, in contrast, moult predominantly during the day (Tamm & Cobb, 1976). Since lobsters tend to forage nocturnally, continuous illumination can inhibit feeding and negatively affect growth; conversely hyperactivity induced by constant darkness can become an energy drain with similar effects (Aiken, 1980). Juvenile *J. edwardsii* under laboratory rearing conditions generally grew more slowly under either long dark or long light photoperiods, than they did when day lengths were more evenly balanced towards a 12L : 12D cycle (Crear *et al.*, 2003).

1.4.3 Food limitation

Larvae and postlarvae

Lobster larvae in culture with more food develop faster, grow larger, and survive better, although excess food can result in suboptimal conditions for growth (Waddy *et al.*, 1995). As in many other crustaceans, lobsters require foods rich in polyunsaturated fatty acids, carotinoids and astaxanthin pigments derived from both algal and animal sources (McConaugha, 1985; Kittaka, 1994, 2000). The larvae of clawed and spiny lobsters are omnivorous, and consume zooplankton and suspended particles (Kittaka, 1994, 2000; Ennis, 1995). While the postlarvae of clawed lobsters are also planktivorous, the puerulus postlarvae of spiny lobster species are non-feeding (Kittaka, 1994, 2000). In *Homarus*, larvae reared on a diet consisting of other crustaceans – either naturally occurring live zooplankton or commercially available brine shrimp – are more robust and grow faster than those reared on other foods (Lee & Wickins, 1992; Aiken & Waddy, 1995). As long as sufficient energy reserves have accumulated, growth of larval American lobsters is largely independent of food supply; however, starved postlarvae arrest the moult cycle in stage C and eventually die (Juinio *et al.*, 1992). Readers are referred to Lee and Wickins (1992), Phillips *et al.* (1994a), Aiken and Waddy (1995) for a more comprehensive treatment of optimal stocking density of lobster larvae and postlarvae in culture.

Little is known of the extent to which growth and development of lobster larvae in the wild may be subject to food limitation. One of the few studies to examine this question, evaluated levels of daily protein synthesis in American lobster postlarvae off the southern New England coast as determined by RNA : DNA ratios (James-Pirri & Cobb, 1997). They found significant year-to-year differences in the percentage of what were deemed poorly nourished postlarvae, although the consequences of this variation for subsequent growth and survival were unclear. Postlarvae had consistently higher levels of protein synthesis than newly-settled benthic lobsters, which was attributed to the change from a planktonic to a benthic existence.

Juveniles and adults

In the benthic stages, as in the larvae, starvation or low quality food can delay the moult, and the lobster can suffer so-called ‘moult death syndrome’ (Lee & Wickins, 1992; Waddy *et al.*, 1995). In general, juveniles require more food as a percent of body weight (10% per day, but not more) than do adults (Waddy *et al.*, 1995; Mente *et al.*, 2001). Levels of serum protein are a good predictor of both intermoult period and weight gain per moult (Castell & Budson, 1974; Mente *et al.*, 2001). Many studies have been conducted to evaluate the influence of both natural and artificial foods on growth, much of which has been summarised in the reviews cited above. A few more recent studies are worth mentioning. Crustaceans are an important component in the diet of many lobsters. For example, mature *H. americanus* reared on rock crabs (*Cancer irroratus*) grew significantly faster than on an artificial diet without crab even when the calorific content was greater (Gendron *et al.*, 2001). But a diet consisting of molluscs in some cases results in better growth; in rearing experiments with *J. edwardsii*, lobsters reared on a diet of mussels (*Mytilus edulus*) grew faster than those fed a formulated shrimp feed (Thomas *et al.*, 2003). In an apparent interaction between diet and the temperature sensitivity of growth, weight gain in *J. edwardsii* was found to be more temperature sensitive on a diet of prawn than on mussel (Crear *et al.*, 2000).

Evidence of food limitation of growth in wild populations is more prevalent and convincing for spiny lobsters than for clawed lobsters. A dramatic example is the widespread response of the Cape rock lobster, *J. lalandi*, to an El Niño-related anomaly that affected food supply (Pollock *et al.*, 1997; Hazell *et al.*, 2002). Between 1990 and 1994, coastal upwelling along the South African coast failed, nearshore temperatures rose, and primary production dropped, leading to a die-off of the ribbed mussel, *Aulacomya ater*, a principal food of this lobster. Consequently, the lobsters moved to deeper, normally less-productive water and growth increments declined coast-wide. Remarkably, in the first documented cases of negative growth in a wild lobster population, the average shrinkage per moult was recorded to be as great as 3%. A concomitant reduction in size at maturity also occurred during these years (Cockcroft & Goosen, 1995; Pollock *et al.*, 1997). A historical analysis of population size structure suggests that conditions were often favourable for growth earlier in the twentieth century than during its last quarter (Cruywagen, 1999). While the Cape rock lobster can be an opportunistic feeder (Barkai & Branch, 1988), recent trophic studies suggest that regional differences in response to these events depend on the the availability of its preferred planktotrophic prey, *A. ater* and the barnacle, *Notomegabalanus algicola* (Mayfield *et al.*, 2000). Similarly, for Australia's western rock lobster, *P. cygnus*, Joll and Phillips (1984) found that consistent differences in lobster growth rates among different reefs were related to the food availability. Stomach contents of lobsters living in 'high-growth' populations were dominated by molluscs and contained a diversity of other animal and algal material, whereas diets of lobsters in 'slow-growth' populations were dominated by coralline algae and were less diverse. A depth-wise decline in the growth rates of *J. edwardsii* in southern Australia has also been attributed to a gradient in food availability (McGarvey *et al.*, 1999).

1.4.4 Density effects

Larvae and postlarvae

Larval and postlarval stages of lobsters occur in nature at such low densities that intra-specific crowding is never likely to be a factor in growth. But in culture, density effects are well known, the adverse effects of high density being food limitation, interference, cannibalism, and disease. Optimal stocking densities for maximum growth and survival of different lobster taxa are discussed by Lee and Wickins (1992) and Waddy and Aiken (1995).

Juveniles and adults

The benthic stages of lobsters are far more prone to density-dependent effects, both in culture and in the wild. Clawed lobsters tend to prefer and grow better in a solitary existence, and often do not do well under communal rearing conditions (Waddy *et al.*, 1995). Far lower densities than those used for spiny lobsters have adversely affected survival, moulting frequency and increment both in culture (Van Olst *et al.*, 1976; Aiken & Waddy, 1978) and in field enclosures (Wahle *et al.*, 2001). Communally-reared American lobsters are cannibalistic, especially if not provided shelter, and at the extreme, in rearing tanks with no shelter, only a single large lobster has remained at the end of four-month trials (Waddy *et al.*, 1995). Communal rearing could be viable, even preferable, for *Homarus* if juveniles reared on substrata with plenty of shelter were periodically sorted into similar-sized groups and then restocked, thereby avoiding the adverse effects of larger individuals on smaller ones through growth inhibition and cannibalism (Aiken & Waddy, 1988). In field enclosures consisting of cobble substratum, Wahle *et al.* (2001) observed a significant interaction between stocking density and the thermal environment such that the growth of first year lobsters in the warm regime (12–17°C) was significantly affected by density, but in the cool regime (10–15°C) there were no density effects, presumably because lobsters had not grown big enough in the four-month trial to begin to crowd each other. On the other hand, per capita survival in this experiment, while unaffected by differences in thermal regime, was adversely affected by the higher stocking density treatments, both with the same and older age classes.

Despite the solitary and aggressive nature of *Homarus*, other than from laboratory and field enclosure experiments, we know of no compelling evidence of density-dependent effects on growth in the wild. For *N. norvegicus* though, Tuck *et al.* (1997) reported an inverse relationship between population density and both estimated maximum adult size (L_∞) and the size at maturity (Tuck *et al.*, 2000), perhaps suggesting this species is more likely to be subject to density-dependent food limitation than *Homarus.*

Because spiny lobsters are social and gregarious they lend themselves well to culture at high density (Booth & Kittaka, 1994, 2000). In fact, juvenile stocking densities as high as 200 individuals per m^2 have not only been employed, but result in higher growth than solitary rearing (Lee & Wickins, 1992; Booth & Kittaka, 2000). It is therefore somewhat ironic, given their sociality, that most examples of density effects on growth in the wild by way of food limitation come from spiny lobsters. In three cases, *J. edwardsii* in southern Australia (McGarvey *et al.*, 1999), *P. marginatus* of the Hawaiian Islands (Polovina, 1989), and *P. gilchristi* in South Africa (Groeneveld, 1997), significantly smaller adult body size, or onset of maturity, or slower growth, was attributed to higher local population densities. In all cases, the populations were thought to be food limited at high density. Experimental manipulation of density in the field to evaluate growth effects has only been reported for *P. cygnus* in Western Australia (Ford *et al.*, 1988). In this case, reduced-density populations experienced lower per capita mortality, but no growth effects. In captivity, *J. edwardsii* tolerated high densities but suffered adverse growth effects: young juveniles reared at a density of 200 per m^2 experienced 40% less weight gain than those stocked at 50 per m^2, but survival in the two treatments was the same (Booth & Kittaka, 2000).

1.4.5 Space and shelter

Space limitation can affect growth in the same way as crowding (Van Olst *et al.*, 1976). American lobsters, *H. americanus*, housed in individual cages within culture tanks have been shown to grow at the same rate as those reared communally in the same kind of tank at the same density (Aiken & Waddy, 1978). Growth rates were found to scale with the area provided per individual such that unlimited growth was obtained with areas greater than $75 * CL^2$ (CL = carapace length), whereas growth was limited when the per capita area was reduced to $18 * CL^2$. Thus, provided there was enough space, individual cages did not hinder growth and had the added benefit of preventing cannibalism. Structurally-complex habitat, whether shell, rocks, or vegetation can enhance survival and therefore carrying capacity by segregating individual lobsters (Van Olst *et al.*, 1976; Aiken & Waddy, 1988; Linnane, 2000). Growth rates of lobsters reared communally in these more naturalistic habitats characteristically vary substantially (Roach, 1983; Linnane, 2000; Wahle *et al.*, 2001). It is not known whether in the wild the structural elements of habitat, apart from the other components of habitat, influence lobster growth.

The space requirements of spiny lobsters appear to be far less than those of *Homarus* probably owing to their social habit. *Jasus edwardsii* for example at 35 mm CL only required 20 cm^2 of space (Booth & Kittaka, 2000) whereas the same-sized *H. americanus* would require 918 cm^2 by the Aiken and Waddy (1978) formula above. With spiny lobsters there is less known about the effect of structure and space on growth. Habitat enhancement has been practised in at least two spiny lobster fisheries, but the impact on lobster growth is doubtful. For example, in the Caribbean, artificial habitats such as casitas and pesqueros have been used to enhance population densities in the fishing grounds for *P. argus*, but to date there is no evidence of any positive effect on growth through trophic enhancement by these structures (Briones-Fourzán *et al.*, 2000; Cruz & Phillips, 2000). Similarly in Japan, more substantial concrete artificial reefs have been widely used to promote spiny lobster larval settlement and to attract older lobsters migrating from offshore, but their role in enhancing lobster growth has not been demonstrated (Nonaka *et al.*, 1989).

1.4.6 Behavioural and social conditions

With the American lobster, Nelson *et al.* (1980, 1983) found that individuals reared several cm downstream from larger individuals were 40% smaller than those reared further downstream. Aiken and Waddy (1988) found that under communal rearing conditions, after lobsters were sorted into narrow size groups and restocked, new behavioural hierarchies became established as previously subordinate lobsters assumed new status thereby altering their growth trajectory.

In spiny lobsters, the first juvenile stages are solitary, but become social in their second year. Accordingly, in *P. cygnus*, growth rates did not differ between solitary and communally-reared individuals, but after the age of three years, juveniles reared in isolation grew significantly more slowly (Booth & Kittaka, 1994; Booth & Kittaka, 2000). Despite the positive effects of sociality on growth in most spiny lobsters, *J. edwardsii* and *H. americanus* juveniles held in captivity downstream from larger individuals experienced slower growth (Booth & Kittaka, 2000). In rearing studies with *P. homarus*, Jong (1993) found that lobsters reared with both sexes together grew more slowly than when sexes were separated. The slow-down was attributed to reproductive activity under mixed conditions. The extent to which these effects operate in wild populations remains unclear.

1.5 Modelling growth

Mathematical descriptors of growth applied to lobsters include general models of animal growth (particularly the well known von Bertalanffy model) and moult process models that explicitly treat the individual components of crustacean growth (moult increment and intermoult duration, or alternatively, moult probability). These model types differ fundamentally with respect to their representation of the increase in lobster size over time. General models of animal growth treat size increase as a continuous process. In contrast, moult process models explicitly represent size increase as discontinuous. Both general model types have been broadly applied to each of the major lobster taxa. Here, we describe the approaches used to develop growth models tailored to lobster populations and key elements of the data requirements and estimation processes.

The moult process models described below do not require information on absolute age. Rather, the growth pattern is determined from some specified starting size based on the time required to make the transition from one size class to another. The application of the von Bertalanffy and other continuous growth models to crustaceans has also been most often developed in the absence of direct information on absolute age. As noted above, the principal sources used to determine growth for most lobster taxa include mark–recapture studies using tags that are retained through the moult. Direct examination of exoskeleton condition following a moulting period (where feasible) has also been used to determine fractions of the population that have moulted in a specified time period (e.g. Ennis, 1972; Sheehy *et al.*, 1999). Observations based on aquarium studies provided a valuable basis for comparison with field estimates of growth (but see the caveats in Section 1.3) and provide the only source of information on known size-at-age relationships. More recently, estimated age based on lipofuscin analysis has been employed in the development of models of lobster growth (Sheehy *et al.*, 1999; Tully *et al.*, 2000; Sheehy & Bannister, 2002).

A full representation of the variability in growth of lobsters is crucial in the development of demographic models (Fogarty, 1986; Punt *et al.*, 1997). Variability in growth of individual lobsters can lead to widely divergent sizes at age (Fig. 1.1), reflecting the effect of quantum changes associated with moulting and in the probability distributions of moult increments. An examination of laboratory-reared individuals reveals that the number of moults at different ages can differ markedly (Fig. 1.2), leading to a broad range in size at age. While most models of lobster growth have focused on deterministic representations of the mean size as a function of time, important advances have been made in developing stochastic models that attempt to represent the full variability in size as a function of time. Here, we review progress in model development of growth processes for lobsters progressing toward a representation of the full variability in growth.

1.5.1 Continuous growth models

The von Bertalanffy growth model has been extensively used in a number of lobster taxa (Table 1.2, Fig. 1.4). The form of the von Bertalanffy model as applied to lobster is:

$$L_t = L_\infty[1 - e^{-k(t-t_0)}]$$

where L_t is the carapace length at time t, L_∞ is the asymptotic size, k is the rate at which the asymptotic size is approached and t_0 is the hypothetical age at zero carapace length. This model has been broadly applied to exploited fish populations. Its analytical convenience and use in other models (including size-based mortality estimators) has led to its application to crustacean populations (see Cobb & Caddy, 1989). An oft-cited concern with the application of the von Bertalanffy model to crustaceans is that it cannot capture the distinctive discontinuous growth of these taxa. Furthermore, biological characteristics such as the occurrence of a terminal moult cannot be adequately represented. It should also be noted that the actual age is not known and most estimates of the von Bertalanffy model for crustaceans involve certain assumptions concerning the age of the smallest individuals represented. Here, we present estimates of the parameters of this model because of their utility in a comparative view of lobster growth (Table 1.2, Fig. 1.4), and because this model has been extensively employed in mortality and yield estimation and modelling of lobster populations.

Parameters of the von Bertalanffy growth equation have been estimated using two primary methods: (1) tag-recovery information and (2) estimating growth from moult increment and moult probability data. This entails in both cases first assigning an age to the initial size. It should be noted that von Bertalanffy parameter estimates derived from mark–recapture studies are sensitive to the size range represented and outliers in the data. The truncated size distribution available for tagging in heavily exploited lobster populations greatly influences the parameter estimates and results in biased estimates. For the case where recoveries of individuals with known size at recapture and time-at-large (TAL) is available, it is possible to develop estimates of the von Bertalanffy parameters L_∞, and k. We can recast the von Bertalanffy model as:

$$L_{i+1} = L_i + (L_\infty - L_i)(1 - e^{-k(TAL)})$$

where L_i is the carapace length of the ith lobster at release and L_{i+1} is the recapture size. Rearranging to a form amenable to linear regression (Fabens, 1965) we have:

$$\frac{L_{i+1} - L_i}{TAL} = k\left(L_\infty - \frac{L_{i+1} + L_i}{2}\right)$$

and L_∞, and k can be readily determined from the regression. This method has been applied to a broad array of crustacean populations. Campbell and Phillips (1972) proposed a related method in application to mark–recapture data. It should be stressed that the interpretation of the parameters differs when the estimates are based on mark–recapture data rather than the case where the actual age of marked individuals is known (Francis, 1988). In a number of applications, the premoult–postmoult relationship has been used in an adaptation of the well-known Ford–Walford approach (see Ricker, 1975) for estimating the parameters of the von Bertalanffy model. Note that this will result in an overestimate of the growth if only those individuals that have moulted are included in the analysis. Given estimates of the asymptotic size and the parameter k, the age of the ith instar is given by:

$$t_i = -\frac{1}{k}\log_e{}' \frac{L_\infty - L_i}{L_\infty}$$

Table 1.2 The von Bertalanffy growth parameters employed for selected lobster taxa by region. Coefficients *k* and t_o parameterised for annual units except where otherwise noted; the latter not provided in all cases.

			von Bertalanffy parameters		
Species/Region	Source	Sex	*Linf*	*k*	t_o
Nephrops norvegicus					
Irish Sea	Hillis (1979)	Male	60.0	0.16000	0
		mature Females	56.0	0.10000	0
		Males & immature Females	76.0	0.14000	1
		mature Females	56.0	0.11000	1
Firth of Clyde, Scotland	Tuck *et al.* (1997)	Male	56.1	0.18550	−0.115
Skagerrak, Sweden	Ulmestrand & Eggert (2001)	Male	72.9	0.13800	0
		mature Females	64.0	0.05600	0
Homarus gammarus					
Ireland	Gibson (1967) in Saila & Marchesseault (1980)	Females	217.0	0.09400	0.344
Norway	Uglem *et al.* (2005)	Both sexes	179.3	0.11700	0.185
Homarus americanus					
Bay of Fundy, Canada	Campbell (1983a)	Males	281.0	0.06500	0.760
		Females	207.0	0.08900	0.420
Port Maitland, Nova Scotia, Canada	Campbell (1983b)	Males	135.0	0.19300	1.224
		Females	108.0	0.37200	2.262
Jasus edwardsii					
S Australia^a	MacGarvey *et al.* (1999)	immature Female	138.0	0.42000	
		mature Female	430.0	0.19000	
Fiordland, New Zealand	Annala & Bycroft (1988)	Male	202	0.12500	−0.37
		Female	165	0.04900	−0.386
Gisborne, New Zealand	McKoy & Esterman (1981)	Males	118	0.29	−0.36
Stewart Is, New Zealand	McKoy (1985)	Males	121	0.26	0.36
		Females	137	0.17	0.49
Jasus lalandi					
Western Grounds, S Africa	Groeneveld (1997)	Male	111.2	0.09200	
		Female	96.1	0.12900	
Eastern Grounds, S Africa	Groeneveld (1997)	Male	95.8	0.05000	
		Female	78.5	0.06500	
Palinurus gilchristi					
Aglhas Bank to Port Elizabeth, S Africa	Groeneveld (1997)	Male	111.00	0.09200	
		Female	96.00	0.12900	
Port Alfred, S Africa	Groeneveld (1997)	Male	96.00	0.05000	
		Female	78.00	0.06500	
Palinurus elephas					
Corsica	Marin (1987) in Ceccaldi & Latrouite (2000)	Male	166.00	0.15100	−0.348
		Female	136.00	0.18500	−0.342
Panulirus cygnus					
W Australia^b	Phillips *et al.* (1992)	Males	165.6	0.00026	
		Females	163.5	0.00026	
Seven Mile Beach, W Australia	Sheehy *et al.* (1998)	Males	158.8	0.17000	0.85
		Females	125.0	0.19000	0.78
Panulirus argus					
Cuba	Phillips *et al.* (1992), Baisre & Cruz (1994)	Males	250.3	0.27000	
		Females	170.9	0.39000	

Table 1.2 *continued*

			von Bertalanffy parameters		
Species/Region	Source	Sex	*Linf*	*k*	t_o
Panulirus homarus					
Durban, S Africa	Smale (1978) in Arellano (1989)	Male	120.00	0.17700	
		Female	94.20	0.33700	
Panulirus ornatus					
Torres Strait, Australia[b]	Phillips *et al*. (1992)	Males	150.7	0.00157	
		Females	163.5	0.00157	
Panulirus penicillatus					
Red Sea	Plaut & Fishelson (1991)	Males	141.30	0.04970	
		Females	84.70	0.10660	
Enewetok Atoll, Marshall Islands	Ebert & Ford (1986) in Arellano (1989)	Males	146.00	0.21100	
		Females	96.50	0.58000	
Cagayan, Phillippines	Arellano (1989)	Males	161.00	0.13100	
		Females	153.00	0.17200	

a. Average of 11 study areas.
b. Parameterised for daily units.

where L_i is the carapace length of the *i*th instar. The intermoult duration between successive instars under this formulation is given by:

$$t_i - t_{i-1} = \frac{1}{k}\log_e{}' \frac{L_\infty - L_{i-1}}{L_\infty - L_i}$$

It is then possible, in principle, to represent the mean size as a step function with size increases occurring following each intermoult period.

A modification of the von Bertalanffy model to account for seasonal growth can be specified as:

$$L_t = L_\infty{}' \; 1 - e^{-k(t-t_0) - \frac{Ck}{2}[\sin 2 \;\; (t-t_s)]}$$

where C is a parameter controlling the amplitude of seasonal fluctuations, t_s specifies the start point of the sinusoidal oscillation, and all other terms are defined as before (see Pauly & Neal, 1984 for an application to shrimp populations). This model qualitatively reflects the cessation of growth during the cold winter months in temperate waters. Tully *et al*. (2000) employed a seasonal von Bertanlaffy specification to model an index of European lobster growth based on lipofuscin content as a function of estimated age at three temperature levels (Fig. 1.5).

Modelling growth in weight

Although growth in linear size dimensions occurs at discrete intervals at each moult, the growth process itself is continuous and the change in weight of an individual with time is appropriately represented as a continuous function. The relationship between carapace length and weight can be represented by the simple allometric relationship:

$$W_t = aCL^b$$

where a and b are coefficients. The von Bertalanffy model expressed in terms of weight is then:

$$W_t = W_\infty[1 - e^{-k(t-t_0)}]^b$$

where W_∞ is the asymptotic weight. The von Bertalanffy model expressed in terms of weight has an inflection point at early time steps. The equivalent expression for the seasonally varying von Bertalanffy model expressed in terms of weight is:

$$W_t = W_\infty{}' \; 1 - e^{-k(t-t_0) - \frac{Ck}{2}[\sin 2 \;\; (t-t_s)]} \quad {}^{b}$$

We feel that this representation can be particularly valuable as a model of lobster growth in seasonal environments.

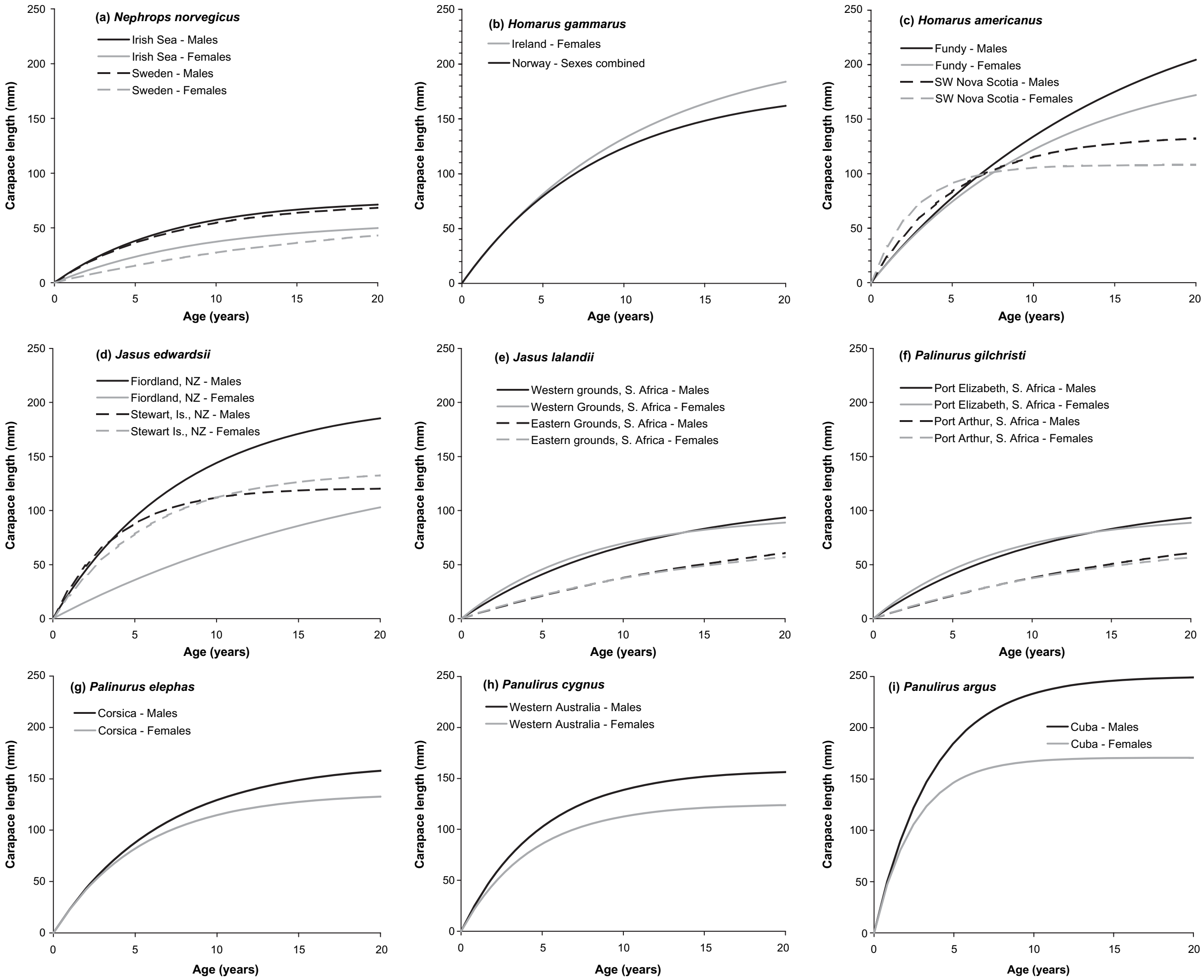

Fig. 1.4 Selected von Bertalanffy curves for a variety of clawed and spiny lobsters. Examples from contrasting geographic areas shown to illustrate within-species variability for males and females except where data not available. In most cases, the curves were fitted to growth data from lobsters near or above the harvestable size and therefore may not represent the growth trajectory of younger stages well. Sources of curves cited in Table 1.2.

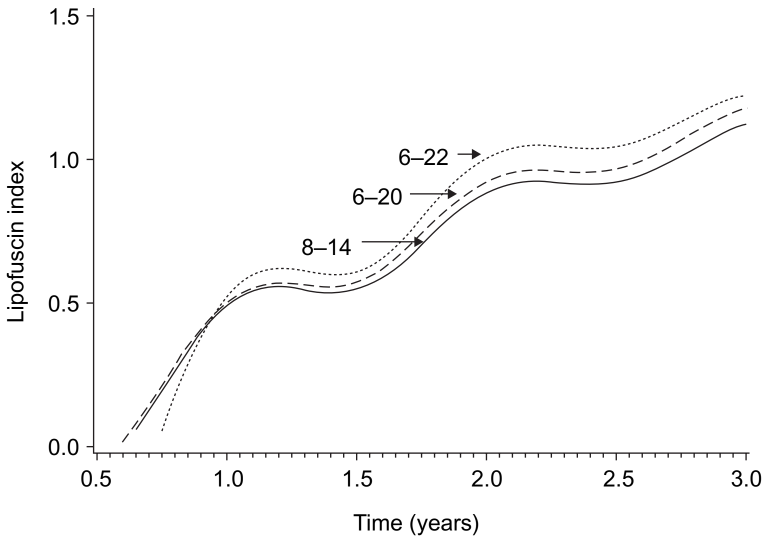

Fig. 1.5 Predicted lipofuscin index of European lobsters, *Homarus gammarus*, under different temperature regimes (6–20°C, 6–22°C, 8–14°C) using a seasonal von Bertalanffy-type function.

Botsford (1985) developed a lobster growth model for lobsters reared in an aquaculture system. If the rate of growth in linear dimensions (e.g. carapace length) is constant we have the simple expression:

$$\frac{dL}{dt} = k$$

and translating length to weight using the allometric relationship above gives:

$$\frac{dW}{dt} = KW^{v}$$

where K is a function of the growth constant k and the parameters of the length–weight relationship and v is given by $(1 - 1/b)$. This is a well-known growth model (Parker & Larkin, 1959). For the case of isometric growth $b = 3$ and therefore $v \sim 0.67$. The relative growth rate:

$$\tfrac{1}{W}\frac{dW}{dt} = KW^{v-1}$$

is therefore a declining function of body weight as has been observed for many aquatic organisms.

Sheehy *et al.* (1999) applied a logistic function to model European lobster growth in weight. The model was also applied to model growth in linear dimensions. In this case, ages were assigned, based on a lipofuscin index. The weight at time t can be expressed:

$$W_t = \frac{W_\infty}{1+\left(\frac{t}{t^*}\right)^{-g}}$$

where g and t^* are coefficients. As with the von Bertalanffy model for growth in weight, this model exhibits an inflection point at early ages. An illustration of the resulting growth function for male and female *H. gammarus* is provided in Fig. 1.6.

1.5.2 Moult process models

Moult process models explicitly represent the discontinuous patterns of size increase in crustaceans. The carapace length (L) at successive instars can be expressed in the simple recursive form:

$$\bar{L}_{i+1} = \bar{L}_i + \quad L_i +$$

where L_i is the carapace length of the ith instar, L_i is the moult increment of an individual with premoult size L_i and is a random error term. In general, both the intermoult duration and the moult increment is a function of premoult size, temperature and other factors such as food supply, popula-

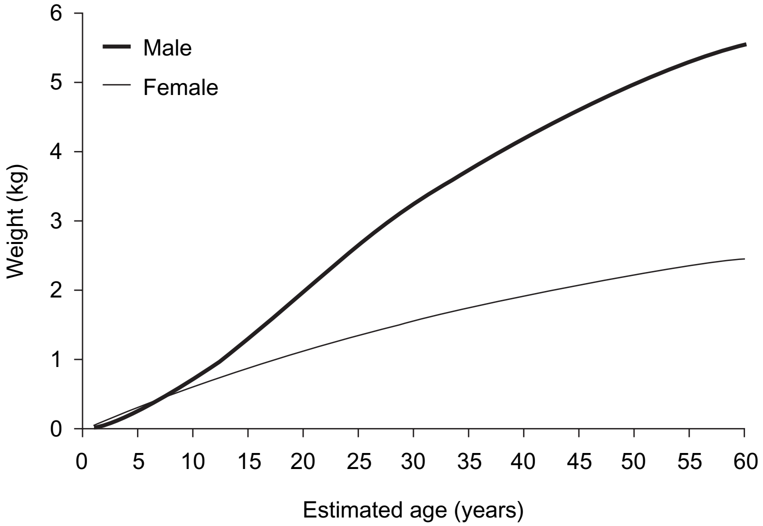

Fig. 1.6 Predicted length-at-age of male and female European lobsters, *Homarus gammarus*, using a logistic growth model (Sheehy *et al.*, 1999).

tion density, biological condition (including limb loss), and other factors.

Approaches taken to determining the intermoult period necessarily differ for lobster taxa exhibiting well-defined seasonal moulting periods (principally in temperate–boreal systems) and those exhibiting continuous, non-synchronous moulting patterns in tropical and subtropical systems. Accordingly, these cases are treated separately below.

Moult probability and intermoult duration

The clawed and spiny lobsters in temperate regions typically exhibit well-defined moulting periods. Estimation of moult probabilities have been based on techniques that capitalise on this feature. Moult probability has been most commonly estimated using the 'anniversary' method of Hancock and Edwards (1967) based on tagging studies. In this technique, the proportion of lobsters having moulted during a specified time period (usually one year ± some tolerance factor) is calculated for different size classes. Note that if the moult probability is known exactly, it is the inverse of the intermoult duration. The moult probability for an individual in the *i*th size class is given by:

$$\hat{p}_i = \frac{N_{m,i}}{N_{n,i} + N_{m,i}}$$

where $N_{m,i}$ is the number of individuals in size class i that moulted during a specified time period, $N_{n,i}$ is the number that did not moult in the time period.

Estimation of moult probability based on mark–recapture studies can be biased if tags are lost during moulting. For example, estimated tag loss in studies of American lobster stocks range from 9 to 12% (Cooper, 1970; Russell, 1980; Fogarty & Idoine, 1988). Similarly, if mortality is associated with moulting, the estimate of the proportion moulting will be biased. The corrected estimate of the proportion moulting adjusted for moult-related tag loss and mortality is:

$$\hat{p}_i = \frac{N_{m,i}\,[(1-TL)(1-M_T)]^{-1}}{N_{n,i} + N_{m,i}\,[(1-TL)(1-M_T)]^{-1}}$$

where $N_{m,i}$ is the number of individuals in size class i that moulted during a specified time period, $N_{n,i}$ is the number that did not moult in the time period, TL is the fraction of individuals that lost tags during the moult and M_T is the fraction of tagged lobsters that died due to the tagging process (assumed to occur immediately after release, Fogarty & Idoine, 1988).

Ennis *et al.* (1982) based moult-probability estimates on examination of shell condition of American lobsters (see Ennis, 1972). This technique holds the potential for obtaining moult probability estimates based on larger sample sizes and

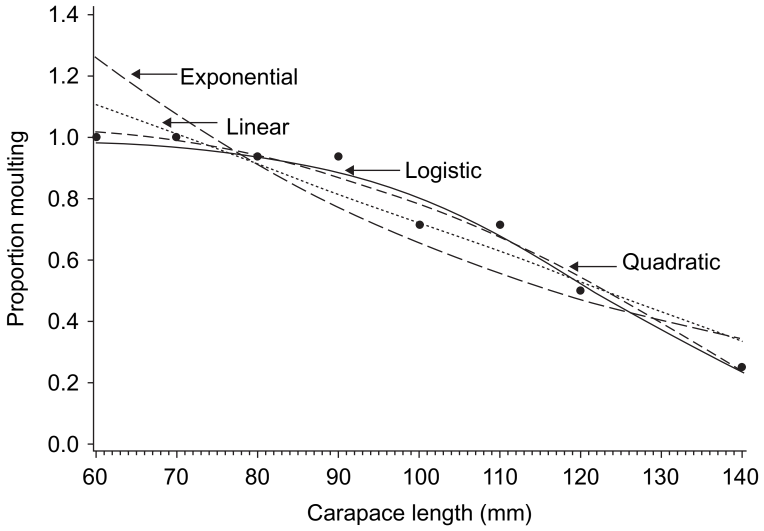

Fig. 1.7 Application of alternative moult probability models, including linear, exponential, quadratic, and logistic, to offshore male American lobsters, *Homarus americanus*.

with lower cost than tagging studies and deserves broader application. It has proved exceedingly difficult to obtain a sufficient number of recaptures to define the moulting probability at larger sizes (Fogarty & Idoine, 1988; Sheehy *et al.*, 1999).

In general, the probability of moulting within a specified time period is a function of premoult size, water temperature, and other factors such as food supply, density, and reproductive state (particularly for females). The moult probability can then be specified as:

$$p_i = f(L_i, X_i) +$$

where $f(^\bullet)$ indicates a general function of premoult carapace and a sequence of auxillary biotic and abiotic variables (X_i) affecting the moulting process, and   is a random error term. In virtually all published cases, the moult probabilities have been expressed as a function of premoult carapace length only. Several model forms have been used (reviewed in Fogarty, 1995). These include linear:

$$f(\ ) = a_0 + a_1 L_i +$$

quadratic:

$$f(\ ) = a_0 + a_1 L_i + a_2 L_i^2 +$$

exponential:

$$p_i = (1 + e^{a_0 + a_1 L_i})^{-1} +$$

and logistic:

$$f(\ ) = a_0 e^{-a_1 L_i +}$$

where a_0, a_1, and a_2 are constants (to avoid the proliferation of parameters and symbols, we have reused these symbols in each model form; note however that the interpretation can differ in different models). These different models in some instances make substantially different predictions of the moulting probability as a function of size (particularly for the smaller and larger size classes represented in the samples). An illustration of these four models applied to an offshore American lobster population is depicted in Fig. 1.7. The models differ with respect to the error assumptions made. The linear and quadratic models assume a normal error structure with zero mean and constant variance. The exponential model assumes a lognormal error structure. The fitting procedure employed for the logistic regression case explicitly recognises that the data employed in the analysis comprises counts (number of lobsters moulted and the total number of recaptures) and employs a binomial error structure. This would seem to be most appropriate for data of this type. Note that it is possible to incorporate a binomial error structure in the linear, quadratic, or exponential models in the context of a generalised linear model, but to date, this approach does not appear to have been employed.

Incorporation of additional factors affecting the moulting probabilities can be readily accomplished. Temperature is particularly relevant in this regard. For example, Ennis *et al.* (1982) estimated annual moulting probability for *H. americanus* for different water temperatures (cumulative-degree-days) in Comfort Cove, Newfoundland. Campbell (1983b) also demonstrated that temperature strongly affects the annual moult probability of American lobster off Nova Scotia. Similar observations have been made in culture systems (see Van Olst *et al.*, 1980). These results have important implications for understanding interannual variation in production of lobsters. An extended logistic moult probability model which can accommodate additional explanatory variables (e.g. temperature) can be developed as:

$$p_i = \left(1+e^{a+a_1L_i+\quad b_iX_i}\right)^{-1}+$$

where L is the premoult length, X is an auxillary variable (e.g. temperature), b_i are coefficients for the auxillary terms and all other terms are defined as before. Quadratic or higher order effects for premoult size and the auxillary variables can, in principle, be specified in this formulation by including additional terms in the model.

For lobster taxa characterised by moulting throughout the year it is possible to determine the proportion moulting based on mark–recapture data as:

$$\hat{p}_i = \frac{TAL}{IP_i}, TAL < IP_i$$

where TAL is the time at large and IP_i is the intermoult period. This estimator assumes that moulting is non-synchronous (Munro, 1974; Restrepo & Hoenig, 1988; Hoenig & Restrepo, 1989). For $TAL > IP_i$, $p_i = 1.0$. In this application, returns from a mark–recapture experiment for each size class i are grouped according to time at large in pre-arranged intervals and the proportion having moulted in each time interval is computed. If the assumption of continuous, non-synchronous moulting is met, the relationship between the proportion moulting and the time at large will be linear through the origin. A simple linear regression through the origin of the proportion moulting on the time at large will therefore yield an estimate of the intermoult duration (IP_i, equal to the inverse of the slope of the regression). It is recommended that estimates be based on the lower part of this linear function (e.g. up to values of $p_i < 0.5$).

Again, we can express the relationship between the intermoult period as a general function:

$$IP_i = f(L_i, X_i)+$$

where IP is the intermoult period and all other terms are defined as before. The functional forms applied to lobster taxa have been reviewed by Verdoit *et al.* (1999) and include polynomial:

$$f(\,) = a_1 + a_2L_i^d +$$

where d is a 'shape' coefficient with special cases of linear (d = 1, Mauchline, 1977), and cubic (d = 3, Kurata, 1962) in addition to the general form above (Castro, 1992) and log-linear:

$$f(\,) = e^{a_0+a_1L_i+}$$

Illustrations of the relationship between intermoult duration and carapace length for selected lobster species of *Panulirus* are provided in Fig. 1.8. Verdoit *et al.* (1999) also employed a two-phase model for female Norway lobsters in which intermoult duration was treated as two separate constant functions of size for immature and mature lobsters; males were modelled using a single constant function over all size classes.

Size increase per moult

In general, the moult increment can be specified as:

$$Y_{i+1} = f(L_i, X_i)+$$

where Y_{i+1} is the measure of either size or size increase for the i + 1 instar and all other terms are defined as before. Three different representations of Y_{i+1} have been modelled including the postmoult size (L_{i+1}), the moult increment ($Li = L_{i+1} - L_i$) and the proportional increase in size $(L_{i+1} - L_i)/L_i$.

The relationship between premoult and postmoult size (the so-called Hiatt growth diagram or the Gray–Newcombe diagram (Botsford, 1985)

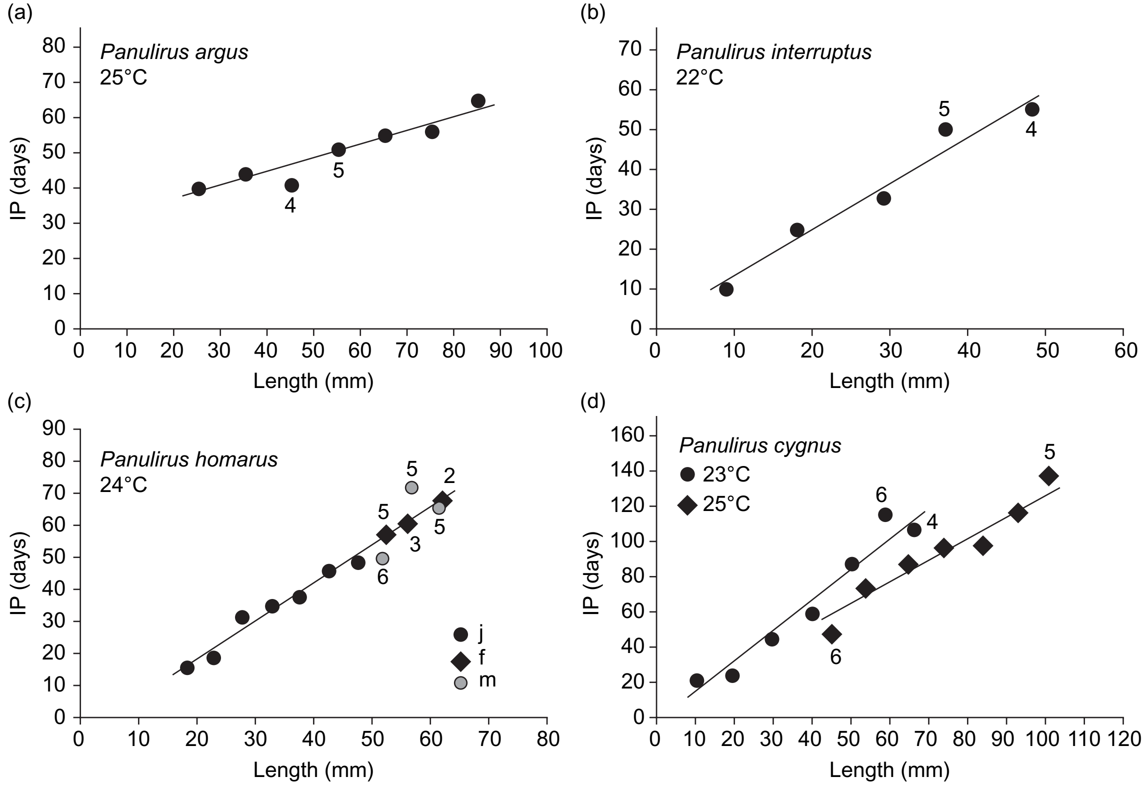

Fig. 1.8 Intermoult period (IP) as a function of size for four species of *Panulirus* at specified temperatures (from Smith, 1997).

has been commonly used to describe crustacean growth. Again, attention has centred on the dominant effect of the premoult size. The general form of the Hiatt–Gray–Newcombe relationship is:

$$L_{i+1} = a_0 + a_1 L_i^{a_2} +$$

Simple linear functions ($a_2 = 1$) have typically been employed in applications to most crustacean species.

The dominant component of the postmoult size is the premoult size and it is therefore not surprising that a close relationship is indicated in this representation (Hartnoll, 1982; Botsford, 1985). An inflection in the premoult–postmoult relationship at the size of maturity has been noted in some crustaceans. Hiatt (1948) proposed that conjoined linear models with an intersection near the size at maturity be used in this case (see also Somerton, 1980). The Hiatt or Gray–Newcombe model for a two-phase premoult–postmoult relationship is:

$$L_{i+1} = a_0 + a_1 L_i + \quad , L_i \quad L^*$$

$$.$$

$$L_{i+1} = L^* + a_0 (L_i - L^*) + \quad , L_i > L^*$$

where L^* is the inflection point. Although linear models have most often been employed, alternative non-linear specifications have been advocated. Wilder (1953) employed the power model:

$$L_{i+1} = a_0 L_i^{a_1} +$$

for the premoult–postmoult relationship.

For the relationship between the moult increment and premoult size, Mauchline (1976) suggested the log-linear form:

$$L_i = L_i e^{a_0 + a_1 L_i +}$$

Mauchline (1976) further suggested that the apparent inflection at maturity was an artefact and that a hyperbola was a more appropriate functional form, although this argument was rejected by Botsford (1985). Misra (1957, reported in Easton & Misra, 1988) proposed an alternative non-linear form based on an allometric relationship between pre- and postmoult size:

$$L_{i+1} = b_0 x^{a_0 + a_1 L_i} e^{b_1 L_i + \;_i}$$

where b_0 and b_1 are parameters and all other terms are as before. The relationship between the percentage increase per moult and the premoult size has also been used to describe growth in crustaceans. This representation is problematic because of a confounding of the dependent and independent variables (premoult size appears on both sides of the equation, complicating interpretation of the statistical significance of the relationship) because it imposes a hyperbolic functional form on the relationship.

As noted by Botsford (1985) the marginal increase in fit in premoult–postmoult relationships using the different model forms described above is generally small. Furthermore, this representation tends to obscure the levels of variability in the moult increment and the changes in increment as a function of premoult size. An illustration is provided for male American lobsters (Fogarty, 1986) where it is clear the Hiatt–Gray–Newcombe relationship obscures the pattern of variability (Fig. 1.9). The relationship between moult increment and premoult size would appear to provide the most informative representation of growth per moult (Botsford, 1985; Fogarty & Idoine, 1988) and it is recommended that this approach be generally adopted in preference to the premoult–postmoult relationship. It is recommended that the full

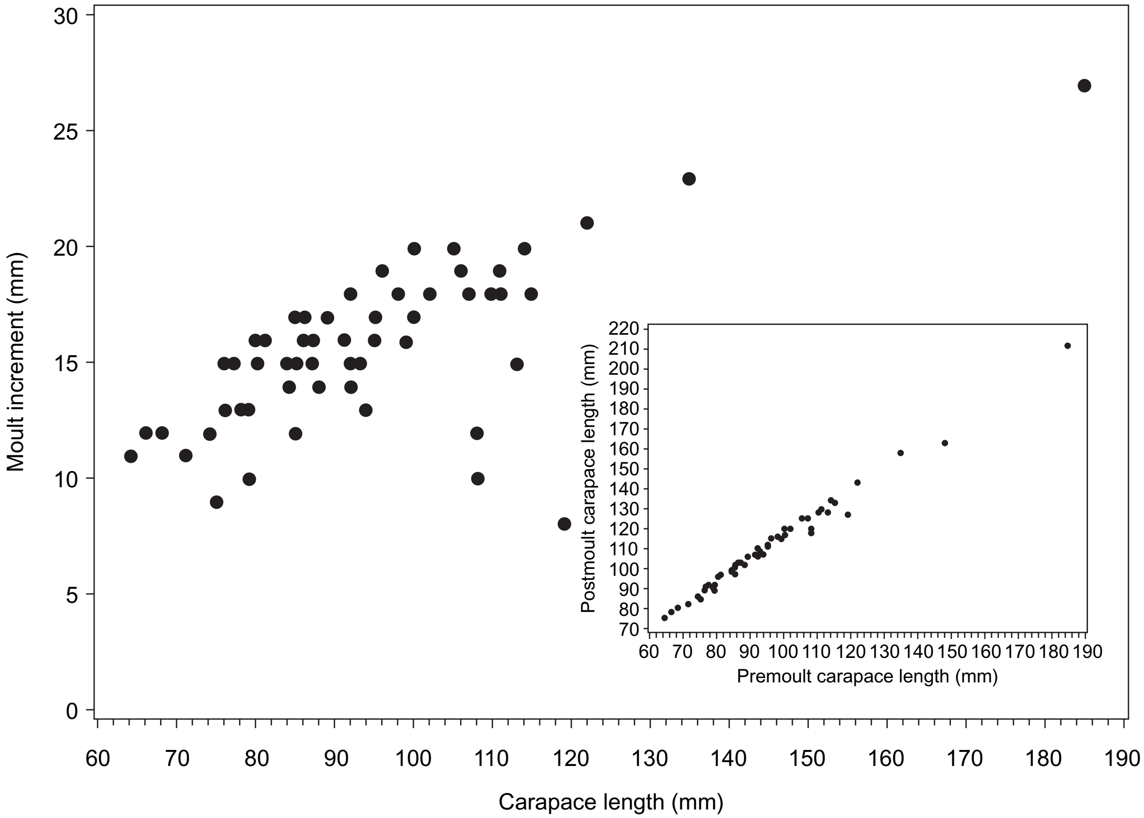

Fig. 1.9 Relationship between moult increment and premoult size for male offshore American lobsters, *Homarus americanus*, and the corresponding premoult–postmoult relationship (inset).

probability distribution of moult increments as a function of premoult size be specified and used in the development of crustacean growth models where possible.

Mean growth

Models of crustacean growth have most often been cast in terms of the mean size as a function of time. Even in cases where a fuller representation of growth variability has been made, summaries of mean length as a function of time have been made. The estimates of moult probability per unit time and moult increment can be combined to give an estimate of mean size as:

$$\bar{L}_{t+\quad t} = \bar{L}_t + p_L \quad L +$$

where L_t is the mean length at time *t*, and $\quad L$ is the moult increment for lobsters of size *L* and p_L is the proportion moulting at size *L*. An illustration of an empirical growth model derived in this way for an American lobster population is provided in Fig. 1.10, demonstrating sexual dimorphism in growth (Fogarty, 1986).

1.5.3 Scaling time

The models described above treat elapsed time as the relevant dimension on which to map changes in lobster size. Alternative specifications based on either geometric series of time units (Caddy, 2003) or an integrated measure of time and temperature expressed as degree-days have also been developed and utilised in models of crustacean growth with specific application to lobster populations.

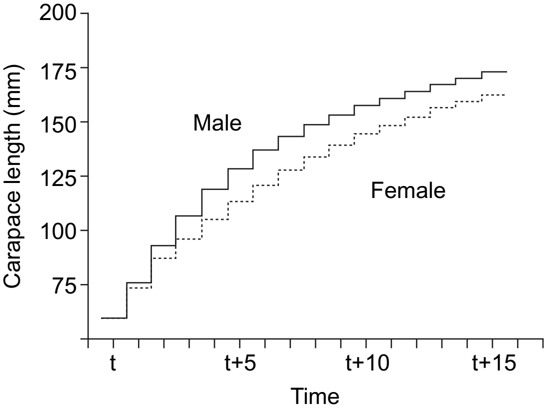

Fig. 1.10 Mean size at the end of successive growth years for male and female American lobsters, *Homarus americanus*, (Fogarty, 1986).

Gnomonic intervals

Caddy (2003) introduced the concept of 'gnomonic' intervals with application to crustacean growth. A gnomon is a geometric growth interval (*sensu* D'Arcy Thompson, 1966). In application to crustacean growth, Caddy suggested that the intermoult intervals progressively increase as a constant proportion throughout the life of the individual. If the intermoult period increases by a constant proportion with successive moults, the initial intermoult interval can be expressed:

$$IP_0 =$$

where IP_0 is the initial intermoult interval and is a constant. The *i*th intermoult interval is then given by:

$$IP_i = \qquad ^{i}$$

The method requires information on the intermoult durations for each successive moult sequence and therefore is practically constrained to applications where individuals have been reared in the laboratory or other controlled settings and the moult history can be documented. Caddy (2003) reported that the hypothesis of gnomonic growth intervals could not be rejected for any of the 11 crustacean growth series he examined. An illustration of the method applied to *P. argus* is provided in Fig. 1.11. For taxa in which growth is seasonal, deviations from the simple geometric series of intermoult durations can be expected due to temperature and other environmental cues affecting the moulting process. To capture the intrinsic seasonality in this case, a simple modification employing a sinusoidal oscillation was proposed (Caddy, 2003):

$$IP_i = \qquad ^{i} + \quad \sin[2 \quad (t-r)/ \quad]$$

where is the amplitude, r is the phase, and is the periodicity (set to 1 year in this case. We note that the function could also be modified by direct incorporation of a temperature function.).

Given a specification of the expected intermoult durations starting at a specified instar, and a pre-

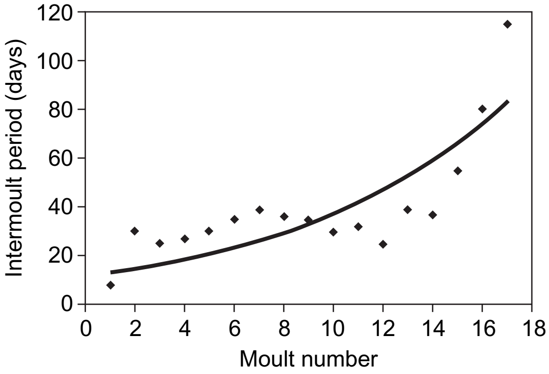

Fig. 1.11 Intermoult period at successive instars using the gnomonic growth progression of Caddy (2003) for *Panulirus argus*.

dictive measure of the expected moult increment for that instar, a complete growth curve can be generated recursively. Caddy (2003) defined this function in terms of the Hiatt growth diagram and the gnomonic time interval.

Physiological time units

An alternative to the specification of crustacean growth models is to use physiological time units specified as degree-days (Curry & Feldman, 1987). The duration of a biological process such as growth in ectotherms can be expressed as a function of the cumulative temperature sum during a specified time interval. The situation where the process requires some minimum temperature level to operate can be directly incorporated into the specification. In this case, the number of degree-days per calendar day is:

$$t_{\mathrm{dd}} = \overline{T}_{\mathrm{t}} - T_{\mathrm{min}}$$

for the case where $T_{\mathrm{t}} > T_{\mathrm{min}}$ and $t_{\mathrm{dd}} = 0$ for the case where $T_{\mathrm{t}} < T_{\mathrm{min}}$ (Curry & Feldman, 1987). This approach has been widely applied to insect populations (Curry and Feldman, 1987). The relationship between the developmental time and the developmental rate as a function of temperature is depicted in Fig. 1.12. The degree-day measure can be directly substituted for more conventional measurements of time in crustacean growth models. An illustration of the rectification of temperature effect on intermoult period using the degree-day method is provided in Fig. 1.13 for *P. cygnus* (Smith, 1997).

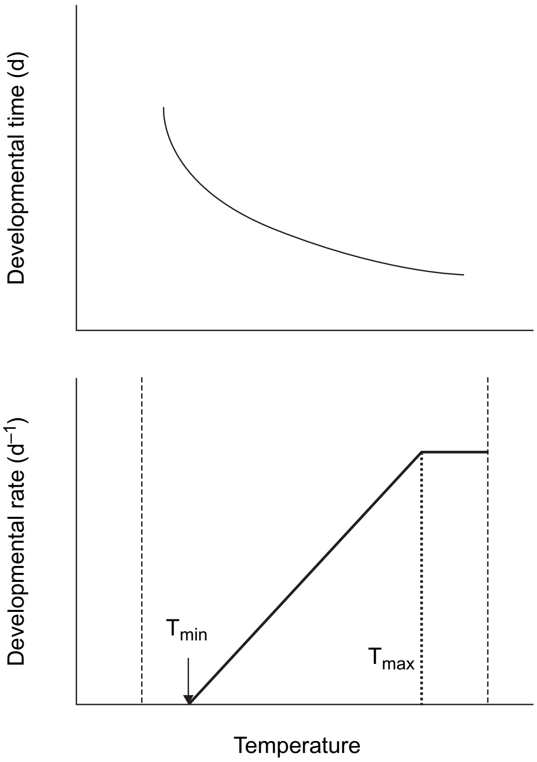

Fig. 1.12 Developmental time (upper) and corresponding developmental rate (lower) as a function of temperature. For developmental rate, upper (dotted vertical line) and lower (x-axis intercept) temperature limits at which growth occurs are specified. The dashed lines indicate lower and upper lethal temperature limits.

1.5.4 Modelling variability in growth

The moult process and continuous growth models described above have typically been employed to describe the mean size of individuals at successive time steps and they generally do not consider individual variability in growth. As we have seen, substantial variability can exist in growth trajectories of individual lobsters (Fig. 1.1). In principle, given information on the variance of the various parameters of the model, it would be possible to define confidence intervals for the size-at-time. Under

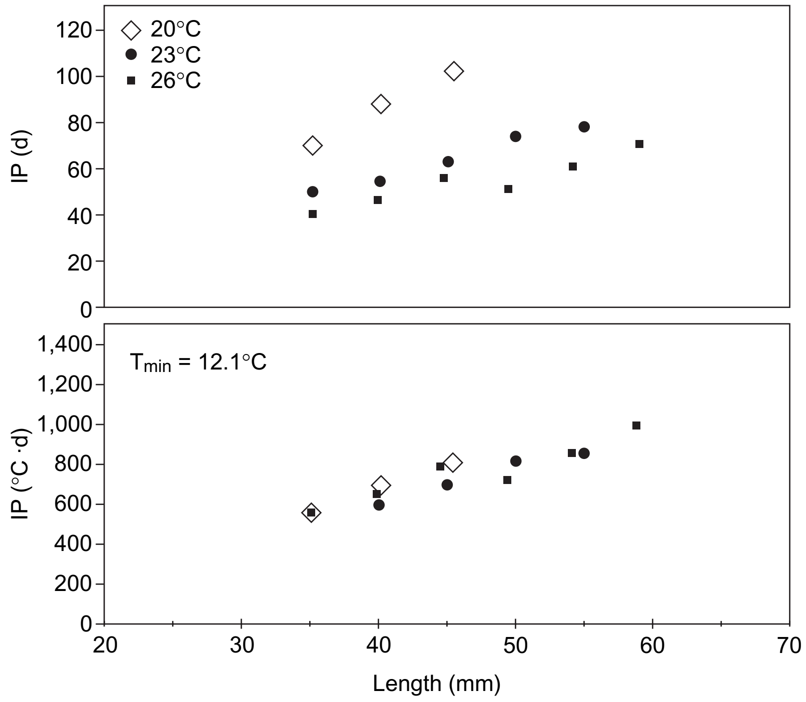

Fig. 1.13 Intermoult period of *P. cygnus* as a function of size at three holding temperatures (upper) and intermoult period represented as degree-days as a function of size demonstrating the rectification for temperature effects (Smith, 1997).

further assumptions, it would be possible to define the full probability distribution of sizes at each time step. The models and approaches described below have been explicitly developed to describe the variability in the growth process. In these models, probability distributions have been used to characterise key aspects of moulting dynamics.

Distributed delay models

Idoine (1985) described growth of the American lobster in terms of a sequence of distributed delays. In this context, a particular moult is specified as a 'delay' and each delay can be characterised in principle in terms of factors such as sex, age and environmental conditions (Idoine, 1985).

We are fundamentally interested in the number of individuals entering a moult group (or delay), the time spent in each stage, and the number exiting this stage (Fig. 1.14). The inter-individual variability is captured in the specification of the time spent in each stage, which is defined by a probability distribution of outcomes. In this application, the particular probability distribution chosen is a special case of the Gamma distribution, called the Erlang distribution. The form of this distribution describing the time required to pass through a moult is determined by a 'shape' parameter ( ) specifying the order of the delay and by the variance of the process. The full probability distribution for the time spent within a moult group is given by:

$$y = {}^{\prime}\frac{\quad}{{}_{t}} \quad \frac{{}^{-1}}{(\quad -1)!}e^{-\frac{\quad}{\quad}}$$

where is a 'shape' parameter, and is the mean of the distribution, and is time. The parameter is a function of the mean and variance of the time spent within a moult group:

$$= \frac{{}^{2}_{t}}{{}^{2}_{t}}$$

and for application of the Erlang distribution, this parameter is taken to be an integer. If cannot be taken as an integer, the factorial term in the above distribution is replaced by a gamma function.

An illustration of the shape of the probability distribution specifying the transit times within a

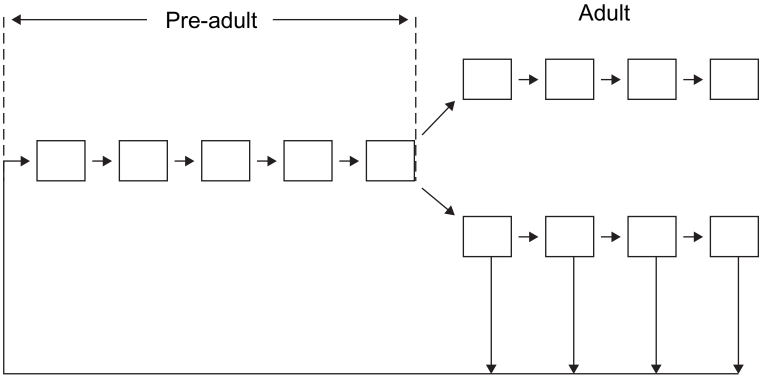

Fig. 1.14 Representation of a multistage-distributed delay process for application to lobster growth (Idoine, 1985). Each stage represents a delay. The time required to pass through the stage is specified by an Erlang probability distribution.

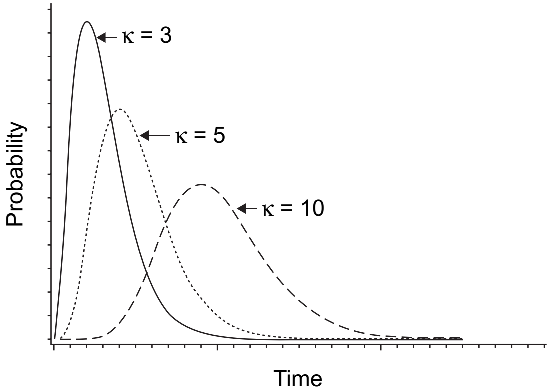

Fig. 1.15 Examples of the Erlang distribution function for different values of the shape of parameter . As increases, the probability distribution approaches the normal distribution.

moult is provided in Fig. 1.15 for different levels of the shape parameter. As increases, the shape of the distribution approaches a normal probability distribution. Given information on moult increments for each moult group, it is possible to construct the growth curve for the population.

Extension of the distributed delay concept to encompass time-varying distributed delays has been explored (e.g. Manetsch, 1976). Such a model structure allows consideration of seasonal or other temporal trends in defining growth patterns.

Simulation and matrix representations

We can provide an alternative representation of variability in growth by specifying the transition probabilities between different size groups within specified time periods. The transition probabilities are a function of the moulting probabilities within the time interval and the probability distribution of moult increments. To capture these features, and additional complexities such as the interplay between the reproductive cycle in females and growth processes, and moult-related mortality, Fogarty (1986) and Fogarty and Idoine (1988) developed a simulation model describing the evolution of the size structure of American lobsters over time. Verdoit *et al.* (1999) also employed a simulation approach to represent variability in lobster growth and uncertainty related to estimation of growth parameters. For male Norway lobsters, the 5th and 95th percentiles from the bootstrap simulations are very wide, largely reflecting the uncertainty in growth estimates, while those for females are relatively narrow (Fig. 1.16).

Wahle *et al.* (2004) examined the effects of variable growth on recruitment in *H. americanus*, to provide forecasts of relative recruitment based on observed settlement indices. The simple projection model:

$$n_t^* = \underset{a}{} p_a n_{t-a} s^a$$

was used where n_t^* is the population index for newly recruited lobsters in year t, p_a is the fraction of surviving individuals that will recruit to the fishery at age a, n_{t-a} is the settlement index in year t–a, and s is the annual survival fraction. Estimates of the time required to reach legal size were based on laboratory-reared individuals. The fraction

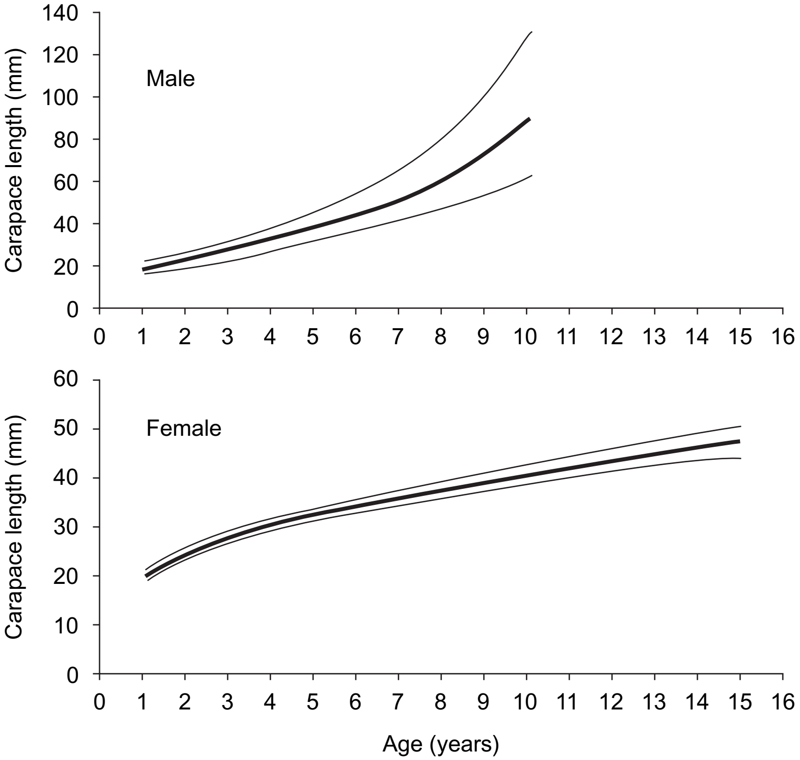

Fig. 1.16 Growth of male and female Norway lobsters, *Nephrops norvegicus*, with representation of variability in growth estimates with the 95th (upper thin lines) 50th (middle lines) and 5th (lower thin lines) percentiles based on bootstrap simulations.

reaching the minimum legal size at each age was determined and used to specify the p_a. A constant survival fraction was employed. The minimum time required to reach legal size under hatchery conditions was four years and the maximum was eight years in these analyses.

We can also describe the evolution of the size composition over time in terms of a size transition matrix. The probability of moving from the *i*th to the *j*th size class can be specified as:

$$T = \begin{bmatrix} p_{1,1} & p_{1,2} & p_{1,3} & \cdots & p_{1,n} \\ p_{2,1} & p_{2,2} & p_{2,3} & \cdots & p_{2,n} \\ p_{3,1} & p_{3,2} & p_{3,3} & \cdots & p_{3,n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ p_{n,1} & \cdots & \cdots & p_{n,n-1} & p_{n,n} \end{bmatrix}$$

where the elements on the main diagonal ($p_{i,i}$) represent the probability of a lobster remaining within the same class during the time interval. Note that

$$\sum_{j=1}^{n} p_{ij} = 1 \text{ and } 1 \geq p_{ij} \geq 0.$$

All the elements below the main diagonal represent increases in size during the time interval. Decreases in size under certain environmental conditions have been noted for some lobster taxa (e.g. the Cape rock lobster, *J. lalandii* off South Africa, Cruywagen, 1997) and are well known in other crustacean taxa such as euphausiids. Accordingly, we have allowed for shrinkage in size by permitting non-zero elements above the main diagonal.

Note that the $p_{i,i}$ are related to the estimates of moult probability derived earlier (see Section 1.5.2) as:

$$p_{i,i} = [1 - p_i]$$

and the non-diagonal elements of the matrix represent the probabilities of changing in size and moving into a specified size category.

Given empirical estimates of the probability of moulting or staying the same size in a specified time interval and the probability of moving into different size classes for those that do moult based on mark–recapture information or other sources, it is possible to specify the elements of the transition matrix without underlying assumptions concerning the form of the growth function or the distribution of transition probabilities.

Punt *et al.* (1997) applied this general approach to model the growth dynamics of *J. edwardsii* under the constraint of positive growth increments and assuming that growth follows a Schnute (1981) general growth function. Normal and Gamma probability distributions were used to represent variability in the growth process (deviations from the predicted growth). This approach holds the advantage of reducing the number of parameters to be estimated to two per row.

Degree-day models

Smith (1997) employed this general approach in the development of models of crustacean growth to permit direct incorporation of temperature-dependent growth processes. Smith characterised the intermoult period as comprising two components: a ‘required’ time element which reflects physiological constraints on moulting processes and which can be taken to represent a minimum time to moult for individuals of a specified size and physiological state, and a ‘variable’ component representing the effects of exogenous factors on the moulting process. The intermoult period (expressed as degree-days) was taken to be a linear function of premoult size and a shifted exponential probability distribution was used to specify individual variation in the intermoult period.

The shifted exponential probability–density function is:

$$y = {}' \frac{1}{\ } e^{-\frac{-}{\ }}$$

where is a shape parameter, is a parameter representing the minimum time between moults and is time. Smith (1997) employed a two-phase specification for the intermoult period comprising a fixed ( ) and a variable ( ) component:

$$IP = \ (L) + \ (L)$$

where we have a linear model describing the minimum intermoult period:

$$(L) = {}_0 + {}_1L$$

and a separate function describing the variable component:

$$(L) = {}_0 + {}_1L$$

An illustration of this approach applied to *P. cygnus* is provided in Fig. 1.17 where the lower line

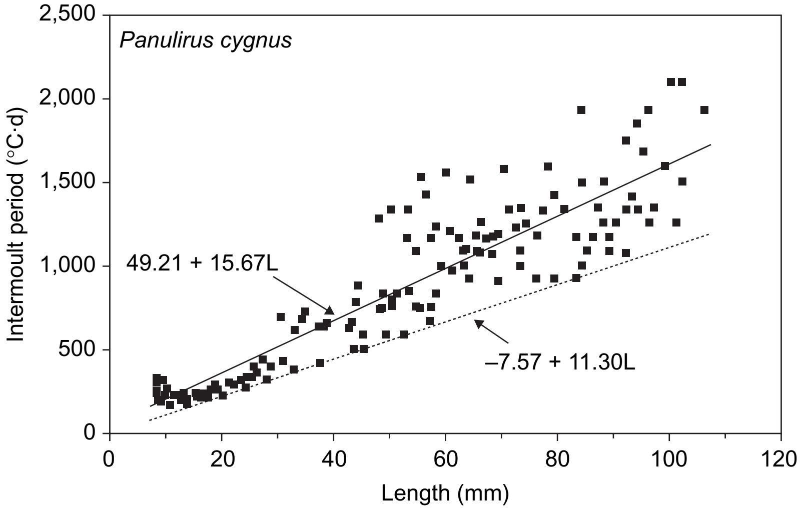

Fig. 1.17 Illustration of the two-phase intermoult period model of Smith (1997) comprising a minimum time component (lower line) and a variable component reflecting environmental influences on intermoult period (upper line).

provides the demarcation point for the minimum intermoult period and the upper line is the maximum likelihood estimate for the variable component of the intermoult period. The combined function gives the expected intermoult duration comprising the fixed and variable components. Given estimates of the moult increment, it is possible to construct the entire growth function.

1.6 Conclusions and future directions

Despite the divergent larval forms of spiny and clawed lobsters, the benthic stages of the various taxa have much more congruent patterns of growth and maturation. All lobsters have indeterminate growth, the absence of a terminal moult permitting lobsters to continue to grow after sexual maturity, with the multiple reproductive instars all capable of producing eggs. The size and age at maturity can vary a great deal from as small as approximately 30 mm CL to greater than 100 mm, and as young as 2–3 years or as old as 8–10. Proportional growth per moult is typically greater in small, younger lobsters than in large, older ones. General patterns of incremental growth are quite well described near the commercially-exploited size range, but as a rule, less is known about growth rates of early juveniles in nature. The onset of maturity inhibits growth more in females than in males because of the greater reproductive investment. Also associated with the onset of maturity are sex-specific patterns of allometric growth of the claws, legs, pleopods, and abdomen. Because initial size and early growth can have an important bearing on an individual's growth trajectory, it is important to conduct more long-term studies on juvenile growth in the wild.

A range of tools are available to evaluate the age–size relationship. We reviewed methods commonly used for both direct and indirect assessments of growth and age determination in lobsters. Tagging is perhaps the most widely used direct means to obtain growth information on the wild stock, but workers should be aware of the inherent biases that can be introduced to estimates of growth by size-selective removal, tag loss, tag-related mortality and trauma. Recognising that size is often not an accurate proxy for age, the determination of age has posed one of the greatest challenges to crustacean biologists. Physiological age markers, such as lipofuscin, the 'age pigment' represent a useful proxy for age in some taxa (e.g. *H. gammarus*, *P. cygnus*). As noted above, the method is expensive, time consuming and may not be generally practical at present. And because the accumulation of lipofuscin can be sensitive to environmental change, particularly temperature, it will still be important to calibrate the index accordingly. In the end, for fishery scientists it may be more worthwhile to invest in a detailed understanding of spatial and temporal variability in the age–size relationship at the population level. Monitoring programmes that follow cohorts from the time of larval settlement and build an understanding of the processes resulting in an observed size composition will be particularly useful toward that end.

Growth is subject to substantial modulation by environmental variability. Temperature is likely to be the single most important environmental factor explaining regional and temporal variability in growth among lobsters. Not surprisingly, the overriding influence of temperature on growth is most apparent where thermal extremes are greatest, for example, in the western north Atlantic within the geographic range of *H. americanus*. Trophic effects on growth have been most widely reported among spiny lobsters. The Cape rock lobster, *J. lalandii*, is perhaps the most extreme example of 'bottom-up' control on population size and body growth, largely modulated by the effect of El Niño-driven changes in primary productivity that, in turn, influence the abundance of an important suspension feeding prey of the rock lobster. Perhaps because of their social habit, negative density-dependent effects on growth have been more often reported for spiny lobsters, than for clawed. The one exception is the relatively cryptic, deep water *N. norvegicus* which also can experience lower growth rates at high density. While much emphasis has been placed on the survival value of sociality in spiny lobsters, food limitation may be one of its costs.

Much less is known about the heritable component of growth variation in lobsters. It is well known that much variation exists in growth rates even among siblings raised under identical conditions. While regional differences in growth have been well characterised in many locations and may largely be explained simply by environmental differences, we are aware of no studies on lobsters that have rigorously evaluated how much those differences are the heritable product of population differentiation. This void is probably due to the difficulty of conducting the necessary multi-generation studies to make such an evaluation. Analysis of the genetic structure of lobster populations (e.g. Ovenden & Brasher, 2000) coupled with detailed growth studies may help disentangle these effects.

We described a broad range of growth models, many of which have been developed for use in lobster population dynamic modelling. These fall into two categories: (1) continuous growth models, and (2) moult process models. Continuous growth models have been most broadly applied although important advances have been made in the development and application of moult process models. There is currently no generally accepted functional form for the moult increment component or for the intermoult duration (alternatively, moult probability) as a function of size. We suggest that the size increase component be represented using the relationship between moult increment and premoult size rather than premoult–postmoult relationships. Current information suggests that a linear function is generally suitable for this purpose. More importantly, the probability distribution of moult increments in different size classes should be specified wherever possible. The relationship between intermoult duration and size is more difficult to determine because of methodological limitations but information is accruing for a number of lobster taxa based on both field and laboratory studies. The polynomial model suggested by Castro (1992) provides sufficient flexibility to encompass most probable forms of the relationship. Smith (1997) argues that most often a simple linear model (a special case of the Castro model) will suffice. The implications of the model choice can be quite significant, particularly if projections are made beyond the range of the available data and so the functional form chosen is quite important. For the case where moult probability as a function of size is modelled, we recommend the use of logistic regression. This approach allows proper consideration of the underlying error structure and is constrained to biologically reasonable values.

Significant advances have been made in development of stochastic growth models for lobsters. Variation in the time spent in different size classes has been modelled using several different probability distributions that permit a representation of intrinsic variability in growth. For modelling approaches in which moult probabilities are specified, a natural representation of variability in growth emerges because of the fundamental moult–no moult structure and the resulting quantum change in size of moulted individuals. Moult increment is a smaller component of overall variability in growth but it is nonetheless important. To date, relatively little attention has been devoted to attempts to capture the sources of variability in the moulting process by incorporating exogenous variables in crustacean growth models. The development of models based on degree-day formulations to measure ‘physiological’ time are very promising in this regard. In principle, the functional relationships described above for the size increase and the intermoult duration (or moult probability) components can be easily extended to incorporate factors such as temperature, condition (including limb loss), food supply, etc. Attempts to incorporate these factors directly in models should be encouraged. These factors can be considered covariates in the specification of moult increment–size and intermoult duration–size relationships. Consideration of temporal trends in the components of growth should also be accorded higher priority (e.g Brandao *et al*., 2004).

Finally, much more information is required on individual variability in growth patterns. Up to now, information of this type for lobster taxa has been limited to laboratory observations. It is not known in general if there are ‘fast’ and ‘slow’ growth forms or whether these patterns might be under genetic control as noted above. All models of lobster growth to date assume that the growth pattern is a function of size alone, without consideration of the past growth increments or intermoult durations. Consideration of whether growth increment or time between moults is conditional on past growth has not been undertaken for lobsters. In other crustaceans, it has been possible to develop conditional expectations for moulting based on past history (e.g. McCaughran & Powell, 1977) and similar approaches should be applied to lobster species wherever possible. Such an overall approach may lead to development of individual-based models for lobster populations incorporating the true range of variability in demographic parameters. We feel that such a representation would substantially advance the current state of the art.

There is a need to incorporate in growth models the important intrinsic (heritable) and environmental factors that cause variability in growth and a need to continue the exploration for an accurate proxy for age. The refinement of age pigment methods should continue, but at the same time it is necessary to better understand the factors that contribute to variability in growth so we can better simulate the size trajectory of a cohort in terms of both the mean and variance in size with time. For that it will be necessary to place more emphasis on long-term field studies that do the difficult work of monitoring the fate of cohorts through time.

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Chapter 2

Reproduction

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2.1 Introduction

Because many lobster species support valuable fisheries, their reproduction has been investigated since the onset of commercial exploitation. Female size at onset of maturity and fecundity were the main focus of these studies as these are important parameters in assessing the state of the stocks. Over the last 20 years, however, in response to the needs of aquaculture and more sophisticated fisheries models, as well as the quest for a deeper understanding of lobster autecology, there have been an increasing number of *in situ* and experimental studies that have expanded our understanding of the complexities of lobster reproduction. Now it is becoming evident that lobsters have complex social and reproductive behaviours including mate choice and competition, that there is subtle interplay between growth and egg production, that there can be maternal influences on egg size and larval health and that male size can also affect larval production.

Rather than merely provide an update of lobster reproduction eloquently summarised and reviewed by Aiken and Waddy (1980), Phillips *et al.* (1980), Quackenbush (1994), Talbot and Helluy (1995), Waddy *et al.* (1995), and Chubb (2000) we have used the mating system as a model upon which to integrate selected findings, especially those of recent years, contrast the differences between lobster groups and identify where more research is required. The backdrop for this review is our personal yet increasingly shared ‘bias’ that intense exploitation of select sex/size/maturity classes has the potential to negatively impact the mating system of lobsters (Cobb, 1995; Wahle, 1997; MacDiarmid & Butler, 1999; Gosselin *et al*., 2003) as of other animals (e.g. Rowe & Hutchings, 2003; Carver *et al*., 2005). Our purpose is to propose a more holistic view of lobster reproduction, focusing on female and male interactions and reflecting the consensus among evolutionary biologists and the growing awareness among fisheries scientists, that all components of mating systems – not simply female attributes – are important for ensuring the conservation of, and maximum economic returns from marine resources (e.g. Conover & Munch, 2002; Shuster & Wade, 2003; Alonzo & Mangel, 2004).

A mating system is the interaction of a suite of co-evolved anatomical, physiological and behavioural traits that characterise reproducing individuals with their population ecology in a variable environment, all of which determine mating and reproductive success. Thus, we review those aspects of lobster anatomy, physiology and behaviour directly impacting on reproduction as well as how key features of the structure of local populations such as population density and dispersion, sex ratio and size structure, affect mating success. In the last section we examine the potential for, and actual impact of, exploitation on lobster mating systems.

2.2 Reproductive morphology

2.2.1 *General patterns*

Lobsters conform to the generalised decapod reproductive pattern with separate sexes, paired ovaries or testes lying dorsally in the body cavity, leading via paired oviducts or vasa deferentia to reproductive apertures or gonopores at the base of the third pair of walking legs in females and the fifth pair in males (Meglitsch, 1967). The abdominal pleopods in the female are biramous and the inner branch (endopod) develops long setae specialised to carry eggs during the incubation period. The fifth walking leg in females terminates in a small pincer and is used to groom the setae and manipulate the egg mass. The detailed morphology of reproductive structures in lobsters has been reasonably well described for those species that support large commercial fisheries (e.g. Aiken & Waddy, 1980; Phillips *et al.*, 1980; Talbot & Helluy, 1995) but small, rare or non-commercial species remain largely ignored.

2.2.2 Sperm delivery and storage

A basic difference between the spiny and slipper lobsters (Palinuridae and Scyllaridae) on the one hand and the clawed lobsters (Nephropidae) on the other is the sperm delivery mechanism in males and sperm storage in females. In spiny and slipper lobsters, the male sperm transfer organ is the gonopore itself and sperm is passed to the female's external sternal region. In the spiny lobster genus *Panulirus*, there is an interesting trend from simple to complex mating structures in both males and females that reflects patterns of speciation (George, 2005). Males of more primitive species such as *P. cygnus* have a simple gonopore while the more recently evolved species such as *P. homarus* have a complex gonopore with an associated pointed and serrated penile process terminating in a distinct clump of setae (Fig. 2.1A) that may aid mate–mate recognition, direct sperm placement, detect a previously deposited spermatophore and/or be used to remove the spermatophore placed by another male (Sections 2.5, 2.6). In the more primitive species, the female sternum is typically unmodified and completely calcified while in the more recently evolved species, upon maturation the sternum develops soft, fleshy, decalcified windows separated by distinct calcified ridges with the numbers and extent of windows increasing with female size (Fig. 2.1B). This modified sternum is likely to be a specialised spermatophore reception area (Velázquez, 2003) and may play a role in sperm maintenance (Section 2.6). These structures may themselves have helped to initiate and maintain recent speciation in *Panulirus* (George, 2005). Sperm transfer and deposition structures in slipper lobsters are poorly described but more closely resemble those in spiny lobsters. In male clawed lobsters the first pair of abdominal pleopods are modified into intromittent organs, the gonopods, which deliver spermatophores from the sperm ducts that open at the base of the fifth walking legs into the median seminal receptacle that lies between the fourth and fifth pair of walking legs on the ventral surface of the female (Farmer, 1974; Talbot & Helluy, 1995) (Fig. 2.1C, D).

2.3 Maturation

2.3.1 Indicators of maturation

Size at onset of maturity (SOM) is a key metric of the reproductive capacity of populations and thus is important in stock assessments, fisheries management and any study requiring definition of the breeding population. Alterations in SOM among areas, or over time, may indicate the impact of the environment and/or exploitation on the lobster population. There are three basic indicators of maturity that can each be assessed by one or more criteria: (1) morphological maturity is detected by development of external body parts representing secondary sexual characters, (2) physiological maturity is reflected in the development of gonads and accessory glands, and (3) functional maturity is revealed by internal or external features or behaviour indicating past or current breeding activity. The adequacy and congruence of these indicators and criteria and their usefulness in estimating SOM depends on the species, population and extent of sampling.

SOM is usually estimated by plotting the percentage that are mature against classes of some body size measure and estimating the size at which 50% are mature. Alternatively, SOM may be determined from changes in allometry by classical intersect methods (e.g. Hartnoll, 1974) or by the less subjective method of smoothing splines (Watters &

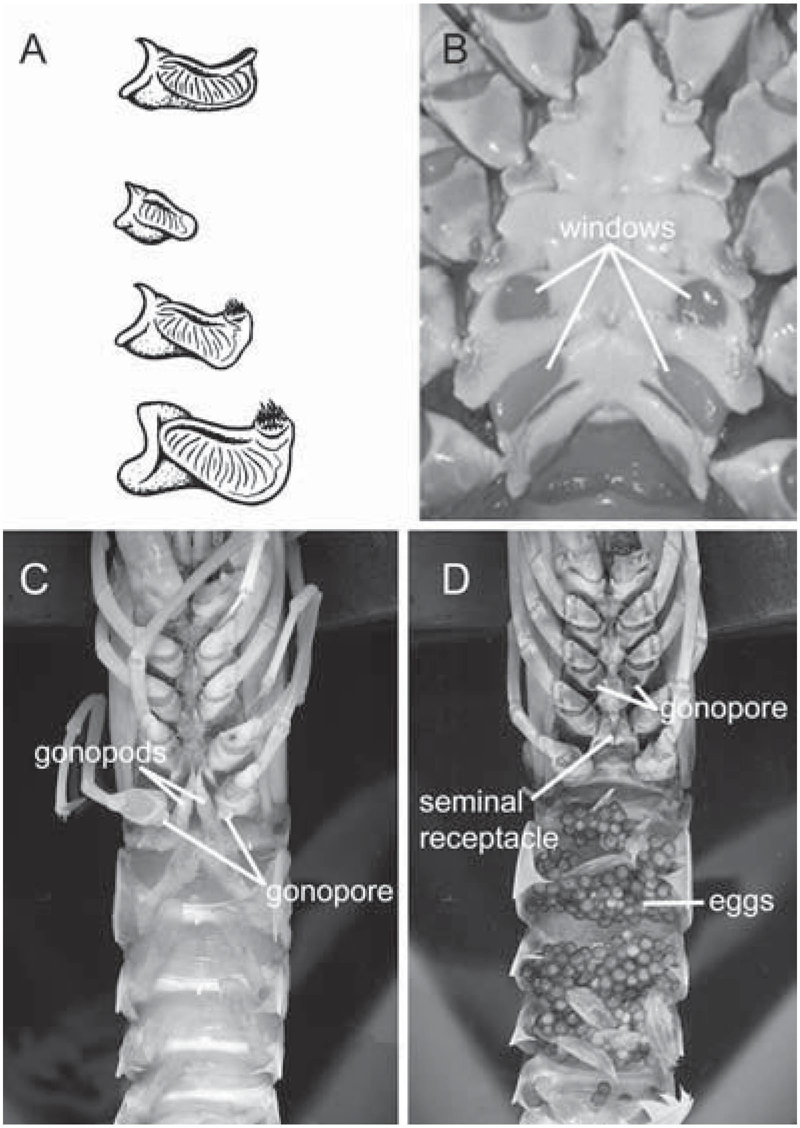

Fig. 2.1 Penile process of mature *Panulirus cygnus* (A top) and development of male penile process in juvenile, subadult and mature *Panulirus homarus rubellus* (bottom sequence in A); sternal plate of a mature female *Panulirus homarus homarus* showing fleshy decalcified windows (B); reproductive structures in male (C) and female (D) *Metanephrops challengeri* (A and B from George, 2005 reproduced with permission of RSNZ Publishing).

Hobday, 1998, but also see DeMartini *et al*., 2005). All measures will bias estimates of SOM if the sampling method preferentially captures either mature or immature lobsters of a certain size. This could occur for instance if lobsters change habitats when they mature and only one habitat is sampled or if mature and immature lobsters of the same size vary in their catchability (e.g. Farmer, 1974; Tully *et al*., 2001). Chubb (2000) and DeMartini *et al*. (2005) provided excellent reviews of the merits of the different approaches.

2.3.2 Female size at onset of maturity

Female SOM has been estimated using functional criteria of egg-bearing, the presence of fresh or spent spermatophores and resorbing ova, physiological criteria of ovary colour and size, oocyte size and development of cement glands on pleopods, and morphological criteria of abdomen and pleopod development. In females of temperate-water species that brood just a single annual clutch of eggs over an extended period, there is a high probability that the incidence of egg-bearing across the entire size range midway through the incubation period will yield accurate estimates of SOM (e.g. Annala, 1991). In many other species, females do not have a discrete breeding season or do not brood in every season/year and therefore SOM may be biased if the percent of females berried is the only criterion used to determine sexual maturity. This occurs if truly immature females are not, or cannot, be distinguished from mature but reproductively inactive females thereby generating an overestimate of SOM (DeMartini *et al.*, 2005). For instance, small egg-bearing females may be under-sampled due to their mating/spawning later in the reproductive season and/or small females may spawn less frequently than large females (Section 2.4). Frequently, this bias is countered by including other maturity measures such as the presence of ovigerous setae on the pleopods or fresh or eroded spermatophores on the sternal plates (Chubb, 2000). However, the presence of spermatophores is apparently not reliable in *Homarus americanus* and *Nephrops norvegicus* because physiologically immature females sometimes mate (Farmer, 1974; Aiken & Waddy, 1980; Waddy & Aiken, 2000). In *Homarus*, the development of cement glands on the pleopods is a particularly useful criterion of physiological maturity and imminency of oviposition for postmoult and intermoult females, as it is highly correlated with ovary development and can be assessed without killing the female (Aiken & Waddy, 1980; Tully *et al.*, 2001). Alternatively, in the spiny lobster genus *Panulirus* the development of decalcified windows on the female sternum (George, 2005) can be used to determine maturity (e.g. Lindberg, 1955; Velázquez, 2003).

Female maturity has also been estimated by allometric changes in the length of the pleopods, the length of pleopodal setae or the width of the abdomen relative to carapace length (CL) which all change in preparation for first spawning (Stewart *et al.*, 1997; Lizárraga-Cubedo *et al.*, 2003, Kulmiye, 2004; DeMartini *et al.*, 2005). This approach has the advantage that reproductively inactive yet mature females can be correctly classified as mature, but can lead to an underestimate of SOM if maturity is attributed to individuals that have not yet matured physiologically. For example, in *Homarus* the female ratio of abdomen width to carapace length (AW/CL) begins to increase and diverge from the male ratio 3–4 moults before female physiological/functional maturity (Krouse, 1973; Aiken & Waddy, 1980). Therefore it is recommended to score female maturity on the basis of some threshold value of the ratio AW/CL at which females are usually functionally mature. In some studies, no change in abdomen allometry has been detected (e.g. Comeau & Savoie, 2002) but this is often associated with under-sampling of the smallest and probable immature size classes (e.g. Tully *et al.*, 2001). We agree with DeMartini *et al.* (2005) and recommend that easily measured appendage length to body size relations should be routinely applied to provide estimates of female SOM in lobsters, but only after this approach has been validated by undertaking histological studies of gonad maturation.

2.3.3 Male size at onset of maturity

SOM is more difficult to assess in male than in female lobsters. Male physiological maturity has been determined by the presence of mature spermatozoa in vasa deferentia of several spiny lobsters (Heydorn, 1969a; Berry, 1970; MacDiarmid, 1989a; Turner *et al.*, 2002) and in the clawed lobsters *Homarus americanus* (Krouse, 1973) and *Nephrops norvegicus* (Farmer, 1974), but this need not indicate functional maturity. For example, male *H. americanus* may become physiologically mature at <50 mm CL but they are not willing or able to mate even in the absence of competition until 1–2 moults later when they exceed 65–70 mm CL (Aiken & Waddy, 1980; Ennis, 1980; Conan *et al.*, 2001). Aiken and Waddy (1980) have suggested the use of vasa deferentia weight relative to CL as an indicator of male maturity. However, this is likely to be a very poor indicator of male maturity in heavily-exploited populations, as studies on crabs indicate that dominant mature males may become severely depleted of sperm (Rondeau & Sainte-Marie, 2001; Kendall *et al.*, 2002; Hines *et al.*, 2003) such that their vasa deferentia are no larger than those of truly immature males.

Male function maturity is very difficult to assess in the field (Lawton & Lavalli, 1995) but is often assumed to be associated with a change in the dimensions of the first cheliped in clawed lobsters or of the second or third walking legs in spiny lobsters, relative to CL. Cheliped size is important to male *Homarus* for securing territory (dens) from, and asserting dominance over rival males, and for sexual display and coercing females (Elner & Campbell, 1981; Atema & Voigt, 1995). The extreme development of the second and third walking legs of males in some spiny lobsters enables them to extract females from their dens (Berry, 1970; Lipcius *et al.*, 1983; Bertelsen & Horn, 2000). The change in the size of the cheliped or walking leg usually occurs after physiological maturity and it can be detected by plotting the metric of cheliped or leg size versus CL for both mature and immature lobsters with SOM indicated by the point of upward deflection (George & Morgan, 1979).

Morphological criteria have now been widely used to determine male SOM in the spiny lobster genus *Panulirus* (see review in Chubb, 2000; Kulmiye, 2004). In *Jasus edwardsii*, the relative width of the first walking leg, especially the merus (= meropodite) that becomes broad and massive and carries large stout spines in large males, shows a distinct upward deflection at a size coincident with first observed male courting activity in mid New Zealand (A. MacDiarmid, personal observation), while the same measure in legs two and three does not (Fig. 2.2) and is likely to be a good candidate for external determination of SOM. Similar methods developed for male *Homarus americanus* are based on the ratio of crusher propodus (= propodite) volume over CL (or $CL^3/100$) plotted against CL with the point of divergence between the male and female pattern taken to be male SOM (Aiken & Waddy, 1989). Recently, Conan *et al.* (2001) contended that cheliped size diverges between sexes in a gradual and monotonic fashion from early juvenile stages, without any point of upward deflection in male allometric plots that might reflect the onset of maturity. However, early juveniles were not represented in their analysis and the number and CL range of other lobsters was too small (especially with regard to potentially mature individuals) to offer a real perspective on the development of chelipeds in the female and male. Figure 2.3 shows the allometry of crusher claw length relative to CL for most of the size range of benthic stages of *H. americanus*. Both sexes exhibit an initial phase of crusher claw positive growth allometry (slope of ln-transformed data >1) from settlement to ∞20–25 mm CL, followed by a phase of

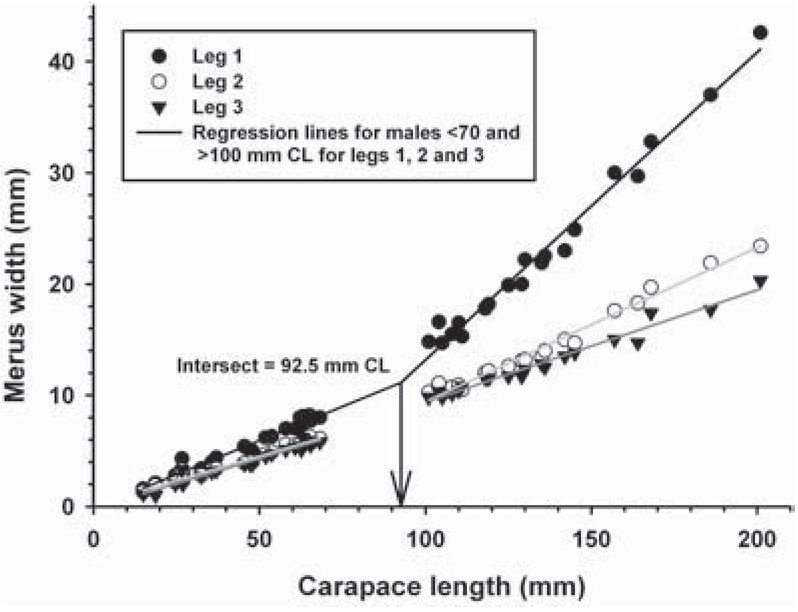

Fig. 2.2 Meropodite width as a function of carapace length (CL) for legs 1, 2 and 3 in male *Jasus edwardsii* from mid New Zealand. Separate regression lines for males <70 and >100 mm CL for legs 1, 2 and 3 are shown. The CL corresponding to the intersection of the separate regressions for leg 1 is also indicated.

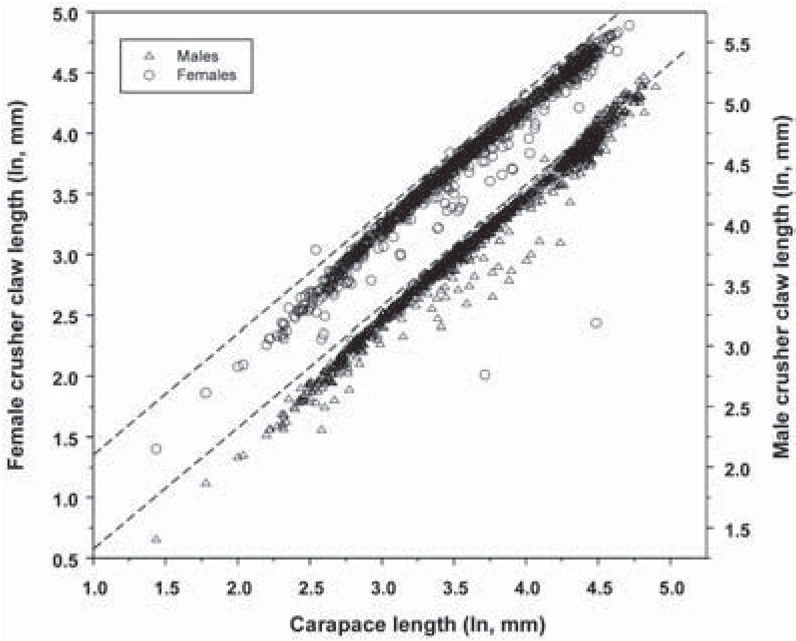

Fig. 2.3 The size relationship between crusher claw length and carapace length (both ln-transformed) for female (circles and left ordinate axis) and male (triangles and right ordinate axis) *Homarus americanus* from the Magdalen Islands, Québec. Included are two dashed reference lines with a slope of one (isometry).

isometric growth (slope = 1) up to ∞70 mm CL. Above this size, males again exhibit crusher claw positive growth allometry and start to express functional maturity (see above) while females continue to have isometric growth, as confirmed for lobsters of 80–175 mm CL by MacCormack and DeMont (2003). We conclude that the allometry of secondary sexual characters for characterising male maturity should be retained as a standard method. The development of the penile projection in the spiny lobster genus *Panulirus* (Heydorn, 1969b; George, 2005) and of the gonopod in clawed lobsters (Fig. 2.1A, C) might also be useful for determining male size of functional maturity (as in brachyuran crabs, e.g. Hartnoll, 1974).

2.3.4 Variation in SOM among species

Published values of lobster SOM reveal extreme variability among species (Tables 2.1 and 2.2). In *Nephrops norvegicus*, female maturation may be reached at 21 mm ocular CL and a weight of ~5 g (Tuck *et al.*, 1997, 2000) while in the packhorse lobster *Sagmariasus verreauxi*, female SOM occurs at 160 mm CL or ~2.2 kg, a massive 440-fold difference in weight (Booth, 1984). Nevertheless, amidst this variability two clear patterns emerge. First, in almost all species of lobsters investigated to date, males mature at a slightly larger body size than females (10.4% on average, Table 2.1). Second, SOM appears to be a constant relative to asymptotic size, as observed by Charnov (1990) in 27 populations of pandalid shrimp. Table 2.2 lists the data available for 53 populations of 18 lobster species. A plot of SOM against estimates of *L*′ for females shows a strong positive relationship ($r^2 = 0.87$, $n = 45$, $F = 284$, $p \ll 0.001$) at a slope of 0.60 (Fig. 2.4). The more sparse data for males appear to follow the same trend. Despite the uncertainty of estimating *L*′ , especially in heavily exploited populations, this plot indicates a fundamental relationship between SOM and growth in lobsters. Maturation is accompanied by a profound change in the biochemistry of female lobsters with large associated energy costs to somatic growth due to biosynthesis of lipids and their being sequestered in developing oocytes (Zoetendyke, 1990; Tuck *et al.*, 1997; Rosa & Nunes, 2002). Metabolic costs for males in terms of sperm production and time and energy spent searching for and courting females, also interacting with other males has hardly been investigated for any lobster species, but

Table 2.1 Estimates of male and female size at onset of maturity (SOM) in 12 species of lobster. SOM is the difference between male and female SOM expressed in mm or percentage of female SOM. GSI = gonadosomatic index.

Family, species, site	Female SOM (CL mm)	Male SOM (CL mm)	SOM mm (%)	Method	Reference
Palinuridae					
Jasus edwardsii	87.5	92.6	5.1 (5.8)	F: mid-point of size class with 50% setose or egg bearing; M: GSI vs body weight intersect method	Reanalysis of data in MacDiarmid (1989a)
NE New Zealand					
Palinurus elephas					
Columbretes Is, Spain	76.5–77.2	82.5	5.3 (6.9)	F: maturity ogive based on ripe ovaries or egg bearing; M: gonad weight vs CL	Goñi *et al.* (2003)
Panulirus guttatus					
Loee Key Reef, Florida	∞38	48	∞10 (26.3)	F: smallest size class with 50% egg bearing; M: 2nd leg length vs CL intersect method	Sharp *et al.* (1997)
Florida Keys	32.0	36.0	4.0 (12.5)	F: mid point of size class with 50% setose or egg bearing; M: 2nd leg length vs CL intersect method	Robertson & Butler (2003)
P. marginatus					
Ohau Island	58.6	63.6	5.0 (8.5)	F: leg length vs CL intersect method; M: leg length vs CL intersect method	Prescott (1984)
Necker Island	60.7	59.5	–1.1 (–1.8)		
P. homarus homarus				F: pleopod exopod length vs CL intersect method; M: 2nd leg length vs CL intersect method	
Kenya	50.5	57.5	7.0 (13.9)		Kulmiye (2004)
P. cygnus				F: maturity ogive based on presence of eggs or spematophore; M: 1st leg length vs CL intersect method	
Fremantle	97	107	10 (10.3)		Grey (1979)
Geralton	96	98	2 (2.1)		
P. japonicus	43	52	9 (20.9)	F: pleopod vs CL intersect method; M: 1st leg vs CL intersect method	Minagawa & Higuchi (1997)
Oshima, Japan					
P. versicolor	65	72	7 (10.8)	F: 5th leg length vs CL intersect method; M: 3rd leg length vs CL intersect method	George & Morgan (1979)
Indo-west Pacific					
Scyllaridae					
Ibacus peronii	50.4	45.0	–5.4 (–10.7)	F: maturity ogive based on ovary stage; M: smallest mature male	Stewart *et al.* (1997)
SE Australia					

Table 2.1 *continued*

Family, species, site	Female SOM (CL mm)	Male SOM (CL mm)	SOM mm (%)	Method	Reference
Nephropidae					
Nephrops norvegicus Firth of Clyde	21–34	29–46	8–12 (36.7)	F: abdomen width vs CL; M: crusher length vs CL	Tuck *et al.* (2000)
Homarus americanus					Gendron *et al.* (1994),
Gaspé, Canada	89.5	98	8.5 (9.5)	F: abdomen width/CL vs CL; M: crusher propodite index vs CL	
Grand Manan, Canada	108.1	110.1–130	11.9 (11.1)	F: maturity ogive based on cement glands on pleopods; M: crusher propodite index vs CL or crusher height vs CL	Campbell & Robinson (1983), Aiken & Waddy (1989), Fig. 3 in Elner & Campbell (1981)
Homarus gammarus					
Firth of Forth, Scotland	79.0	80.0	1.0 (1.3)	F: abdomen width/CL vs CL; M: crusher propodite index vs CL	Lizárraga-Cubedo *et al.* (2003)
Hebrides, Scotland	98.0	110.0	12.0 (12.2)		

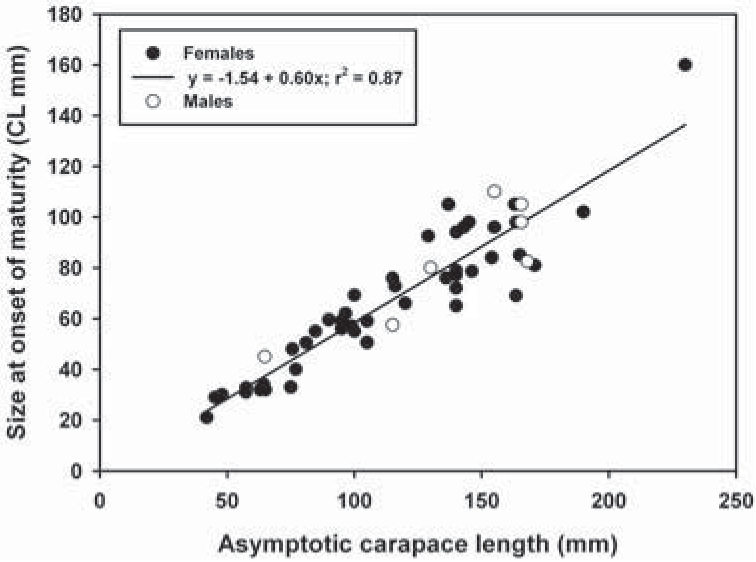

Fig. 2.4 Size at onset of maturity versus asymptotic carapace length (L_∞) for the female and male lobsters listed in Table 2.2. Also shown is the regression line and equation for females.

Table 2.2 Size at onset of maturity (SOM), asymptotic carapace length (L_{∞}) and relative size at onset of maturity (RSOM = SOM/L_{∞}) for 53 populations of 18 species of lobster. Data are for females unless stated otherwise.

Family, species, site	SOM	L_{∞}	RSOM	Reference
Palinuridae				
Sagmariasus verreauxi				Booth (1984)
Northern New Zealand	160	>230	<0.69	Pollock (1997)
Jasus edwardsii				
Thompson-Caswell Sds, NZ	85	165	0.52	Annala *et al*. (1980)
Stewart Island, NZ	105	137	0.77	McKoy (1985)
Jasus lalandii				
Marshall Rocks	57	99	0.57	Beyers (1979)
Min:	59	95	0.62	Pollock (1997)
Max:	66	120	0.55	
Jasus tristani				
Inaccessable Is	56	95	0.59	Pollock (1991)
Nightingale Is	59	105	0.56	
Palinurus gilchristi				
South Africa Min:	55	100	0.55	Pollock & Augustyn (1982)
Max:	65	140	0.46	Pollock (1997)
Palinurus elephas				
Corsica	76	136	0.56	Ceccaldi & Latrouite (2000)
Columbretes Is, Spain: females	77.2	140	0.55	Goñi *et al.* (2003)
Columbretes Is, Spain: males	82.5	168	0.49	
Panulirus penicillatus				Plaut (1993)
Gulf of Aqaba	55.0	84.7	0.65	Plaut & Fishelson (1991)
Enewetak Atoll, Marshall Is	62	96.5	0.64	Ebert & Ford (1986)
Panulirus argus				
Cuba	81	170.9	0.47	Baisre & Cruz (1994)
Venezuela	105	163	0.64	Yallonardo *et al.* (2001)
NE Brazil	84	154	0.54	Fonteles-Filho (1994)
Panulirus guttatus				
Min:	32	63	0.51	Caillouet *et al.* (1971)
Max:	40	77	0.52	Pollock (1997)
Venezuela	48	75.6	0.63	Robertson (2001)
Florida Keys	32	65	0.49	Losada-Tosteson *et al*. (2001)
Panulirus cygnus				
Male:	98–105	165.6	0.59–0.63	Phillips *et al*. (1992)
Female:	69–98	163.5	0.42–0.60	Grey (1979)
Panulirus ornatus				MacFarlane & Moore (1986)
Torres Strait	>78.6	146.2	0.54	Phillips *et al.* (1992)
Panulirus homarus				
Sri Lanka	59.5	>90.0	0.66	Jayakody (1989)
Shuwaniyah, Oman	69.2	>100	<0.69	Mohan (1997)
Sudh, Oman	75.9	>115	<0.66	
Mugsyl, Oman	72.8	>116	<0.63	
Panulirus homarus homarus				
Kenya: males	57.5	115	0.50	Kulmiye (2004)
Kenya: females	50.5	105	0.48	

Table 2.2 *continued*

Family, species, site	SOM	$L_{\prime}$	RSOM	Reference
Scyllaridae				
Ibacus peronii				
Coffs Harbour: males	45.0	64.8	0.69	Stewart *et al.* (1997)
Coffs Harbour: females	50.4	81.1	0.62	Stewart & Kennelly (2000)
Nephropidae				
Nephrops norvegicus				
Min:	21	42	0.50	Pollock (1991)
Max:	33	75	0.44	Pollock (1997)
Firth of Clyde Stn 2	32.7	57.5	0.57	Tuck *et al.* (1997 & 2000)
Firth of Clyde Stn 3	29.1	46.8	0.62	
Firth of Clyde Stn 4	29.0	45.3	0.64	
Firth of Clyde Stn 4	31.0	57.4	0.54	
Firth of Clyde Stn 6	34.0	64.4	0.53	
Metanephrops challengeri				Cryer & Oliver (2001)
East coast North Island, NZ	30	48	0.62	Annala *et al.* (2004)
Homarus americanus				
Min:	72	>140	<0.51	Pollock (1997)
Max:	102	>190	<0.54	
Homarus gammarus				
North-west Ireland: females	96.0	>143.0	0.67	Tully *et al.* (2001)
West Ireland: females	92.5	>129.0	0.72	
South-west Ireland: females	94.0	>140.0	0.67	
South-east Ireland: females	96.0	>155.0	0.62	
Firth of Forth, Scotland: males	80	>130	0.62	Lizárraga-Cubedo *et al.* (2003)
Firth of Forth, Scotland: females	79	>140	0.56	
Hebrides, Scotland: males	110	>155	0.71	
Hebrides, Scotland: females	98	>145	0.68	

is high in other crustaceans (e.g. Robinson & Doyle, 1985). Some large male *Jasus edwardsii* rarely leave their den for the duration of the six-week mating season (MacDiarmid *et al.*, 1991) and male feeding rates plummet during this time (Kelly *et al.*, 1999) potentially leading to a loss in nutritional condition.

2.3.5 Variation in SOM among populations

The literature presents a confusing picture of variation in SOM among populations of the same species. SOM may vary within a species in response to age, growth rate, seawater temperature, density, food availability, other environmental variables or their interaction. SOM in New Zealand female *Jasus edwardsii* is negatively related to average seawater temperature and appears to be unrelated to age (Annala *et al.*, 1980), whereas in Tasmania, the same species reaches SOM at a smaller size in the southern, cooler, slow-growing populations and at a larger size in the northern, warmer, fast-growing populations (Punt & Kennedy, 1997; Punt *et al.*, 1997; Turner *et al.*, 2002). In contrast, in *J. lalandii*, SOM appears to be age rather than size specific (Beyers & Goosen, 1987). Summer water temperature seems to be the overwhelming natural factor determining female SOM in *Homarus americanus*, with animals maturing at smaller sizes as temperature increases (e.g. Waddy *et al.*, 1995, Comeau & Savoie, 2002). In the spiny lobster *Palinurus gilchristi*, SOM is highest in the areas of faster growth (Groeneveld & Melville-Smith, 1994). Female *Nephrops norvegicus* in the Atlantic and Mediterranean mature between 3 and 3.5 years of age but over a range of locally determined sizes (Orsi Relini *et al.*, 1998; Tuck *et al.*, 2000), while males reach sexual maturity between 4 and 5.5 years depending on local growth rates (Tuck *et al.*, 2000). SOM of *N. norvegicus* in the Firth of Clyde is negatively correlated to catch rate and burrow density (Tuck *et al*., 2000). There is also evidence from *J. edwardsii* in Tasmania, *P. marginatus* from Necker Island and *H. americanus* that SOM varies over time at one location, presumably in response to movement between populations, intense fishing, or a change in temperature, density or some other environmental variable (C. Gardner, unpublished data; Waddy *et al*., 1995; Tuck *et al*., 2000; Landers *et al*., 2001; DeMartini *et al*., 2003). Clearly, a more systematic experimental approach is required to determine the critical environmental and social factors influencing SOM. In addition, because SOM can be dynamic in time, it should be assessed on a more regular basis in species subject to exploitation (e.g. DeMartini *et al*., 2005).

2.4 Timing and duration of female receptivity

2.4.1 Importance for the mating system

The degree of temporal synchronicity and extent of female receptivity contribute to shape the mating system, as they dictate the number of potential mates and competitors, and hence the intensity of sexual competition and ultimately the potential for sexual selection. The intensity of female sexual competition increases with greater synchrony and shorter period of female receptivity. On a seasonal basis, female receptivity is most synchronised in warm temperate species such as *Jasus edwardsii* and *Palinurus elephas* that have only one brood per year in a short, well-defined reproductive season that may last as little as six weeks at a locality (e.g. MacDiarmid, 1989a; Hunter, 1999). Tropical species of spiny lobsters on shallow reefs may reproduce more or less continuously throughout the year (Chubb, 2000; MacDiarmid & Kittaka, 2000; Kulmiye, 2004) with individual females successively mating and brooding 4 times per year (e.g. Briones-Fourzán & Lozano-Álvarez, 1992). In *Homarus americanus*, a temperate species with long brooding periods, mating occurs mainly in the second half of the boreal summer (July–September) with individual females either moulting/brooding annually, alternating one year of moulting with one year of brooding, or alternating moulting in one year with two to three consecutive years of brooding (Ennis, 1984; Waddy & Aiken, 1986; Comeau & Savoie, 2002). Small female lobsters from all environments typically breed less frequently and/or later in the breeding season than large, multiparous females (see reviews in Waddy *et al*., 1995; Chubb, 2000; Groeneveld, 2000; Robertson, 2001; Goñi *et al*., 2003; Kulmiye, 2004).

2.4.2 Link to moulting schedules

The timing of mating and spawning in most female lobsters is intimately linked to moulting schedules. As sperm stored internally or externally by the female are lost at ecdysis, mating in lobsters takes place some time after the female moults, though the delay may vary from a few minutes to several months even among females of the same species. In females with a limited window of receptivity and attractiveness to males, mating normally must occur within a 24–48 hour period either just after moulting as in *N. norvegicus* or up to 63–73 days after moulting but immediately prior to egg extrusion as in the rock lobsters *Jasus edwardsii* and *S. verreauxi* and the spotted spiny lobster *Panulirus guttatus* (Farmer, 1974; MacDiarmid *et al*., 1999; Robertson, 2001; Moss *et al*., 2004). In females with extended receptivity and attractiveness to males, the moult–mate interval can be considerably longer, up to 97 days in *P. cygnus* (Chittleborough, 1976). In *H. americanus*, although females usually mate within minutes to hours of moulting (Templeman, 1940; Aiken & Waddy, 1980; Atema, 1986; Talbot & Helluy, 1995) when their receptivity is at its peak, uninseminated females exhibit a secondary peak of receptivity shortly before oviposition and will be mated if the opportunity arises (Waddy & Aiken, 1990). Additionally, female *H. americanus* may top up their sperm supplies any time during intermoult, which may last for up to three years (Dunham & Skinner-Jacobs, 1978; Waddy & Aiken, 1990; Waddy *et al*., 1995). Species in which females have synchronous mating and limited receptivity are more at risk of being mate-limited than species with females having asynchronous mating and extended receptivity.

2.4.3 Environmental influences

Seasonal progressions in day length and/or water temperature are the obvious environmental factors influencing the timing of lobster reproductive cycles but this influence has been explored in few species. Laboratory experiments have determined that long days enhance female gonadal development and spawning frequencies in *Panulirus argus* and *P. japonicus*, while warmer temperatures significantly accelerate these processes in these species (Lipcius & Herrnkind, 1987; Matsuda *et al.*, 2002) as well as in *P. cygnus* (Chittleborough, 1976). With short days, ovarian development in *P. japonicus* depended on temperature (Matsuda *et al.*, 2002). In *Homarus americanus*, photoperiod has little influence on regulation of spawning in shallow inshore populations (Waddy *et al.*, 1995) and the length of the female reproductive cycle is related to the number of degree-days in a particular season (Comeau & Savoie, 2002). Latitudinal and interannual variation in the onset and proportion of female *Jasus edwardsii* mating appears to be triggered by an autumnal decline in temperature with 50% mating at a temperature of 16°C (Walker & Bentley, 2000).

2.4.4 Daily timing

Individual daily scheduling of reproductive activity can affect the potential number of mates and competitors but it is not clear for the majority of lobster species whether mating has a higher probability at particular times of the day and how this links with other activities. The best information comes from laboratory studies of the Caribbean spiny lobster *P. argus* where mating took place during the day and night but peaked during crepuscular periods (Lipcius & Herrnkind, 1985). In *Homarus americanus* and *H. gammarus* no laboratory or field study has monitored lobsters continuously over time during the mating season and thus it is not known with certainty if mating is more frequent at a particular time of day, although Dunham and Skinner-Jacobs (1978) reported equal numbers of matings during light and dark phases. In *Nephrops norvegicus*, mating apparently occurs only at night (Farmer, 1974).

2.5 Mate attraction, recognition, choice and competition

2.5.1 Finding a mate

When females are receptive for only a short period of time they must quickly find or attract mates. Additionally, for males and especially females, reproduction is costly in terms of energy, time and foreclosure of further mating opportunities (Debuse *et al.*, 1999). It is essential, therefore, that lobsters recognise and mate a member of the same species and furthermore choose and perhaps compete for a mate that helps to maximise their own reproductive success.

2.5.2 Olfactory, visual, auditory and tactile cues

Olfactory, visual, auditory and tactile stimuli may play a role in the attraction, recognition and choice of mates in different lobster species. In *H. americanus* there is clear evidence of female distance-attraction to males (but not the reverse) in response to male urine-borne chemical cues and disruption of this key mechanism reduces the frequency of females approaching male dens and the time they spend attempting to enter (Bushmann & Atema, 1997). However, urine from the opposite sex is important to both female and male *H. americanus* for proximate recognition and evaluation (of sex or maturity status), courtship and normal mating behaviour, while submissive posturing may relax male aggressiveness (Atema & Voigt, 1995; Bushmann & Atema, 1997, 2000). The extensive work on *H. americanus* has stimulated interest in the role of olfaction in reproduction in other species. Raethke *et al.* (2004) found that while receptive female *Jasus edwardsii* distinguish males from females and juveniles using olfaction, they select among potential mates using both olfaction and visual cues. The visual sense in spiny lobsters is well developed especially in the large-eyed shallow-water tropical members of the genus *Panulirus* (Meyer-Rochow, 1975, 1988). We suspect that while in clawed lobsters, olfaction plays the critical role in determining mate attraction, recognition and choice, in spiny lobsters, vision is likely to play an important role increasing from least critical in *Jasus* to most critical in the recently evolved species such as *P. ornatus*.

Spiny lobsters in the clade Stridentes also possess a stridulating organ (Patek, 2001) and in at least one species it is used to attract mates. In *Palinurus elephas*, stridulation by a reproductive female attracts mature males from a radius of at least 15 m, but on first contact regular calls stop and other males cease to react (Mercer, 1973). In the laboratory, males move towards an underwater speaker broadcasting female stridulation. Similar female stridulation and male reaction has been observed in *P. homarus* (Berry, 1970) and it is likely to occur in other members of this clade.

2.5.3 Mate recognition

In temperate lobsters with few, if any, closely related sympatric species, mate recognition is probably subsumed into the problem of mate choice. However, in some speciose genera of lobsters, mate recognition may be an important first hurdle to successful reproduction. It is interesting to note in this regard two features of the spiny lobster genus *Panulirus*. First, the decalcified windows on the female sternum and the male penile processes that develop at maturity (George, 2005) (Fig. 2.1A, B). These distinctive male and female structures may be critical in enabling individuals to mate preferentially with their own species. George (2005) noted that most of the species with simple male and female reproductive structures occur with no or only one sympatric species while those with complex structures are often widespread within the Indian and Pacific Oceans and co-occur with closely related species on many reefs. The distinctive reproductive morphology may be of fundamental importance in initiating and maintaining speciation within the group. Second, this mechanism may be aided by the bright colours and strongly contrasting patterning, especially at the base of the antennae, around the eyes and on the legs of many species in this genus; all areas that are prominent to a potential mate during courtship.

2.5.4 Operational sex ratio

The relative importance of mate choice and competition in lobster breeding systems will vary among species and between males and females depending on the operational sex ratio (OSR – the ratio of mature males to receptive females), the variance in mate quality and the cost of breeding expressed as either mortality associated with reproduction or time spent dealing with the result of previous matings (Reynolds, 1996; Kokko & Monaghan, 2001; Shuster & Wade, 2003). The degree of mate choosiness for one sex should increase with the degree of opposite-sex bias in OSR, the variance in mate quality, and the cost of breeding (Gibson & Langen, 1996; Kokko & Monaghan, 2001). Mate competition, likewise, will vary dependent on the OSR and the cost of breeding (Kokko & Monaghan, 2001). Spatial aspects including reef size and lobster density and patchiness may also be important in determining mate availability, choosiness and competition (e.g. Robertson, 2001), especially in species such as *Homarus gammarus* and *H. americanus* where males defend breeding site resources (Debuse *et al*., 2003).

The OSR in lobsters may be skewed heavily towards males, as individual females are receptive for only a portion of the reproductive period (Section 2.4). A strong male bias in the OSR results in mature males competing with others for access to scarce receptive females and in all lobster species studied so far, mature males are aggressive toward one another during the reproductive season (see Lawton & Lavalli, 1995 and MacDiarmid & Kittaka, 2000 for reviews). Male–male aggression affects their local spatial dispersion, normally resulting in large male lobsters monopolising one or more dens and/or asserting territorial control over prime habitat (Karnofsky *et al*., 1989; Karnofsky & Price, 1989; MacDiarmid, 1994; Atema & Voigt, 1995).

2.5.5 Indicators of mate quality

In lobsters, variance in mate quality is usually a function of body size because this greatly affects the number and sometimes the quality of eggs and sperm on offer (Sections 2.6, 2.8) as well as the

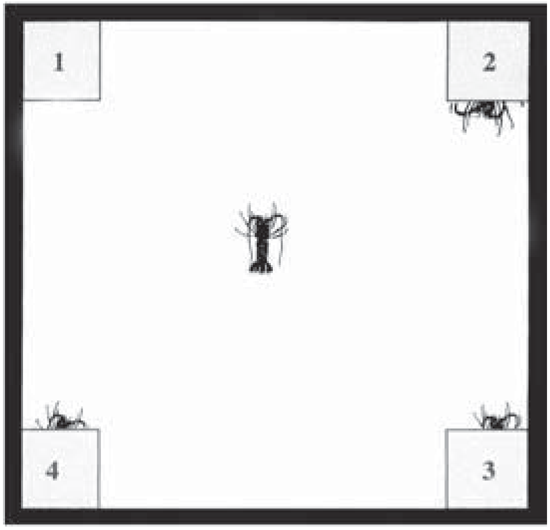

Fig. 2.5 Experimental set up for determining female mate choice in *Jasus edwardsii* and *Panulirus argus*. Each test female lobster was given 24 hours to select a shelter that was empty or had a tethered female, small mature male or a large mature male. At least 20 replicates were run per experiment and were analysed using a log-linear goodness-of-fit test with 0.25 n (the number of replicates) as the expected use of each shelter type if the category of occupant did not affect female selection (MacDiarmid *et al.*, 2000).

capability of males to protect recently moulted females. At least in some clawed lobsters there is presumption or evidence that nutritional status also has a strong influence on egg/sperm number and quality and/or dominance (Harrison, 1990; Vye *et al.*, 1997; Gendron *et al.*, 2001). However, although bigger may often be better, there can be practical limits to the size of a mate (Berry, 1970). For example, early observations suggested that female *Homarus americanus* could not be mated by males >7% smaller or >21% larger in CL due to physical limitations (Templeman, 1934), but a recent investigation indicates these limits are substantially underestimated (Gosselin *et al.*, 2003).

Subsequent experimental studies (e.g. Fig. 2.5) indicate that mate selection in the temperate species *Jasus edwardsii* is much more precise than it is in the tropical *Panulirus argus* and more precise for the larger individuals (MacDiarmid *et al.*, 2000; MacDiarmid & Stewart, 2005a; M. Butler, unpublished data). Likewise, though competition amongst males is common to both genera, competition amongst females appears to be more overt in *J. edwardsii* and more apparent among larger individuals. This is probably because in this species the variance in mate quality is higher and the cost of mating greater, especially for larger individuals. In *J. edwardsii* there are larger rewards for mating with a larger partner (e.g. more sperm, larger eggs, more robust larvae, etc.) and more dire consequences when suitable mates are not found (e.g. significant reduction in annual egg production by females, long-term ovarian damage in unmated females, lost mating opportunities for males; (MacDiarmid & Butler, 1999; MacDiarmid *et al.*, 1999, 2000; Mauger, 2001; MacDiarmid & Stewart, 2005b) (Sections 2.6, 2.7).

In *Homarus americanus*, females usually search for males and prefer to mate with the dominant one, typically the largest in the neighbourhood (Atema & Voigt, 1995). Females may prefer large males because of their bigger dens, greater protective value and more generous offering of sperm (Cowan & Atema, 1990; Atema & Voigt, 1995; Bushmann & Atema, 2000, Gosselin *et al.*, 2003). However, the possibility that males are less likely to mate or have a lesser mating frequency in years when they moult is a confounding factor, as small males often may not be 'receptive' to females because they usually moult annually while larger males moult only every two to three years (Waddy *et al.*, 1995). Among males of similar size and moult stage, dominance can be predicted by plasma protein level, a likely indicator of nutritional status, and to a lesser extent by cheliped dimensions and exoskeleton calcium concentration (Vye *et al.*, 1997). Dominant and subordinate males apparently do not differ in the volume of urine they emit over relatively long periods of time, so recognition of dominance by receptive females and competing males may be more related to the quality (i.e. chemical composition) of urine and/or the fine temporal pattern of its release (Karavanich & Atema, 1998; Breithaupt & Atema, 2000; Bushmann & Atema, 2000). Male acceptance of females appears to be based primarily on criteria of maturity and whether they have already mated (Waddy *et al.*, 1995).

2.5.6 *Courting and copulation*

Courting and cohabitation in spiny and clawed lobsters have previously been thoroughly reviewed (Atema & Voigt, 1995; MacDiarmid & Kittaka, 2000). The courting frontal approach in spiny lobsters has been observed to occupy from several minutes to 11 days prior to copulation (Lipcius & Herrnkind, 1985; MacDiarmid, 1989b). In *Jasus edwardsii*, the length of the courting period is unrelated to female size but increases with male size (MacDiarmid, 1989b; MacDiarmid & Butler, 1999), perhaps an attempt by females to monopolise preferred males. Female *Homarus americanus* cohabit with a male for an average of 12 days when mating is associated with the female's moult, but cohabitation appears to be brief when mating occurs during the female's intermoult (Atema & Voigt, 1995). Cohabitation time, however, actually depends on the size of female and male *H. americanus*. In moult-associated mating, females cohabited about five times longer with large (116–131 mm CL) than with small (81–84 mm CL) males and cohabitation time was positively correlated with female size, but only when the male was large (Gosselin *et al*., 2003). These last authors suggested that associations with small males were terminated by females because of the low value of the male, while associations with large males were protracted because the female benefited from thorough protection while the male increased his chances of being the sole sire of the next clutch and perhaps became more conspicuous to other mate-searching females. Cowan & Atema (1990) have provided some evidence that female *H. americanus* can stagger their moult to mate with a preferred male (but see Hazlett, 1991 and the authors' rebuttal).

2.6 Copulation and sperm transfer and storage

2.6.1 *Copulation and ejaculate size*

Copulation in lobsters is usually very brief, typically lasting less than a minute in nephropid (Farmer, 1974; Talbot & Helluy, 1995) and in palinurid lobsters (MacDiarmid & Kittaka, 2000). Males of several lobster species deposit a spermatophore that is positively related to female size (Berry, 1970; MacDiarmid & Butler, 1999; Mauger, 2001; Robertson, 2001; Gosselin *et al*., 2003), but it is unclear whether the assessment of female size takes place during courtship, perhaps visually or via olfaction, or during copulation, via perhaps a simple mechanical feedback to the gonopore at the base of the fifth walking leg which is used to clasp the female. The elaborate penile projections in spiny lobsters in the genus *Panulirus* may be a mechanism to aid spermatophore positioning and determine female maturity or size (George, 2005).

In three species of spiny lobster and one species of clawed lobster, small males pass less ejaculate (sperm) than large males (MacDiarmid & Butler, 1999; Mauger, 2001; Robertson, 2001; Heisig, 2002; Gosselin *et al*., 2003). Moreover, in *Jasus edwardsii*, *Panulirus guttatus* and *P. argus*, clutches fertilised by small males are smaller than clutches fertilised by large males, and in the latter species, spermatophore size influences clutch weight more than female size (MacDiarmid & Butler, 1999) (Fig. 2.6). Whereas female clawed lobsters may mate repeatedly to compensate for deficient sperm reserves (Waddy & Aiken, 1990; Gosselin *et al*., 2003, 2005), female spiny lobsters normally mate only once before each successive brood. Laboratory experiments with *P. argus* show that a combination of mechanical and chemical cues from the spermatophore inhibits the female from mating again (Heisig, 2002). Experimental removal of the spermatophore induces the female to mate again. Occasionally, females will remove spermatophores, particularly those deposited by small males (e.g. MacDiarmid & Butler, 1999), but it is unclear whether males are able to forcibly remove spermatophores to induce females to mate. In *Homarus americanus*, female receptivity and male willingness to mate may also be mediated by the presence of sperm in the female (Waddy *et al*., 1995).

2.6.2 *Sperm availability*

Sperm regeneration in male lobsters may take a considerable period. In *Jasus edwardsii*, sperm is

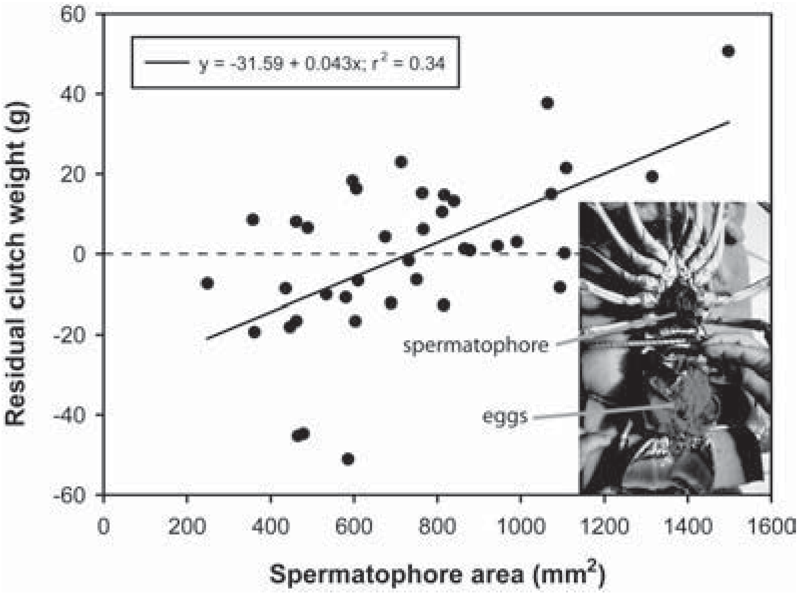

Fig. 2.6 Residuals of clutch weight versus female carapace length as a function of spermatophore area in *Panulirus argus argus* (data from experiments described in MacDiarmid & Butler, 1999). The regression (solid) line and equation are shown. The dashed horizontal line indicates zero residual. Note that most negative residual clutch weights are associated with small spermatophores and large positive residuals are associated with large spermatophores. Shown inset is a female with a fresh spermatophore on the sternum and a clutch of eggs fertilised from a prior mating.

mostly accumulated in the vasa deferentia over the few months prior to mating each year and then used with little regeneration during the six-week mating period (Mauger, 2001). Laboratory experiments indicate that the amount of sperm available for use depends on the initial size of the vasa deferentia and the cumulative weight of the females already mated by a male that season (Mauger, 2001). Small 500 g (100 mm CL) males that start with small vasa deferentia can supply adequate sperm to only 1–3 similar sized females whereas larger 3 kg males (186 mm CL) can service at least 17–20 females (and probably more as long as their cumulative weight does not exceed about 17 kg) representing an 11-fold increase in the total number of eggs fertilised per season (Gibson & Frusher, 1997; MacDiarmid & Stewart, 2005b).

2.6.3 Sperm storage

The specialised structure of spermatophores has been well reviewed by Subramoniam (1993), also Talbot and Helluy (1995). Recent work by Heisig (2002) shows that in the spiny lobster *Panulirus argus*, sperm is concentrated in the mid-posterior portion of the spermatophore with only low concentrations in the anterior region, the region that often remains on the sternum after the spermatophore has been used to fertilise a clutch of eggs. This suggests in this species that it is unlikely that enough sperm would remain to fertilise all the eggs in a subsequent clutch. In some species of spiny lobsters, the female develops specialised soft, fleshy, decalcified windows on the sternum, with larger females having more windows (George, 2005). It is possible these allow nutrients to pass through the body wall to the sperm and sustain them before they are used up to four months later. As larger females receive larger spermatophores, this explanation provides a reason for larger females to develop additional decalcified windows. Alternatively, these structures may be a female strategy to secure additional sperm. In other species under the situation of light sperm competition, second mating males will often deposit a larger packet of sperm than the first mating male to increase the chances of paternity. This trend may reverse for later mating males (Parker *et al.*, 1996; Galvani & Johnstone, 1998). The decalcified windows may thus mimic a fresh soft spermatophore and induce the males into depositing additional sperm, ensuring females gain sufficient sperm to fertilise their entire clutch. In this situation, the elaborate male penile processes might aid the male to determine if a female has been mated or not. As larger females require more sperm, this explanation also provides a reason for larger females to develop additional decalcified windows. The wide variety of male and female reproductive structures in this genus (George, 2005) presents an ideal opportunity to explore these relationships.

Female lobsters store sperm for varying periods and this capacity may confer greater flexibility in the relative timing of mating and spawning/fertilisation. In the rock lobster genus *Jasus*, males deposit a naked spermatophore (Berry & Heydorn, 1970) which females must use immediately, thus a female has to find a mate at the very peak of her fertility. In other spiny lobsters with specialised, longer-lasting spermatophores (Subramoniam, 1993), mating, egg extrusion and fertilisation may be separated by up to two days as in *Panulirus guttatus* (Robertson, 2001), two weeks as in *P. elephas* (Mercer, 1973; Hunter, 1999), or four months as in *P. interruptus* (Velázquez, 2003). Moreover, in the clawed lobsters with specialised internal sperm-storage organs, sperm may be stored for up to three years before use (Waddy & Aiken, 1986; Talbot & Helluy, 1995). The provision to store sperm for extended periods may be particularly important in tropical and deep-water lobsters with low population densities and consequently low male–female encounter rates. Hypothetically, in lobster species where females do not overtly choose their mate, external sperm storage might offer the opportunity for cryptic mate choice through female assessment and manipulation of attached spermatophores, as suggested for the rock shrimp *Rhynchocinetes typus* (Thiel & Hinojosa, 2003).

2.7 Fertilisation and egg-laying

2.7.1 Polyandry

Several studies have suggested that female lobsters can be polyandrous, whether they store sperm for extended periods or not. This behaviour can result in multiple paternities of eggs in a single clutch when no sperm selection or precedence mechanisms exist. Very strong evidence for multiple paternity using microsatellite markers comes from studies of two species of clawed lobsters. In *Nephrops norvegicus*, 6 of 11 females sampled off the Portuguese coast had clutches sired by 2 or 3 males, with the clutches of larger females tending to have more sires (Streiff *et al.*, 2004), while of a sample of 21 females from the Irish Sea and off Iceland, 47% carried eggs fertilised by two different males, although the genetic contribution of the two was highly skewed (P. Prodöhl, personal communication). Likewise, in *Homarus americanus*, multiple paternity has been detected during development of microsatellite markers (Jones *et al.*, 2003), confirming earlier electrophoretic evidence (Nelson & Hedgecock, 1977). More extensive surveys of female *H. americanus* indicate that 11–28% of clutches at two heavily exploited sites were sired by two or three males whereas no clutch was sired by more than one male at the least exploited site (Gosselin *et al.*, 2005). It is interesting to note that the high incidence of multiple paternity in *N. norvegicus* is associated with an apparent lack of male post-copulatory mate-guarding (see Farmer, 1974), whereas the relatively low incidence in *H. americanus* is associated with overt female choice and generally prolonged female and male post-copulatory cohabitation (Section 2.5).

More equivocal is the evidence for multiple mating in spiny lobsters based on the occurrence of overlaying viable spermatophores. Mota Alves and Paiva (1976) working on *Panulirus argus* and *P. laevicauda* in Brazil, found that the frequency of multiple copulation reaches 43% and increases with female size. In contrast, no evidence of multiple spermatophores has been found during examination of hundreds of female *P. argus* from the Florida Keys (MacDiarmid & Butler, 1999; Bertelsen & Matthews, 2001; Heisig, 2002). The current and anticipated development of microsatellite markers for spiny lobsters (e.g. Diniz *et al.*, 2004) should help to resolve these issues. Multiple paternity has not been found in wild *Homarus gammarus* despite a Europe-wide search and its occurrence in laboratory mating experiments (Ferguson, 2002). Considering that female promiscuity in *H. americanus* appears to be linked to sperm limitation (reviewed in Gosselin *et al.*, 2005) and the apparent similarities between the mating systems of the two species, we hypothesise that the lack of multiple paternity in *H. gammarus* indicates a state of extreme population reduction in which promiscuity is no longer possible due to very low mate-encounter rates.

2.7.2 Sperm to egg ratios and non-mating

Although fertilisation in all lobsters examined to date is external (Paterson, 1969; MacDiarmid, 1988; MacDiarmid & Kittaka, 2000; Aiken *et al*., 2004), a usually rather inefficient mode compared to internal fertilisation, sperm-to-egg ratios appear to be relatively low. Heisig (2002) counted sperm in spermatophores recovered from female *Panulirus argus* and calculated their probable size-specific fecundity. She estimated effective sperm to egg ratios to range from 21–37. No similar data are available for other lobster species, however these values are in the lower range of estimates for brachyuran crabs with internal fertilisation (reviewed in Hines *et al*., 2003).

The impact of partial or absolute sperm limitation on fertile female lobsters appears to vary among species. If female *H. americanus* and *H. gammarus* receive no sperm they may resorb ripe eggs in the ovary, apparently without irreversible damage to the ovary (although the haemolymph may temporarily change to dark green or black), or extrude eggs that are not fertilised (Allen, 1895; Aiken & Waddy, 1980; Waddy *et al*., 1995). In unmated *Jasus edwardsii*, egg resorption also discolours the haemolymph to a strong pink/purple and also results in greatly enlarged, discoloured and scarred ovaries with reduced fertility in the following reproductive season (MacDiarmid *et al*., 1999). In other genera of spiny lobsters where mating is not the required cue for egg deposition, if a female fails to find a mate she simply extrudes the current batch of eggs, which because they are unfertilised, fail to attach permanently to the pleopodal setae beneath the abdomen (MacDiarmid & Butler, 1999).

2.8 Egg brooding and hatching

2.8.1 Partitioning reproductive effort

Lobsters have evolved a range of responses to the problem of partitioning reproductive energy into the number and sizes of eggs and there is considerable variation between and within species. It is clear from the trends in Figure 2.7 that while in general, larger females brood more eggs than smaller females, size-specific fecundity is much greater in spiny lobsters such as *Panulirus argus* than in the clawed lobsters. The other spiny lobster genera and the slipper lobsters fall between these extremes and only the enormous size of *Sagmariasus verreauxi* allows it to produce as many eggs as *P. argus*. Higher fecundity in spiny lobsters is associated with small individual egg size and a prolonged larval phase while the reverse is true of clawed lobsters (Pollock, 1997). In two species of clawed lobster, *Homarus capensis* and *Metanephrops challengeri*, very large egg size may be associated with very low fecundity (Fig. 2.1D) and a greatly abbreviated larval phase (Wear, 1976; Kado *et al*., 1994).

Clutch size in lobsters can be extremely variable among locations and over time. *Nephrops norvegicus* from the Firth of Clyde show a 30% range in size-specific fecundity amongst sites between 4 and 60 km apart (Tuck *et al*., 2000). In *Homarus americanus*, considerable variability in size-specific fecundity has been recorded among areas, but there is no evidence that it has changed significantly in over a century along the coast of Massachusetts (reviewed in Fogarty, 1995). In *Jasus edwardsii*, size-specific fecundity varies significantly and inversely with SOM among some New Zealand localities (Annala, 1991). In contrast, little variation in size-specific fecundity was found in populations of *H. gammarus* around Britain and Ireland (Tully *et al*., 2001; Lizárraga-Cubedo *et al*., 2003). Similarly, there was no difference in size-specific fecundity among populations of the slipper lobster *Ibacus peronii* more than 10 000 km apart in eastern Australia (Stewart *et al*., 1997).

Brood size and growth or nutritional conditions appear to be strongly linked in a number of lobster species. In areas where, or years when, food availability is high, both male somatic growth rates and female brood size in *Jasus lalandii* off southern Africa are high (Beyers & Goosen, 1987; Melville-Smith *et al*., 1995). Similarly, brood size in the deep-water spiny lobster *Palinurus gilchristi* off

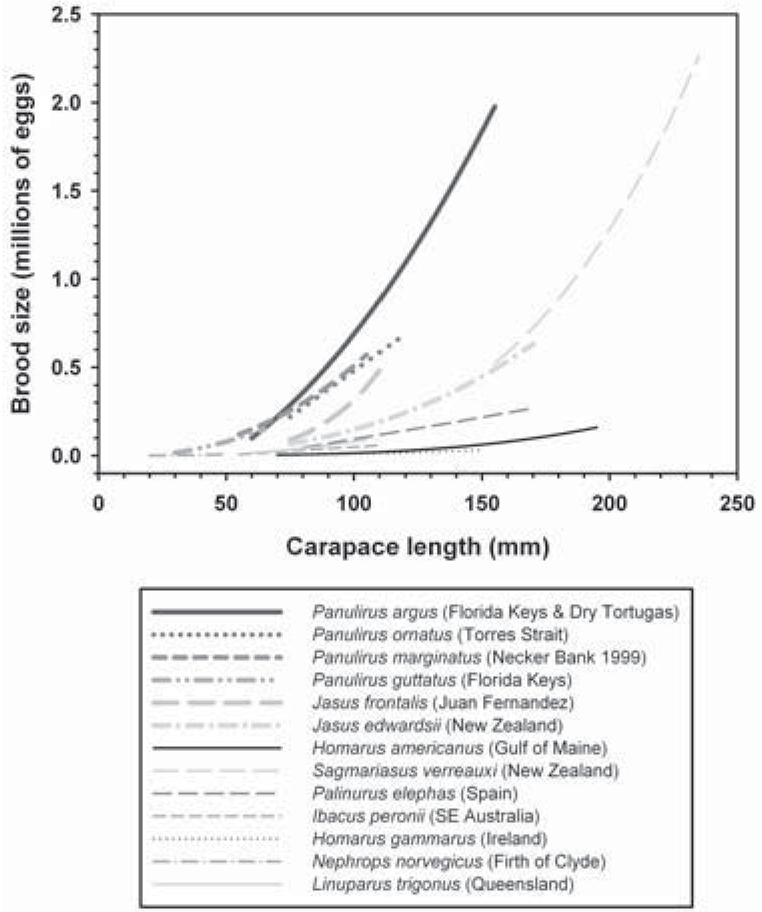

Fig. 2.7 Brood size (millions of eggs) as a function of carapace length in a range of lobster species. The relationships are plotted from equations provided in MacFarlane & Moore (1986), Annala (1991), Fogarty (1995), Stewart & Kennelly (1997), Tuck *et al.* (2000), Bertelsen & Mathews (2001), Robertson (2001), Tully *et al.* (2001), DeMartini *et al.* (2003), Goñi *et al.* (2003) and Haddy *et al.* (2003).

southern Africa appears to be related to growth rate, being high in the fast-growth Agulhas Bank area and low in the slow-growth Port Alfred area (Groeneveld, 2000).

Egg size varies with female size in some lobster species, but not in others. In *Nephrops norvegicus*, egg size is positively related to female SOM and male L' and negatively related to fecundity (Tuck *et al.*, 2000); where growth rate was characterised by a low male L', females had smaller eggs and higher size-specific fecundities. Egg size is positively but only weakly related to female CL in the European lobster *H. gammarus* which would account for about 32% of the variation in egg weight found in lobsters off Ireland (Tully *et al.*, 2001) and 19% of the variation in egg diameter found around the Hebrides (Lizárraga-Cubedo *et al.*, 2003). In the American lobster *H. americanus*, female CL or size class explained about 10–13% of the variation in egg dry weight (Attard & Hudon, 1987; Ouellet & Plante, 2004). According to the last duo of authors, egg quality may be more related to female reproductive experience (primiparous versus multiparous) than to female size *per se*. Large eggs tend to have higher lipid contents and hatch larger larvae that may have better survival characteristics than smaller larvae hatching from smaller eggs (see discussion in Ouellet & Plante, 2004). However, the relationship of egg and larval size with maternal size is often weak, with as much variation within a single brood and among broods of similar sized females (Ouellet & Plante, 2004).

2.8.2 Egg loss

Egg loss commonly occurs during incubation in lobsters (Aiken & Waddy, 1980). In *Nephrops norvegicus*, egg loss can be extremely high ranging from 68% off the Portuguese coast (Figueiredo *et al.*, 1982), almost 50% in the Firth of Clyde (Tuck *et al.*, 2000) to >32% in the Moray Firth (Chapman & Ballantyne, 1980). Tuck *et al.* (2000) found an almost 50% difference between potential fecundity, from histological examination of the ovaries, and actual fecundity from counts of eggs on the pleopods of female *N. norvegicus*. Likewise, egg loss during incubation may be as high as 26% in spiny lobsters (Goñi *et al.*, 2003) and an average of 36% in *Homarus americanus* (Perkins, 1972). Egg loss in crustaceans is positively related to incubation period and negatively related to water temperature (Kuris, 1991) and in lobsters appears to be caused by a combination of disease and nemertean egg predators, although the sampling method, especially trawling, is likely to cause some egg loss (Talbot & Helly, 1995; Chubb, 2000; Tuck *et al.*, 2000).

2.8.3 Brooding migrations

Movements of ovigerous female lobsters to hatch their eggs vary from small local movements to mass migrations. Female spotted spiny lobsters (*Panulirus guttatus*) mate, brood and hatch their eggs on the same small patch of reef (Robertson, 2001). Female *Jasus edwardsii* are less site-bound and move to areas of strong currents at the reef edge or up to 0.5–1 km offshore during the latter stages of egg brooding, sometimes forming large aggregations on sandy substrates, returning inshore after their eggs have hatched (McKoy & Leachman, 1982; MacDiarmid, 1991; Kelly *et al.*, 1999; Kelly & MacDiarmid, 2003). Adult *P. ornatus* undertake a mass spawning migration of about 500 km eastwards across the Gulf of Papua, spawning several times before suffering severe mortality around Yule Island (Moore & MacFarlane, 1984; MacFarlane & Moore, 1986; Dennis *et al.*, 1992), although in other areas ovigerous females appear to undertake more local movement into deeper water to hatch their eggs (Prescott & Pitcher, 1991; Kulmiye, 2004). These movements by ovigerous female spiny lobsters may be to increase the probability that the long-lived phyllosomal larval stages are carried well away from the nearshore reefs where they are preyed upon by planktivorous fish (Kelly *et al.*, 1999). Among the clawed lobsters, ovigerous female *Homarus americanus* undertake seasonal migrations that can exceed 100 km toward shallower areas in summer, apparently to optimise egg development rate (reviewed in Lawton & Lavalli, 1995). Where females hatch may also be important for spatial retention and survival of larvae.

2.9 Lobster mating systems and exploitation

2.9.1 Breeding population size structure

The operation of fisheries in combination with many features of lobster biology and ecology may result in substantial alterations to the mating system (Fig. 2.8). With most, if not all, lobster fisheries taking large pre-reproductive and reproductive individuals, the foremost effects of fishing are to reduce the abundance and size/age structure of animals (e.g. Wahle, 1997; Sardà, 1998). In areas of intense exploitation, few or no reproductive-sized females may remain (e.g. Guzman & Tewfik, 2004). Conversely, the establishment of reserves increases the mean abundance and/or size of lobsters within protected areas (MacDiarmid & Breen, 1993; Kelly *et al.*, 2000; Goñi *et al.*, 2001; Davidson *et al.*, 2002; Rowe, 2002; Acosta & Robertson, 2003). A reduction in the number and size of reproductive females depresses population egg production, especially in species where fecundity is exponentially instead of linearly related to body size (e.g. Bertelsen & Matthews, 2001). In addition, by shifting the balance of egg production from large or multiparous (older) females to small or primiparous (younger) females, selective fishing of large individuals may reduce the quality of eggs (size and energy content) in some lobster species (Attard & Hudon, 1987; Tully *et al.*, 2001; Goñi *et al.*, 2003; Ouellet & Plante, 2004). If egg quality

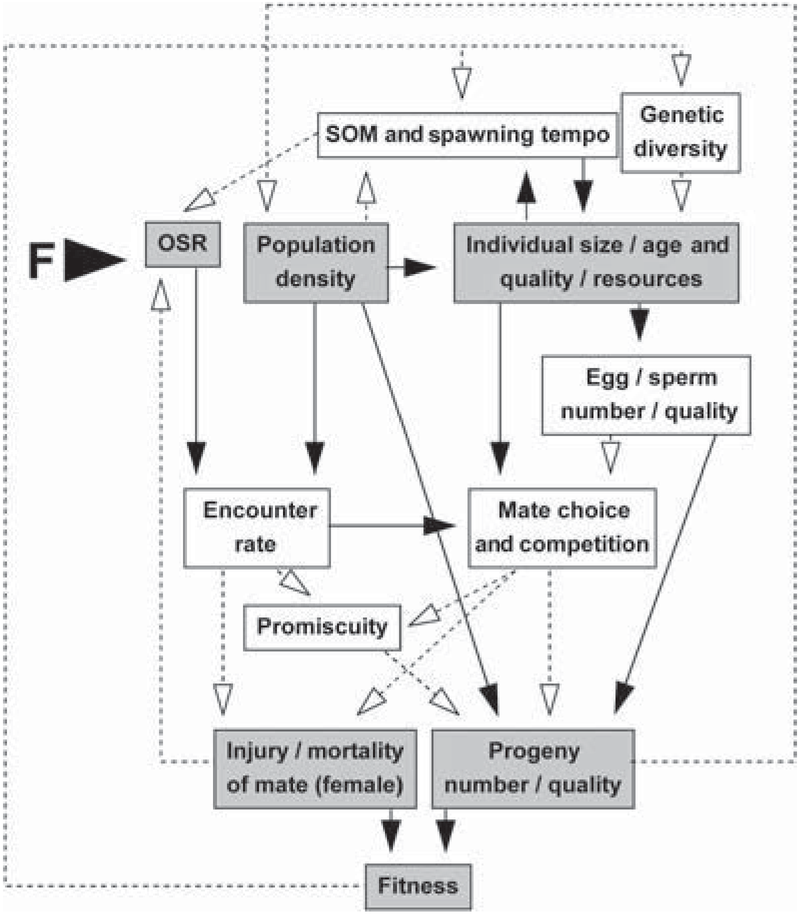

Fig. 2.8 Diagram of the effects of exploitation on lobster mating systems. Fishing (F) modifies the density, size and age structure of mature individuals, possibly leading to changes in their average physiological condition and the quality of breeding site resources they hold. Fishing can also modify the operational sex ratio (OSR) when mortality of mature individuals is biased to one sex. These modifications will alter the number and possibly the quality of eggs and sperm on offer by individual lobsters, the encounter rate of potential mates and the opportunity for mate competition and choice and for promiscuity. As a consequence, some breeding individuals (usually females) may be injured or killed when they cannot find a suitable mate and they depend on one for protection during the moult or postmoult, and the number and quality of progeny may be reduced. Ultimately, these changes may lead to population compensatory responses (change in size for onset of maturity, SOM, and/or reproductive tempo). Additionally, if certain life history traits are heritable and the balance of fitness shifts from one group of individuals to another, the population's genetic structure may be changed over time. Demonstrated or likely effects are denoted by full lines and arrowheads and hypothetical effects are denoted by dashed lines and open arrowheads.

reflects upon larval and juvenile survival (Section 2.8), then negative synergetic effects of decreased egg number and quality are possible. As for males, the reduction in their number and size undoubtedly diminishes sperm supply, although the extent to which this occurs has never been evaluated through sperm-per-recruit models. Until recently, sperm supply was never considered to be a factor limiting lobster population reproductive output (MacDiarmid & Butler, 1999).

2.9.2 Reproductive responses to exploitation

Lobster populations may respond to exploitation and increased mortality through compensatory phenotypic change of reproductive traits. Modest levels of fishing on a virgin population might initially lead to compensatory growth and increased SOM in response to greater resources per capita (Pollock, 1993, 1995), although evidence to support this event is tenuous (see Chubb, 2000). Under intense fishing, however, populations should exhibit decreased SOM as a result of harvesting faster growing individuals (Polovina, 1989; Chubb, 1994, 2000; Landers *et al*., 2001; DeMartini *et al*., 2003). The shift toward smaller SOM may also be accompanied by compensatory changes in female reproductive tempo and brood characteristics. Females may reproduce more frequently as seen in the spiny lobster *Panulirus cygnus* (Chittleborough, 1979). Similarly, it is tempting for us to see in the greater than expected incidence of consecutive and annual spawning among small females of *Homarus americanus* (Comeau & Savoie, 2002), a sign of compensatory population response to very intense fishing along the coast of New Brunswick. In the Hawaiian spiny lobster *Panulirus marginatus*, there has been a startling 36% increase of female size-specific fecundity over a period of two decades starting *c*. 1980, during which the catch per unit effort (CPUE) index of lobster abundance fell fivefold and from 1991 to 1999, the mass of individual eggs increased by 11%, strongly suggesting a density-dependent, compensatory relationship, presumably through the greater availability of prey (DeMartini *et al*., 1993, 2003). Fishing-related changes in the reproductive traits of males have not been scrutinised.

2.9.3 Sex ratio

Many lobster fisheries would appear to have the potential to alter population sex ratio and sexual size dimorphism. Numerous factors could result in sex-biased exploitation. (1) One sex may be more vulnerable to capture due to its greater spatial and/or temporal exposure to fishing gear. In several species, males are more catchable than females and larger males are more so than smaller males (e.g. Tremblay & Smith, 2001; Ziegler *et al*., 2002). (2) In most, if not all lobster species, growth slows considerably more in females than in males at the onset of maturity (Section 2.3). If this occurs at a size smaller than the minimum legal size (MLS), males in a cohort will be fished harder than females resulting in a population sex ratio skewed towards females and a narrowing of the size dimorphism between the sexes. (3) If the difference between MLS and SOM is not the same for females and males, mature individuals of one sex may be more severely depleted than those of the other sex. (4) Several fisheries incorporate a partial or a complete ban on fishing females (e.g. Hall & Chubb, 2001) or take voluntary measures to protect mature females e.g. v-notching in *Homarus* (Daniel *et al*., 1989; Tully, 2001). Moreover, a maximum legal size for females is used or being considered as a management measure to increase the contribution of large (multiparous) females to egg production in some lobster species (e.g. Hall & Chubb, 2001; Fogarty & Gendron, 2004). Overall, it has generally been assumed that lobster fisheries would skew the sex ratio toward females and reduce the size advantage of reproductive males (Childress, 1997; Wahle, 1997; Chubb, 2000). Comparison of populations between reserves and fished areas tend to support the latter expectation, but not the former (Rowe, 2001, 2002; Davidson *et al*., 2002; Goñi *et al*., 2003). This may reflect reality or a misperception caused by census methods, as most studies have relied on trap or diver surveys, which may be biased by sex-differential catchability or visibility for usually cryptic animals.

2.9.4 Sperm limitation and depletion

Density, sex ratio and size structure influence sexual competition, sexual conflict and individual mating success. The density of reproductive lobsters might become so low that some (less desirable) receptive females go unmated due to low mate-encounter rates, especially if the sex ratio is skewed to females (Saila & Flowers, 1965; Ennis, 1980; Daniel *et al*., 1989). The consequences may be reduced larval production, physiological damage to the unmated female because of ovary atrophy,

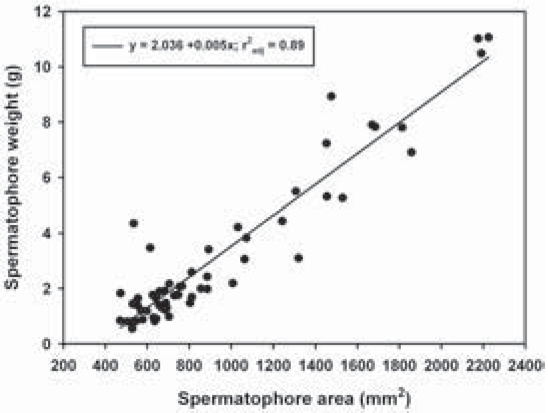

Fig. 2.9 The relationship between the area and weight of spermatophores recovered from the sternum of female *Panulirus argus*.

or injury/death when the female is dependent on males for protection at moulting/mating. Alternatively, all receptive females may be mated, but many may couple with small males that are less fecund or less protective than large males (Sections 2.5–2.7). Investigation of the relationship between sperm offer and resulting fertilisation rates is greatly enhanced in spiny lobster species such as *P. argus* where the spermatophore is external and accessible and there are strong relationships between spermatophore area and weight (Fig. 2.9) and between spermatophore weight and number of sperm (Heisig, 2002). In *Homarus americanus* and *H. gammarus*, the dens of small males may be too small for large females to enter, forcing them to moult in the open with accrued risks of predator- or conspecific-inflicted injury or death (Cowan & Atema, 1990; Debuse *et al.*, 1999; Gosselin *et al.*, 2003). In polygynous species, males (especially those dominant or preferred by females) may become sperm-depleted through frequent mating or may adjust ejaculate-size negatively to mating opportunities, with both scenarios resulting in broods limited in size by sperm availability. These possibilities have not been researched in lobsters so far, but they are well documented in two crab species (Rondeau & Sainte-Marie, 2001; Kendall *et al.*, 2002). Male sperm depletion is likely to be size dependent: in *Jasus*, small males may equally service 1–3 females compared to 17–20 for large males (MacDiarmid & Stewart, 2005b), whereas in *H. americanus*, the numbers may be about 4 and 11 females, respectively (Gosselin *et al.*, 2003). Finally, in potentially polyandrous species such as *Nephrops norvegicus*, *H. americanus* and *H. gammarus* (Debuse *et al.*, 1999; Streiff *et al.*, 2004; Gosselin *et al.*, 2005) a lower density of males may reduce the incidence of female multiple mating or, *a contrario*, promote it (and multiple paternity) as a compensatory mechanism for female sperm limitation (Section 2.7).

2.9.5 Longer-term change

The foregoing discussion of the impact of exploitation on the mating system has considered phenotypic change only. However, sexual competition and sexual conflict are the cornerstones of sexual selection, which is considered to be a potent force in the evolution of reproductive traits and speciation (Shuster & Wade, 2003). With exploitation rates in the range of 0.5–0.8 in many lobster fisheries (e.g. Pollock, 1993; Fogarty, 1995; Fogarty & Gendron, 2004), it is conceivable that in the long-term, fast-growing individuals will be selected out of populations (e.g. Conover & Munch, 2002). In addition, although so far the benefits of female mate choice and multiple mating in lobsters appear to be purely material – more sperm and more protection – we cannot exclude the possibility that these behaviours provide indirect (i.e. genetic) benefits in the form of access to better genes that contribute for example to increased larval survival and population resilience to disease (e.g. Hosken & Stockley, 2003; Neff & Pitcher, 2005).

The degree to which a lobster mating system is altered by exploitation will depend on the extent, intensity and timing of the fishery and on species-specific sensitivity to exploitation. For example, the timing/duration of the fishing season may interact with sex-asynchronous changes in catchability that relate to the moult cycle or mating behaviour (e.g. Tremblay & Smith, 2001; Ziegler *et al.*, 2002), such that sex ratio skew becomes greater when a species is fished in one season than another. Factors of species sensitivity to exploitation include how males react to greater mate availability; the degree to which males can be promiscuous and the rate at which they recover sperm reserves; the possibility of female sperm storage as a safeguard against male scarcity; the frequency, temporal window and spatio-temporal synchronicity of female receptivity; and the possibility that females control moulting/mating to inflate the operational sex ratio and their chances of being mated (Sections 2.4, 2.5). For many lobster species, this critical information is lacking and should be the focus of future research.

2.10 Conclusions

It is clear from this review that there has been a large advance in the understanding of lobster reproduction generally and of their mating systems specifically over the last two decades. The previous review of lobsters acknowledged developments mainly in the field of biology and physiology of reproduction (Aiken & Waddy, 1980). This one informs mainly on the continued uncertainty in the identification of maturity in lobsters and on developments in the knowledge of mating behaviour, recognises that the contribution to reproduction by males may substantially impact female larval output, and reports/identifies pathways by which exploitation may interfere with lobster mating systems. Full understanding of lobster mating systems, however, continues to be hampered by a lack of understanding of fundamental aspects of reproduction in males. These require urgent investigation in most species. Likewise, slipper lobsters and small, rare and non-commercial species generally remain ignored, although they may provide valuable comparison with other exploited species.

The rather invariant relationship between size at onset of maturity and L' across all lobster species (see Fig. 2.4) underscores the utility of reviewing their reproduction as a group. Moreover, the enormous ranges in body size of mature individuals within and between lobster species, and variable partitioning of reproductive energy into the numbers and sizes of eggs, as well as the range in population densities and sex ratios, mean that lobsters offer excellent opportunities for insight into the operation of mating systems generally. For instance, spiny and clawed lobsters provide a valuable contrast with respect to the potential for sperm limitation (high in spiny lobsters due to high fecundity, female monogamy and usually limited receptivity; low in clawed lobsters due to extended receptivity, female polygamy, extended sperm storage and lesser female individual fecundity).

Many of the recent developments in lobster reproduction are based on laboratory experiments. While yielding valuable insights into mating behaviour, the small spatial scales of these experiments may lead to biased appreciation of some aspects of the mating system (see Atema & Voigt, 1995). It is critical that these outcomes are tested in the field on wild populations. Fortunately, because many lobsters are exploited commercially and males in particular are heavily fished, while lobsters of many species increase in abundance in marine reserves, populations with contrasting abundance, size composition and sex ratio are available for study. These should allow insights into the factors shaping the evolution and maintenance of lobster mating systems, gained from small-scale laboratory experiments, to be readily tested at the population scale. We envision that the next decades will bring about a much better understanding of the factors underlying mate choice and competition, promiscuity and multiple paternity, and how these processes through maternal and paternal effects on progeny quality, contribute to population replacement and maintenance of genetic diversity. This information will be critical to conservation of the highly-coveted lobster resource.

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Chapter 3
Behaviour

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> 'Under changed conditions of life, it is at least possible that slight modifications of instinct might be profitable to a species; and if it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable.' – Charles Darwin, 1859

3.1 Introduction

Lobsters are truly remarkable creatures in their bewildering array of behaviours. At each stage in their life, they show a remarkable sensitivity to environmental signals that cue specific behaviours conferring a survival or reproductive advantage. With over 250 million years of fine tuning by the forces of natural and sexual selection, lobsters have acquired a diverse portfolio of behavioural adaptations that allow them to exploit resources across many different habitats, avoid predators, find mates, and release larvae at specific times and places to assure their successful return to appropriate areas. Since behavioural traits are highly plastic, they have the potential to respond quickly to changes in environmental cues and ecological conditions. If these behaviours are heritable, then selection can act to favour those individuals whose behaviours confer the greatest fitness advantage. However, the ability of behavioural traits to track changes in the environment are sometimes limited by competing evolutionary forces and the constraints imposed by development, morphology and the historical effects of evolutionary history. In this chapter, we attempt to identify the important constraints on lobster behavioural evolution due to life history, morphology, physiology, habitat, biotic interactions, and most recently, human habitat alterations and fishing pressure. We will not attempt to summarise the entire historical literature on lobster behaviour, ecology and evolution for there are many other excellent reviews already available (Cobb & Phillips, 1980a, b; Phillips *et al.*, 1994; Factor, 1995; Phillips & Kittaka, 2000). Instead, we will focus on recent research advances comparing the ecological and evolutionary similarities and constraints among a few well-known lobster families to understand both the reasons for their behavioural variation and our potential impact on their future sustainability.

Lobsters are reptant, decapod crustaceans that diverged from a common ancestor during the Permian period (251–290 million years ago; Glaessner, 1969; Holthuis, 1991). Recent reanalysis of both morphological and molecular characters support the idea that species commonly called 'lobsters' are paraphyletic and can be divided into two monophyletic clades (Dixon *et al.*, 2003; Ahyong & O'Meally, 2004). The Homarida clade includes the clawed lobster families Enoplometopidae and Nephropidae and are sister taxa to the freshwater crayfish clade Astacidea. The other clade of lobsters, the Achelata, includes the 'clawless' lobster families Palinuridae (spiny lobsters), Synaxidae (furry lobsters), and Scyllaridae (slipper lobsters) and are sister taxa to the crabs of the Meiura clade (Fig. 3.1). Although the exact relationships of the reptant decapod crustaceans are not yet known and are still vigorously debated, the majority of

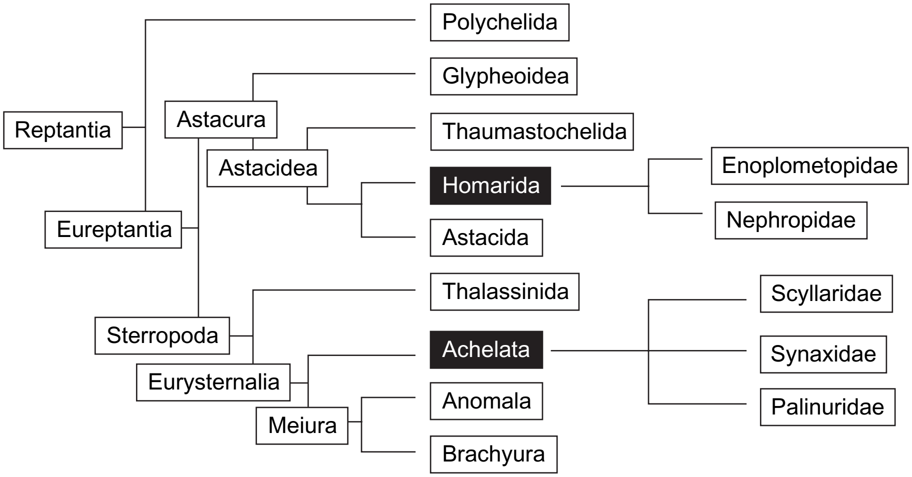

Fig. 3.1 A phylogenetic hypothesis of the decapod crustaceans showing that lobster families are found in two distinct clades (adapted from Dixon *et al*., 2003).

Table 3.1 A comparison of those morphological and reproductive differences between homarid and achelate lobsters likely to influence the evolution of their behaviours.

Character	Homarid lobsters	Achelate lobsters
First pereiopods	enlarged and chelate	reduced without chela
Antennae	reduced and unarmoured	enlarged with spines/armour
Shell thickness	moderate and smooth	thick and armoured
Insemination	internal	external
Fecundity	low	high
Larval duration	short	long

phylogenetic hypotheses agree that clawed and clawless lobsters are not a monophyletic group (Chapter 4).

The impact of having a different common ancestor is most evident in three morphological and three reproductive characteristics that distinguish the clawed and clawless lobsters (Table 3.1). First, the homarid lobsters have chelate first pereiopods whereas the achelate lobsters do not. The presence of major chelae (i.e. claws) has had a profound effect on the evolution of the behavioural repertoire of these lobster groups influencing their ability to manipulate substrates for shelter, establish rank among conspecifics, process larger and more armoured prey, and defend themselves against competitors (Atema & Cobb, 1980; Lawton & Lavalli, 1995).

Second, the achelate lobsters have robust antennae either armed with spikes, as in the spiny lobsters, or flat and armoured, as in the slipper lobsters. These potential weapons as well as a ‘spiny’ carapace are likely to have influenced the effectiveness of anti-predatory defensive behaviours (Barshaw *et al.*, 2003) and the ability to use and defend crevice shelters of a wide range of sizes (Atema & Cobb, 1980).

Third, the homarid lobsters have a moderately thin and smooth shell that is more easily penetrated than the shell of achelate lobsters (Barshaw *et al.*, 2003). Thus, the inability to survive an attack by

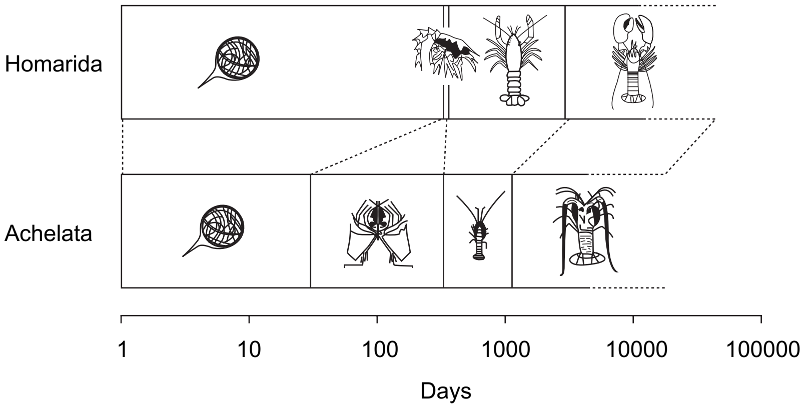

Fig. 3.2 A comparison of the absolute duration of each life history stage for the homarid lobsters (*Homarus americanus*) and the achelate lobsters (*Panulirus argus*). The stages illustrated from left to right are developing embryo, planktonic larva, benthic juvenile and benthic adult. The postlarva stage was omitted as its duration was too short to be compared on the same time scale. Note that days are presented as a common log scale in order to better compare the proportion of time spent in each stage.

piscine predators when outside crevice shelter means that clawed lobsters should adopt a strictly nocturnal activity cycle particularly when predation risk is high, minimise their movement outside crevice shelters, and vigorously defend shelters from conspecifics with non-lethal ritualised behaviours (Atema & Cobb, 1980; Lawton & Lavalli, 1995).

Fourth, copulation in homarid lobsters requires the passing and internal storage of a spermatophore until eggs are ready to be spawned, whereas achelate lobsters attach the spermatophore externally to the ventral surface of the female (Aiken & Waddy, 1980). This subtle difference allows for dramatically different behavioural strategies of both the males and females in exercising mate choice (Waddy *et al.*, 1995; MacDiarmid & Kittaka, 2000).

Fifth, homarid lobsters: (1) have larger eggs (0.5–2.0 mm versus 0.5–0.8 mm), (2) have fewer eggs per brood (600–115 000 versus 50 000–2 000 000), (3) carry embryos longer (9–11 months versus 1–5 months), and (4) have fewer broods annually (0.5–1 versus 1–6) than do the achelate lobsters (Aiken & Waddy, 1980; Waddy *et al.*, 1995; MacDiarmid & Kittaka, 2000). As a result, the parental investment in each larva is considerably greater for clawed lobsters than for clawless lobsters. This may have important consequences on sheltering, aggressiveness and movement of gravid females (Kanciruk, 1980; Lawton & Lavalli, 1995).

Finally, homarid lobster larvae spend much less time in the plankton (0.5–2 months versus 4–22 months) than achelate larvae (Phillips & Sastry, 1980; Booth & Phillips, 1994; Cobb and Wahle 1994; Chapter 7) (Fig. 3.2). This may have important consequences on the movement of gravid females, and their timing and location of larval release (Herrnkind, 1980) as well as on the evolution of larval behaviours. Variation in larval duration has probably influenced speciation (George, 1997), the historical and current geographic ranges of species (Pollock, 1993, 1995), the genetic structure of populations (Ovenden *et al.*, 1992, 1997; Perez-Enriquez *et al.*, 2001), and the potential for local adaptation in behaviour, ecology and morphology (Mohan, 1997; Patek & Oakley, 2003).

Given these differences in morphology and life history, it is not surprising that the homarid and achelate lobsters also have very different levels of sociality (Fig. 3.3). Homarid lobsters are highly aggressive (Scrivener, 1971), form linear dominance hierarchies (Karnofsky & Price, 1989; Atema & Voigt, 1995), and defend dens from conspecifics (Cobb, 1971, 1995). Achelate lobsters are

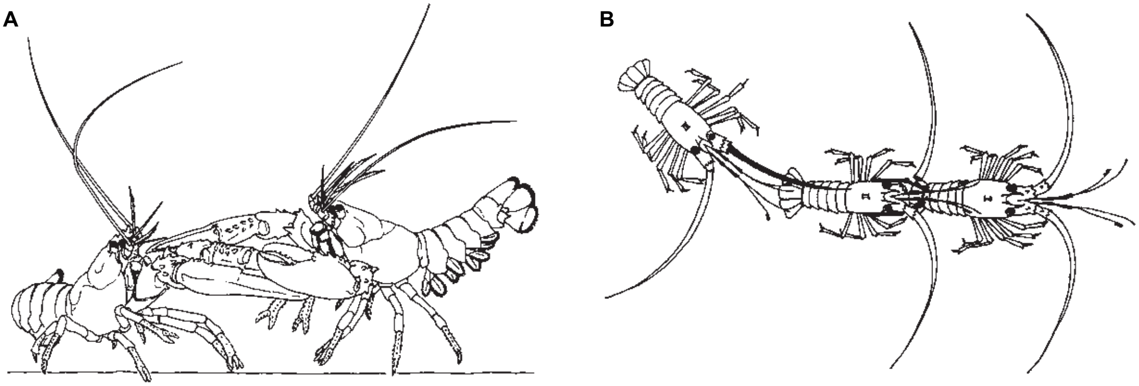

Fig. 3.3 A comparison of the sociality of homarid (clawed) and achelate (clawless) lobsters. (A) An escalated level of aggression during a ritualised fight in *Homarus americanus* (adapted from Atema, 1977). (B) A queue formation during a mass migration in *Panulirus argus* (adapted from Herrnkind, 1969). Clawed lobsters favour aggression over gregariousness while clawless lobsters favour gregariousness over aggression.

highly nomadic (Herrnkind, 1980), share dens with conspecifics (Herrnkind *et al.*, 1975), and even migrate *en mass* in coordinated single file queues (Herrnkind, 1969).

There are at least three possible evolutionary explanations for these differences in the sociality of clawed and clawless lobsters. First, the 'resident-advantage' hypothesis predicts that aggression is favoured over gregariousness to maximise reproductive success through control of a high quality den (Atema & Cobb, 1980). Second, the 'group-defence' hypothesis predicts that gregariousness is favoured over aggression to maximise survival through cooperative group defence of a den (Zimmer-Faust & Spanier, 1987; Mintz *et al.*, 1994; Butler *et al.*, 1999). Finally, the 'guide-effect' hypothesis predicts that gregariousness is favoured to maximise survival when moving between dens (Childress & Herrnkind, 1997, 2001a). Throughout the remainder of this chapter we will consider the evidence supporting these hypotheses for the evolution of lobster sociality.

3.2 Sensory biology and regulation of behaviour

Lobsters, like all arthropods, have a wide array of sensory modalities and a complex neuroendocrine control system. As such, certain lobster species (e.g. *Homarus americanus* and *Panulirus argus*) are regularly used as model organisms for the study of the neural basis of behaviour. A detailed description and review of crustacean sensory biology, neuroethology and behavioural regulation is beyond the scope of this chapter, but thorough historical accounts can be found in Waterman (1961), Ache and McMillan (1980), Ache (1982), Atwood and Sandeman (1982), Sandeman and Atwood (1982), Atema and Voigt (1995), Beltz (1995) and Weise (2002). Instead, we will highlight some of the most recent findings and comparisons between groups.

3.2.1 The senses

Both clawed and spiny lobsters possess a diverse array of chemosensitive and bimodal (chemo-mechanosensitive) sensilla across their body and limbs (Fig. 3.4) (Atema & Voigt, 1995; Beltz, 1995; Beltz *et al.*, 2002; Derby *et al.*, 2002). The greatest concentration of these sensilla occurs on the distal end of the lateral flagellum of the antennules (Atema & Voigt, 1995; Cate & Derby, 2001). Different types of chemoreceptor on the antennules, legs and mouthparts respond sequentially as potential prey is detected, identified, located, and consumed (Derby *et al.*, 2001). Chemoreception in lobsters involves a dual pathway composed of aesthetasc sensilla innervated by chemosensory neurons that project to the olfactory lobes and a

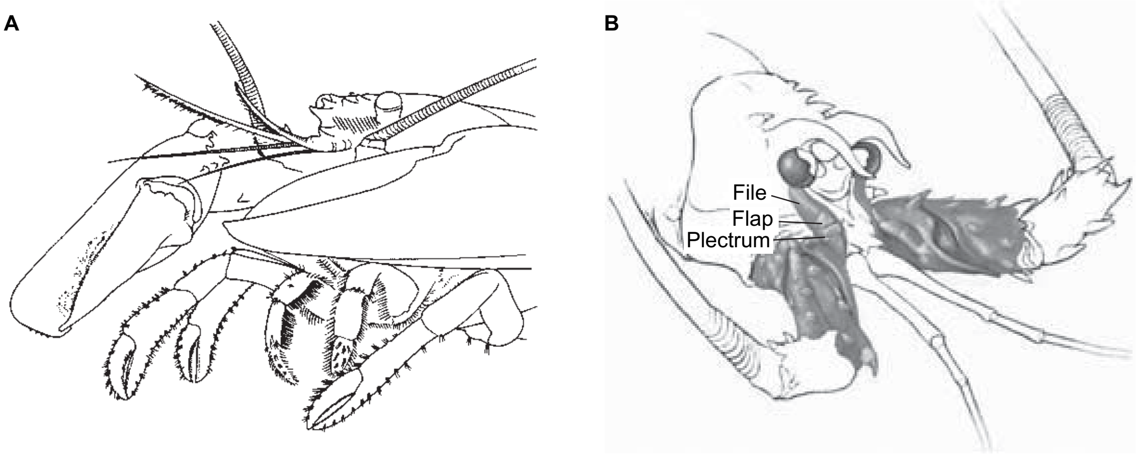

Fig. 3.4 A comparison of the anterior appendages of (A) a homarid lobster (*Homarus americanus*) and (B) an achelate lobster (*Panulirus argus*). Major differences include: the structure of the first perieopod, chelate in (A) and achelate in (B); the first antenna, smooth and flexible in (A) and rigid and spiny in (B); and the presence of a stridulatory organ (file, flap and plectrum) in (B) and absent in (A) (adapted from Atema & Voigt, 1995; Patek, 2002).

variety of 'non-aesthetasc' sensilla innervated by chemo-mechanosensory neurons that project to the lateral antennular neuropils. The functional significance of this dual-pathway system remains a mystery, as it appears that even lobsters lacking one or the other type of sensilla are capable of odour discrimination, odour-associative learning and locating odour sources in naturalistic flow conditions (Steullet *et al.*, 2001, 2002; Horner *et al.*, 2004).

Both spiny and clawed lobsters have the ability to recognise the odours of conspecifics (Zimmer-Faust *et al.*, 1985; Karavanich & Atema, 1998a). Lobsters are capable of distinguishing complex odour mixtures and learning to respond to particular odour components (Fine-Levy & Derby, 1991; Lynn *et al.*, 1994; Atema & Voigt, 1995). This ability to recognise and learn particular odour signatures not only increases the foraging efficiency of an individual, but may also play an important role in the ability of lobsters to find shelters (Nevitt *et al.*, 2000) and recognise opponents they have previously fought (Karavanich & Atema, 1998b). While much of what is known about crustacean olfactory transduction and olfactory-mediated behaviour has come from extensive studies on species of palinurid and homarid lobsters, there still remains much to be discovered in this active and fruitful area of research (Derby, 2000).

Mechanical stimuli (e.g. water movements, touch, etc.) are also important in finding food and conspecifics, avoiding predators, maintaining equilibrium and directional ability, controlling motion, and in detecting vibrations (Wilkens *et al.*, 1996). Lobster antennae are primarily mechanosensitive and multiple contact and non-contact mechanoreceptors are located externally and internally over the entire carapace (Atema & Voigt, 1995). The statocyst is a mechanoreceptive organ located at the base of each antennule and used in spatial orientation and equilibrium (Beltz, 1995). It has been shown that some achelate and homarid lobsters are capable of producing and probably detecting low frequency vibrations (i.e. sound) (Hazlett & Winn, 1962; Offutt, 1970). *Homarus americanus* produces a rasp-like sound (100–300 Hz) by contraction of a modified sonic muscle at the base of the second antennae (Atema & Voigt, 1995; Henninger & Watson, 2005). Palinurids of the Stridentes group (George & Main, 1967) produce sound by means of a 'stick and slip' stridulatory organ at the base of the second antennae (Fig. 3.4) (Patek, 2001, 2002). The functional significance of sound production is not known, but it has been suggested it may startle potential predators. Recent research has found that *Panulirus argus* pairs sound production with rapid whips of their antennae when attacked by triggerfish. Those individuals lacking the ability to make sound during this anti-predatory behaviour were more likely to be eaten than those individuals with intact stridulatory organs (Bouwma & Herrnkind, personal communication). Sound may also potentially serve as a form of intraspecific communication, but whether or not hearing *per se* occurs in crustaceans is controversial (Atema & Voigt, 1995; Lovell *et al*., 2005). Nonetheless, the role of the production and detection of low frequency vibrations at biologically relevant distances, as possible communication signals in the marine environment, is an intriguing area of research given recent attention to the impact of anthropogenic sounds on marine organisms.

While chemoreception and mechanoreception appear to be their primary sensory modalities, lobsters also have well developed visual capabilities. Visual cues may be used in predator avoidance, feeding, and agonistic interactions (Atema & Voigt, 1995). The eyes are lateral and compound, composed of multiple ommatidia (Fig 3.4). While specific information on spatial resolution of lobster eyes is unknown, it is probably poor and monochromatic. Nonetheless it is expected, based upon their structure, that lobster eyes are very effective in detecting low light levels and motion and using this information in specific behavioural contexts (Beltz, 1995; Cronin & Jinks, 2001). Interestingly, extra-ocular photoreceptors found in the sixth abdominal ganglion of some crustaceans have not been demonstrated in the Homarida but appear to be present in at least some of the Achelata (Wilkens & Larimer, 1976).

Both clawed and spiny lobsters are capable of moving long distances (>10 km) and returning to specific locations where they have previously resided (Herrnkind, 1980; Pezzack & Duggan, 1986; Hakkonsen & Anoruo, 1994; Lawton & Lavalli, 1995). Such remarkable feats of navigation have long been of interest to sensory biologists studying animal migration. Lobsters appear to use a diverse combination of guideposts including visual cues (photoperiod and light levels), tactile cues (wave surge and pressure differences), and olfactory cues (conspecific odours and salinity gradients), but the recent experiments have demonstrated that spiny lobsters also respond to small changes in magnetic fields. Lohmann *et al.* (1995) demonstrated that the preferred orientation of the spiny lobster *P. argus* could be altered by reversing the horizontal component of the magnetic field, but were unaffected by a reversal in the vertical component. Boles and Lohmann (2003) went on to demonstrate that: (1) the preferred orientation of displaced lobsters was toward their original point of capture regardless of where the testing was performed, (2) this directional homing tendency remained strong in the absence of cues obtained during the displacement, and (3) a shift in the magnetic field both north and south of the point of capture resulted in significant orientation toward its original location. These elegant experiments suggest that at least one species of lobster has a true navigation sense and that future work should explore the proximate basis of magnetoreception in lobsters.

In addition to the sensory modalities listed above, lobsters have been reported to be able to detect and respond to other environmental stimuli including salinity (Jury *et al*., 1994; Dufort *et al*., 2001), osmolarity (Garm *et al*., 2004) and temperature (Kanciruk & Herrnkind, 1978; Ache, 1982; Jury *et al*., 1994; Crossin *et al*., 1998). While the exact mechanisms mediating these sensory abilities remain to be elucidated, there is a clear role for the ability of lobsters to detect and integrate multiple environmental signals and use this information in adaptive behaviours, including homing, migration and habitat selection. These studies and others continue to demonstrate that many questions remain about how lobsters sense and respond to the complexity of their environment and the role of dynamic stimuli in the expression and evolution of specific behaviours.

3.2.2 Hormones and neuroendocrine control

Lobster behaviour is strongly regulated by four classes of neuroendocrine compounds: steroids, terpenoids, peptides and biogenic amines (Quackenbush, 1986). A cascade of signals, often involving several of these molecular classes, underlies moulting, agonistic and reproductive behaviours (Aiken & Waddy, 1980; Waddy *et al.*, 1995). Changes in environmental cues such as increasing day length leads to reduced levels of peptides such as moult inhibiting hormone (MIH) and/or vitellogenesis inhibiting hormone (VIH) which causes an increase in several steroid hormones such as ecdysone, 20-OH-E, and progesterone (Quackenbush & Herrnkind, 1981, 1983). As a result, moulting and spawning in *P. argus* increases with warm temperatures and long day lengths (Lipcius & Herrnkind, 1985, 1987). The role of the terpenoid hormone, methyl farnesoate, is not as clear for it appears to stimulate gonad maturation in shrimp (Quackenbush, 1994) but was unrelated to gonad maturation in *H. americanus* (Tsukimura & Borst, 1992).

Physiological changes during the moult cycle also correspond to changes in the agonistic interactions of clawed lobsters. Aggression and escape behaviours appear to peak during the midphase premoult stage (D_1 or D_2) while the animal has not yet lost its muscle strength and hard exoskeleton (Tamm & Cobb, 1978; Cromarty *et al.*, 2000). These changes in aggressive state are also correlated with changes in biogenic amines. Dominant clawed lobsters have elevated levels of serotonin and subordinate lobsters have elevated levels of octopamine (Kravitz, 1988). Injection of these two neuromodulators even results in the characteristic postures of dominance (body held high off the substrate) and subordination (body held close to the substrate) (Livingstone *et al.*, 1980). These observations suggest that biogenic amines interact with the steroid hormones to produce an increase in aggression prior to moulting and after spawning (Mello *et al.*, 1999; Kravitz, 2000).

3.2.3 Activity rhythms

In both homarid and achelate lobsters it is generally accepted that they show similar daily activity patterns of inhabiting shelters during the day, showing increased activity near dusk, foraging at night, and then returning to their 'home' shelter before dawn (Atema & Cobb, 1980; Herrnkind, 1980). This convergent behavioural pattern has been reported multiple times in the laboratory and in the field, where lobsters generally become 'restless' as sunset approaches and then emerge from their shelters shortly after sunset (Kanciruk & Herrnkind, 1973; Ennis, 1984; Lipcius & Herrnkind, 1985; Karnofsky *et al.*, 1989; Childress & Herrnkind, 1994; Smith *et al.*, 1999). These patterns probably reflect similar ecological constraints in terms of predator avoidance and feeding requirements and often result in local foraging and meandering movements that are typically less than 300 m/day, but with a large amount of variability in the distance and timing of locomotion within and between individuals. This suggests different behavioural strategies that may depend on size, environment or physiological state (Watson *et al.*, 1999).

There is a substantial body of literature concerning biological rhythms and patterns of locomotory activity of lobsters (Herrnkind, 1980; Lawton & Lavalli, 1995). In most species, both laboratory and field studies suggest or explicitly demonstrate the presence of a circadian rhythm, which is strongly influenced by environmental cues (Kanciruk & Herrnkind, 1973; Lipcius & Herrnkind, 1982; Nagata & Koike, 1997; Smith *et al.*, 1998; Jury *et al.*, 2005). Some laboratory studies have shown that this rhythm is endogenous with a circadian periodicity of approximately 24 hours and peak activity occurring nocturnally (Wildt *et al.*, 2004; Jury *et al.*, 2005). There is a clear role for exogenous stimuli (light, temperature, etc.) to entrain and modulate the endogenous rhythms of lobsters under natural conditions. Light is considered to be an important variable influencing activity patterns in lobsters (Jernakoff, 1987) and in some deep and/or turbid habitats where light levels are consistently low, lobsters are often seen out of their shelters during the day (Karnofsky *et al.*, 1989; Lawton & Lavalli, 1995; Jury *et al.*, 2005). Studies on *Nephrops norvegicus* show that this species often emerges from burrows at approximately the same light intensities, regardless of depth (Aguzzi *et al.*, 2003, 2004). Another intriguing example of the strong inhibitory effect of light on activity is that the full moon has been shown to decrease the activity and subsequent catch of spiny lobsters (Nagata & Koike, 1997). A recent ultrasonic telemetry study in a field mesocosm has also shown that while nocturnal activity was higher under field conditions, there was still a large amount of daytime activity (Golet *et al.*, in preparation), however, this did not appear to be related to low light levels. This is likely because the expression of locomotor activity in lobsters is also strongly affected by additional environmental factors including tides, turbidity, and temperature as well as conspecific interactions and internal physiological state (Herrnkind, 1980; Lawton & Lavalli, 1995).

3.2.4 Environment and behaviour

The physical, chemical and biological characteristics of the environment constrain the evolution of various morphological, physiological and behavioural traits. While we allude to the influence of the environment on behaviour several times throughout the chapter, the examples below demonstrate this point explicitly. First, the interaction between hydrodynamics, habitat, and behaviour is complex and in the case of antennules, the primary olfactory organ in all lobsters, evolutionary diversification is probably due to a combination of habitat constraints, social interaction, and foraging options relative to odour presentation and availability (Goldman & Patek, 2002). There are significant differences in the structure and function of antennules between species and how they are used to capture olfactory information from the environment (Goldman & Patek, 2002). There are differences within and between groups in the speed of flicking, length, orientation and the spacing of the antennules and associated aesthetasc sensilla themselves (Daniel *et al.*, 2001). Another interesting example is that in the scyllarid genus, *Ibacus* has lost certain giant neurons associated with the tail-flip escape response that is commonly used to avoid predators in most other lobsters (Faulkes, 2004). These species do not tail flip and instead utilise alternative defensive strategies such as digging into sand (Faulkes, 2004). Finally, temperature is an important environmental variable that is generally accepted to have a pervasive influence on the behaviour of lobsters (Herrnkind, 1980; Lawton & Lavalli, 1995). For example, pelagic *H. americanus* larvae actively avoid passing through a thermocline, and choose to remain in water warmer than 17°C (Boudreau *et al.*, 1992). Adult lobsters are also capable of behavioural thermoregulation (Crossin *et al.*, 1998) and have been reported to move to shallower, inshore waters to gain the growth or reproductive benefits of warmer coastal temperatures in the spring and/or summer (Ennis, 1984; Pezzack & Duggan, 1986; Karnofsky *et al.*, 1989; Hakkonsen & Anoruo, 1994). Autumn migrations of spiny lobsters (*P. argus*) also seem to be triggered by large drops in temperature, coincident with autumn storms (Kanciruk & Herrnkind, 1978). It is commonly accepted that overall locomotor activity in lobsters is related to temperature, with higher levels of activity at warmer temperatures (Crossin *et al.*, 1998). In addition, ‘temperature is the major factor controlling size at maturity, oocyte maturation, incidence, timing and synchronisation of spawning, success of egg attachment and incubation, and time of hatching’ (Waddy *et al.*, 1995). Thus the feedback of environmental cues on sensory biology, metabolism, locomotion, movement, habitat selection, and anti-predator behaviours are an important component of the life history of these organisms.

3.3 Habitat selection and social behaviour

Habitat selection and social interaction play a significant role in the life history of lobsters (Lawton & Lavalli, 1995; Lipcius & Eggleston, 2000). Survivorship, growth, reproductive success, and movements during different seasons and life history stages are often related to the distribution of critical resources and behavioural interactions with conspecifics in need of those resources (Atema & Cobb, 1980; Herrnkind, 1980; Kanciruk, 1980). Thus significant research effort has gone into studying the ability, process or outcome of selection for habitats that differ in resource availability (e.g. food, mates, temperature, shelters, etc.) and how the need for these resources changes during ontogeny.

3.3.1 *Foraging and feeding*

Lobsters are omnivorous, being mostly predacious but scavenging prey items when available. Gut content studies have found that all lobsters eat a wide variety of benthic invertebrates, but typically have a diet that consists of gastropods, bivalves, chitons, crustaceans, sea urchins, polychaetes and occasionally fish (Lindberg, 1955; Lawton, 1987; Cox *et al.*, 1997). The behavioural ecology of lobster prey and patch selection is not well understood (Fig. 3.5), but observations of lobsters have found that both clawed and spiny lobsters: (1) use olfactory cues to locate potential prey items (Zimmer-Faust & Case, 1982, 1983; Atema & Voigt, 1995; Derby *et al.*, 2001; Grasso & Basil, 2002), (2) forage in a wide range of habitat types including rubble fields, seagrass beds, mussel beds and soft sediments (Fig. 3.5) (Jernakoff, 1987; Karnofsky *et al.*, 1989; Cox *et al.*, 1997), (3) travel distances of several hundred metres in a single evening to reach prey patches (Fig. 3.5) (Herrnkind *et al.*, 1975; Jernakoff *et al.*, 1987), and (4) are rarely observed in direct competition for a food item with conspecifics (Jernakoff, 1987; Lawton, 1987; Karnofsky *et al.*, 1989; Cox *et al.*, 1997). One difference between clawed and spiny lobsters appears to be the willingness of clawed lobsters to return to shelter before processing a prey item (Lawton, 1987). This could be due to differences in handling time of the prey item or behavioural interference from cohabiting conspecifics that may be density dependent. Future research should address the relative importance of prey density (both as naturally occurring prey and as bait) and the functional response of lobsters to variability in prey patches.

As a generalist predator with a widely varying diet, attempts to study the direct impact of lobster predation on community structure have identified only weak trophic links (Chapter 8; but see also Tegner & Levin, 1983; Barkai & McQuaid, 1988). It also appears likely that food availability rarely, if ever, limits lobster population size or density (Berringer & Butler, 2006). Thus, the intense competition for food resources is not likely to have been a major determinant in the evolution of lobster behaviours.

3.3.2 *Sheltering and den sharing*

Both homarid and achelate lobsters reside in crevice shelters during daylight hours (Atema & Cobb, 1980; Herrnkind, 1980). However, the size and type of crevice shelters used, fidelity towards individual shelters, and the behavioural response toward potential shelter competitors, remains one of the greatest contrasts between clawed and clawless lobsters (Fig. 3.6). Some clawed lobsters, such as *N. norvegicus*, create and maintain a system of burrows in soft sediments and as a result are less likely to be shelter-limited (Chapman, 1980). However, clawed lobsters in the genus *Homarus*, are more likely to seek shelters among rubble, under rocks, or in shallow pits in the soft sediment (Cooper & Uzmann, 1980; Spanier *et al.*, 1998). The relative protection from predators offered by these different substrates is quite variable (Barshaw & Lavalli, 1988; Wahle, 1992a) and so early benthic juveniles have low survival if suitable crevices are not available (Wahle, 1992b; Wahle & Steneck, 1992). While clawed lobsters become increasingly agile as they increase in size (and thus reduce their predation risk) they still show high fidelity toward shelters probably due to their necessity during mating and moulting. Spiny lobsters in the genera *Panulirus* and *Jasus* typically seek shelter in crevices beneath rocks, corals or sponges, and under ledges or edges of vegetation (Kanciruk, 1980; MacDiarmid, 1994). Many of these species undergo an ontogenetic shift in habitat use from dwelling full-time in algae, kelp or seagrass as early benthic juveniles, to crevice dwelling as subadults and adults (Butler & Herrnkind, 2000; Chapter 8). Similar to spiny lobsters, the slipper lobster *Scyllarides latus*, prefers crevice shelters under rock ledges and corals with multiple openings (Spanier & Almog-Shtayer, 1992; Spanier, 1994; Spanier & Lavalli, 1998).

Predation pressure on small lobsters is very intense and has probably been a significant force in the evolution of nocturnal activity and diurnal shelter use (Chapter 8). Not surprisingly, many studies have documented the survival advantage conferred on larger lobsters and those individuals in crevice shelter or complex substrates (Eggleston *et al.*, 1990, 1992; Smith & Herrnkind, 1992;

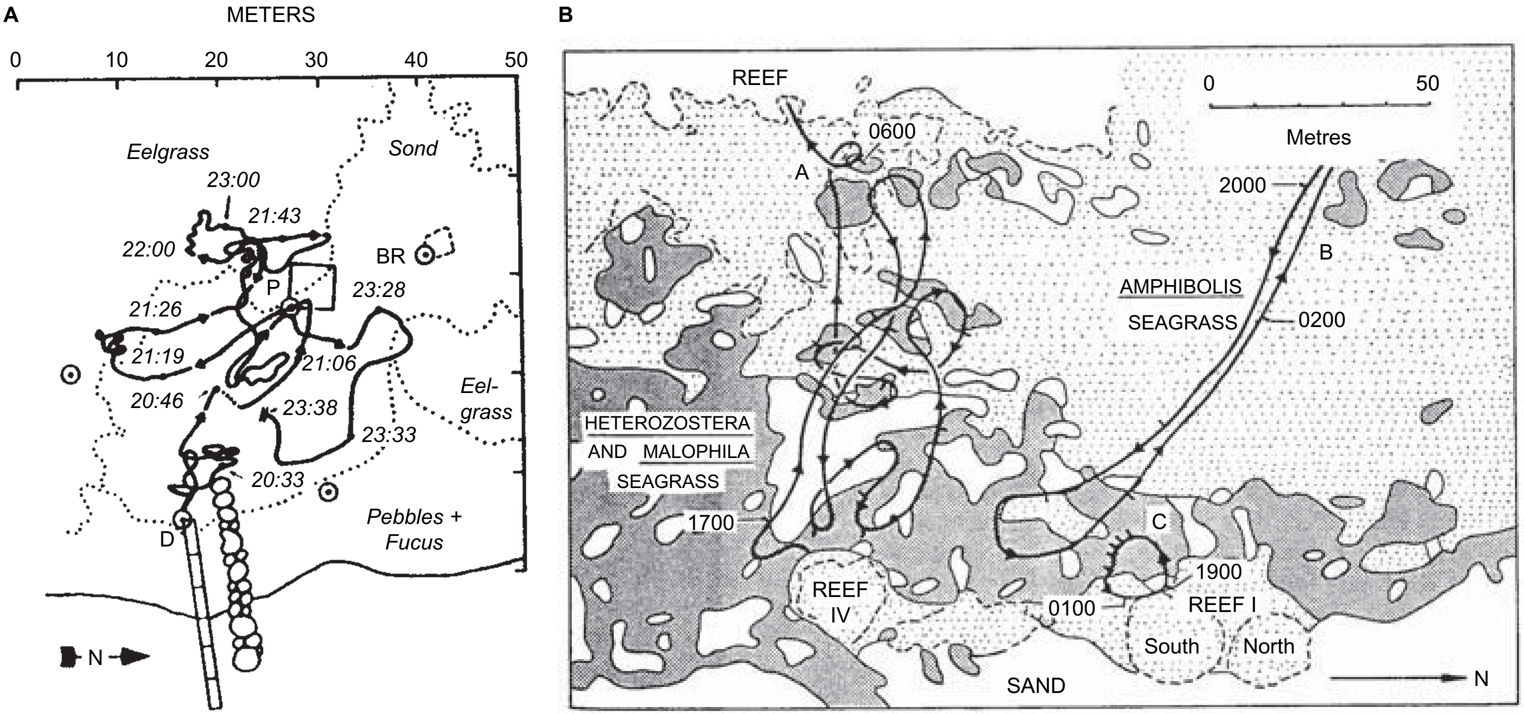

Fig. 3.5 A comparison of the nocturnal foraging movements and prey patch use for (A) a homarid lobster (*Homarus americanus*) and (B) and three achelate lobsters (*Panulirus cygus*). One major difference is that clawed lobsters will occasionally bring large items back to the den for processing (adapted from Jernakoff, 1987; Karnofsky *et al*., 1989).

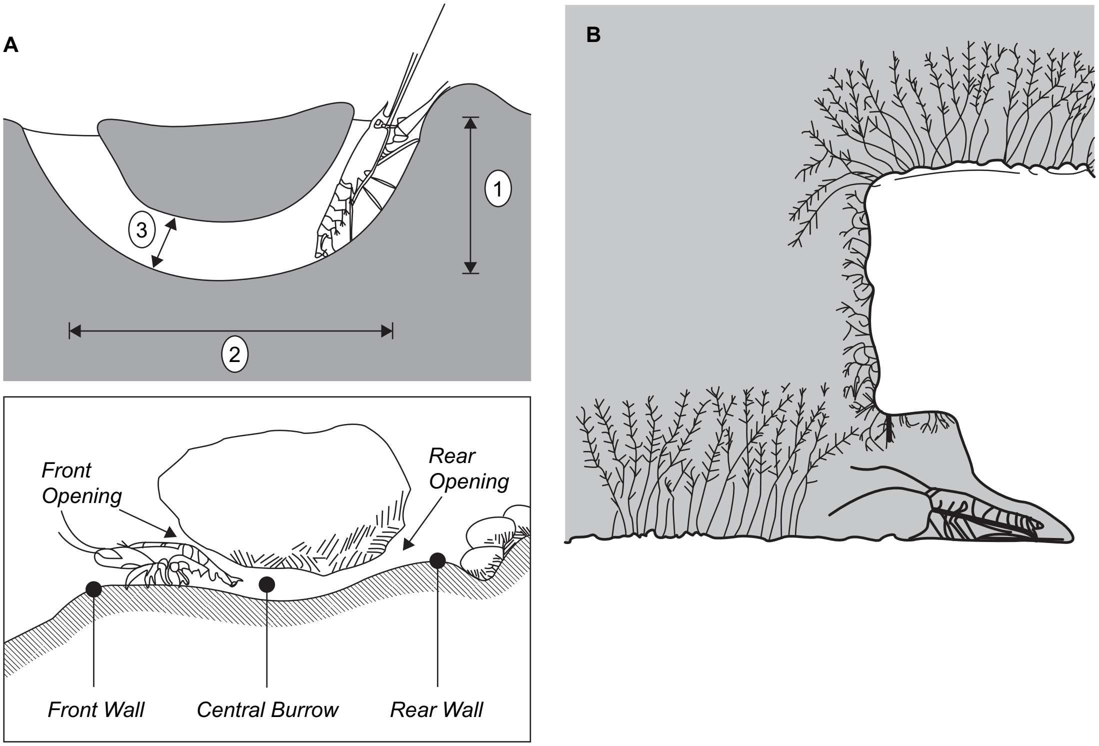

Fig. 3.6 A comparison of (A) two types of burrows occupied by homarid lobsters to (B) the crevices occupied by achelate lobsters. Newly-settled homarid lobsters are capable of constructing their own burrow in soft sediment, but once they become large, they can only modify burrows under rock or ledges (adapted from Dybern, 1973; Botero & Atema, 1982). Newly-settled achelate lobsters often seek shelter in macroalgae or small holes shaded by macroalgae and then move into larger crevices under rocks, corals and sponges (adapted from Jernakoff, 1990). The major difference is that clawed lobsters manipulate the substrate by digging or bulldozing with their claws to create an opening optimally sized for the occupant, whereas clawless lobsters occupy crevices without modification.

Wahle, 1992a, b). However, the mechanism of this sheltering advantage remains a topic of interest as it relates to differences in shelter sharing among conspecifics. Larger clawed lobsters rarely, if ever, share shelters and aggressively defend them from conspecifics (Cobb, 1971; Scrivener, 1971) especially those of the same sex (Bushman & Atema, 1997). Clawless lobsters, in contrast, are regularly observed to share crevice shelters with conspecifics (Herrnkind *et al.*, 1975; Cobb, 1981; Zimmer-Faust & Spanier, 1987; MacDiarmid, 1994).

3.3.3 Ontogenetic habitat shifts

Lobsters have a complex life cycle with different life history stages occupying different habitats (Fig. 3.2). As a result, behaviours that confer an advantage at one stage may not be advantageous at the next stage/habitat. These concomitant changes in behaviour and habitat have the potential to reveal the functional significance of behavioural variation. For example, positive phototaxis and vertical migration in the larvae of lobsters is likely to confer an advantage in terms of dispersal in surface currents (Botero & Atema, 1982; Yeung & McGowan, 1991). However, the negative phototaxis in the postlarval, juvenile and adult stages is advantageous in avoiding diurnal predators during settlement and post-settlement phases (Cobb, 1971; Acosta *et al.*, 1997; Butler *et al.*, 1997; Acosta & Butler, 1999).

Many spiny lobsters also undergo an ontogenetic change in sociality from an asocial early benthic juvenile stage to social subadult and adult stages (Butler & Herrnkind, 2000; Chapter 8). For example, *Jasus edwardsii* first-stage juveniles are often found by themselves, but are increasingly found sharing crevices with conspecifics as they grow larger (MacDiarmid, 1994). This ontogenetic shift in aggregation is mediated by a change in the response to conspecifics' odours at a size when den sharing first confers a survival advantage (Butler *et al.*, 1999). This supports the group-defence hypothesis for the evolution of sociality.

Similarly, *P. argus* first-stage juveniles are also solitary in their macroalgal settlement habitat until they reach about 15 mm carapace length (CL), when they first begin seeking crevice shelters (Fig. 3.6; Marx & Herrnkind, 1985). At that size, they become attracted to conspecific odours (Ratchford & Eggleston, 1998) and respond to the presence of conspecifics by increasing their walking and co-denning in crevice structures (Childress & Herrnkind, 1994, 1996, 2001b). Neither the algal-dwelling asocial juveniles (6–15 mm CL) nor the crevice dwelling social juveniles (15–30 mm CL) benefit from reduced predation when tethered together (Butler *et al.*, 1997; Childress & Herrnkind, 2001a). However, naive individuals were able to find crevice shelters faster when conspecific odour cues were present in the den (Childress & Herrnkind, 2001a). These results support the guide-effect hypothesis for the evolution of lobster sociality.

In contrast to the typical pattern of gregarious den sharing usually found in spiny lobsters, the reef-obligate spotted lobster, *Panulirus guttatus*, is more likely to be found solitarily in deep crevice shelters (Sharp *et al.*, 1997). One difference in the life history pattern of this species is the lack of an ontogenetic habitat shift. The puerulus settles directly on coral patch reefs where it remains for its entire lifespan (Robertson & Butler, 2003). In a phylogenetic comparative analysis of life history and sociality in the genus *Panulirus*, those species with a coral-obligate life style were significantly less likely to show conspecific attraction, den sharing and coordinated defensive behaviours (Childress, 2006). This suggests the guide-effect would no longer confer an advantage since shelters are abundant and long-range movement into unfamiliar habitats is absent. However, *P. guttatus* also have spiny antennae that are greatly reduced in diameter, reducing their effectiveness in thwarting the attacks of triggerfish predators (Bouwma & Herrnkind, in preparation). This suggests that group defence may also no longer be an advantage.

Although co-denning is not a characteristic of adult clawed lobsters, newly settled juvenile *H. americanus* are attracted to conspecific odours (Boudreau *et al.*, 1993a) and have been observed to share shelters or have separate shelters in close proximity (Lawton & Lavalli, 1995). Crevice shelters may also be important in protecting lobsters from strong tidal currents and elevated light levels (Botero & Atema, 1982; Boudreau *et al.*, 1993b). These results suggest an initial guide-effect benefit for clawed lobsters since conspecific attraction could potentially reduce the search time for a suitable benthic substrate at the time of settlement.

Future research on the relationship between lobster habitat and behaviour should address how individuals and populations behaviourally respond to the scale and frequency of natural, environmental and anthropogenic disturbances (e.g. modification of habitats and predator removal by fishing, stochastic events such as hurricanes, sub-lethal effects of pollution, etc.).

3.4 Competition and agonistic behaviour

For many crustaceans with greatly enlarged raptorial appendages, including clawed lobsters, lethality increases with weapon size (Reese, 1983). Larger individuals easily establish dominance over small individuals as claw size is an honest signal of one's resource-holding potential (Cushing & Reese, 1998). However, when these weapons become capable of severely injuring or killing an opponent, most animals develop a form of ritualised fighting to establish dominance without resorting to unrestrained combat (Dingle, 1983). Like the majority of crustaceans, both clawed and clawless lobsters are often aggressive toward conspecifics. These tests of size and strength are actually highly coordinated social interactions that represent a sophisticated system of resource partitioning.

3.4.1 Anti-predatory behaviours

Lobsters employ three strategies to decrease their risk of predation: crypticity, escape behaviours and defensive behaviours. Each strategy is a direct response to the sequential stages in the predation processes: detection of prey, capture of prey and consumption of prey (Lima & Dill, 1990). The effectiveness of each strategy depends on number, size, type, manoeuvrability and experience of the predator. The effectiveness and importance of each strategy also changes during the ontogeny of lobsters. Larval and newly-settled lobsters are vulnerable to the widest range of predators including birds, fish, crustaceans and cephalopods. Larval lobsters are generally cryptic because of their transparent bodies, and in many species, postlarvae settle initially in vegetative habitats and avoid predators by crypticity. Other species immediately occupy crevice shelters scaled closely to their own body size, increasing both crypticity and the probability of escaping a predatory attack (Butler & Herrnkind, 2000). As lobsters grow larger, their suite of predators decreases dramatically. Some predators can now be thwarted by rapid tail-flip escape behaviour, while others can be held at bay by heavy armour and spines and/or skilful use of the claws or first antennae (Barshaw *et al.*, 2003). It is clear that the functional diversification of lobster body plans is to a large extent in response to intense predation pressure at the size that crypticity is no longer an effective strategy. It is at this same size at which the difference in sociality of clawed and clawless lobsters is greatest.

The group-defence hypothesis of lobster sociality suggests that the driving force for aggregation and den sharing is the collective benefit of cooperative group defence. Tethering studies found that *P. argus* (>35 mm CL) had higher survival when tethered in artificial shelters scaled appropriately for their size (Eggleston *et al.*, 1990), and with higher conspecific density (Mintz *et al.*, 1994). Furthermore, untethered lobsters preferred small shelters when alone and large shelters when in groups. These preferences shifted toward medium-sized shelters when predators were present, suggesting that lobsters adopt a strategy of minimising their individual risk through group defence, the dilution effect, or some combination thereof (Eggleston & Lipcius, 1992). Similar results were found in a tethering study of *J. edwardsii* (>40 mm CL) where individuals had 50% greater survival when tethered in shelters with two conspecifics, than those tethered alone (Butler *et al.*, 1999).

Recently, a number of studies have explored the behavioural strategies of *P. argus* alone and in groups when attacked by triggerfish predators. Caribbean spiny lobsters are more likely to come together and remain in a tight outward-facing formation when in the presence of triggerfish predators (Herrnkind *et al.*, 2001). The per capita probability of being killed decreases with increasing group size, suggesting a group-defence benefit above that of the dilution effect (Lavalli & Herrnkind, in preparation). The proximate mechanism underlying this observation appears to be the effectiveness of physically striking the approaching predator with the robust, spiny antennae while producing a rasp from the stridulatory organ. If either the antennae or the stridulatory organ are removed, the effectiveness of this defensive behaviour is reduced (Bouwma & Herrnkind, in preparation).

These observations suggest that sociality in spiny lobsters may have been favoured by cooperative group-defence. However, one scyllarid species, *Scyllarides latus*, also shows a preference for sharing shelters with conspecifics (Spanier & Almog-Shtayer, 1992; Barshaw & Spanier, 1994a). Like panulirids, these scyllarids have significantly higher mortality when tethered in the open versus tethered in crevice shelters (Barshaw & Spanier, 1994b). However, when tethered in groups in the open, these lobsters had no higher survival then when tethered alone (Lavalli & Spanier, 2001). Therefore, the tendency to aggregate in crevice shelters is not likely to be due to cooperative group defence. In fact, the relative predation risk for these slipper lobsters tethered in the open was considerably less than equivalent-sized spiny lobsters

(*Palinurus elephas*) or clawed lobsters (*Homarus gammarus*) suggesting that *Scyllarides latus* relies more on its heavily armoured exoskeleton for protection against predators (Barshaw *et al.*, 2003). Why these slipper lobsters aggregate is still unresolved, but it may be related to their seasonal migration (Spanier *et al.*, 1988) and potential benefit from the guide-effect when seeking crevice shelters in unfamiliar areas.

3.4.2 Shelter competition

Since shelter plays an important role in reducing predation risk, and the availability of suitably-sized shelters may at times be limited, competition for shelter may be critical for survival. This appears to be particularly true for the asocial clawed lobsters in the genus *Homarus*. Although this genus is capable of creating a complete burrow in soft sediment when small, it usually occupies pre-existing crevice shelters once it is larger than 30 mm CL (Fig. 3.6a; Lawton & Lavalli, 1995). These lobsters defend their shelters against intrusion by conspecifics (Karnofsky *et al.*, 1989; Bushmann & Atema, 1997) as well as by interspecifics (e.g. Jonah crabs, *Cancer borealis*, Richards & Cobb, 1986). Laboratory studies of similar-sized male and female juvenile *Homarus americanus* found that males were better able to defend their shelters than females and the effect of prior residency was observed only in male–male interactions but not female–female interactions (Peeke *et al.*, 1998). Dominance in pair-wise interactions is usually determined by sex and size differences, but may also be related to moult stage (Tamm & Cobb, 1978), reproductive status (Mello *et al.*, 1999), claw dimensions, exoskeleton calcification and plasma protein levels (Vye *et al.*, 1997).

3.4.3 Aggression and dominance hierarchy formation

Knowing the aggressive nature of clawed lobsters when paired in the laboratory, how is it possible that *H. americanus* can successfully coexist in nature at high densities? One mechanism is their ability to form highly-structured dominance hierarchies. Clawed lobsters quickly learn their relative rank among local conspecifics and thus avoid repeating aggressive encounters with dominant individuals (Fig. 3.3a). It appears that individuals possess the ability to learn the individual identity of those lobsters previously encountered and remember their relative rank order in the hierarchy for up to seven days (Karavanich & Atema, 1998b). Olfactory cues to the identity of conspecifics appear to be carried in the urine, for blocking urine excretion or ablating the lateral flagella of the antennule is sufficient to eliminate the ability to recognise familiar opponents (Karavanich & Atema, 1998a). Dominant individuals urinate quicker, more frequently and release a greater volume of urine than do subordinate individuals (Breithaupt *et al.*, 1999; Breithaupt & Atema, 2000). Thus, the cost of shelter defence against conspecifics may be greatly reduced if residents remain in areas where their identity is known. This suggests that movement to new locations should be more costly to clawed lobsters than to spiny lobsters, since they will expend greater effort to establish their rank among unfamiliar local residents. This supports the residency-sociality hypothesis.

Since clawless lobsters frequently share shelters, benefit through cooperative group defence against predators, and regularly interact with new unfamiliar conspecifics, one might expect that spiny lobsters would show little intraspecific aggression. However, spiny lobsters have been observed to be aggressive toward conspecifics, pushing one another out of crevice shelters and excluding subordinate individuals from gaining entrance to a den (Fielder, 1965; Berrill, 1975, 1976). Perhaps surprisingly, juvenile *P. argus* tend to show twice the number of aggressive behaviours toward conspecifics than do *Panulirus guttatus* of similar size (Childress, 2006). They also appear to be able to distinguish the odours of familiar and unfamiliar conspecifics, preferring those of unfamiliar individuals. Whether or not spiny lobsters actually prefer to share shelters with unfamiliar individuals in the field is yet untested, but studies of marked individuals in large pens suggest that fidelity to the same den by individual occupants is low (Glaholt, 1990). This also supports the residency-sociality hypothesis for the evolution of sociality.

3.5 Movement and migration

Studies of movements and migration have often been undertaken for lobster species of commercial interest to determine immigration, emigration, mixing of stocks and/or the effect of environmental variables on behaviour. Comprehensive reviews of this literature can be found in Krouse (1980), Herrnkind (1980, 1985), Hakkonsen and Anoruo (1994) and Lawton and Lavalli (1995). Lobster populations generally have individuals that fall into several different behavioural categories, which often make interpretation of movement data relative to distribution and abundance estimates, difficult. Movements may be broadly spatially characterised as: (1) homing–territorial, (2) dispersive–nomadic, or (3) migratory (Herrnkind, 1980). Movement behaviour may also be temporally characterised as: (1) daily, (2) ontogenetic or (3) seasonal–annual. The most common explanations given for the directed movements of lobsters are: (1) the enhancement of growth via increased degree-days (Campbell, 1986) or feeding opportunities (Phillips, 1983), (2) seeking out the best location for release of offspring (Moore & MacFarlane, 1984; Booth, 1997) or (3) avoidance of suboptimal habitats, e.g. high physical disturbance (Herrnkind, 1985), low salinity (Jury *et al.*, 1994), or low oxygen (Cockcroft, 2001). At any specific place and time lobsters seem to fall into two broad categories: (1) residents or (2) transients. For example, Karnofsky *et al.* (1989) studying *Homarus americanus* in a small cove on Cape Cod, Massachusetts, noted that approximately 52% of the population were resident throughout a summer and 48% were transient. What causes one individual to be transient and another to be resident is not clear but may be influenced by sex, size, reproductive status, hormonal state, density of conspecifics, predation/fishing intensity and/or environmental conditions. We explore some of these issues below, but clearly one of the important goals for future research is to more rigorously determine how internal versus external cues influence lobster movements at each life history stage.

3.5.1 Residency and homing

Since all lobsters have a daily activity pattern of nocturnal foraging and diurnal sheltering, it is advantageous for individuals to learn the location of their den (Fig. 3.5). This ability to orient toward and return to a place of residence if displaced, is referred to as homing behaviour (Vannini & Cannici, 1995) and is shared by both the clawed, e.g. *H. americanus* (Karnofsky *et al.*, 1989) and clawless lobsters, *P. argus* (Herrnkind & McLean, 1971), *P. guttatus* (Lozano-Álvarez *et al.*, 2002), *J. edwardsii* (MacDiarmid *et al.*, 1991). The proximate cues associated with returning home to shelter may include wave surge (Herrnkind & McLean, 1971), odours from the den or residents inside the den (Nevitt *et al.*, 2000), or magnetoreception (Boles & Lohmann, 2003). The potential benefits of homing behaviour include a reduction in the time exposed to predators and reducing the costs associated with relocating to areas with unfamiliar conspecifics. Most individuals appear to know the location of, and regularly use, more than one crevice shelter in close proximity to one another (Herrnkind *et al.*, 1975; Karnofsky *et al.*, 1989; MacDiarmid *et al.*, 1991). The benefits of sociality may increase when an individual stops homing to a familiar den and seeks a new shelter in an unfamiliar location where other conspecifics are located.

3.5.2 Nomadism

Herrnkind (1980) characterised nomadic movements as multidirectional relocations that differ in their causative agents from those of seasonal bidirectional migrations. The best known nomadic movements of lobsters are associated with ontogenetic shifts in habitat use. For example, *Panulirus cygnus* undergoes a nomadic relocation from nearshore nursery areas toward offshore reproductive areas as they approach sexual maturity (Phillips, 1983). The adults then remain in these offshore adult habitats year-round even though their reproduction is seasonal (Brown & Phillips, 1994). A similar ontogenetic shift in habitats just prior to sexual maturation is also observed in *P. ornatus* (Moore & MacFarlane, 1984), *P. argus* (David & Dodrill, 1989), and *Palinurus gilcristi* (Groeneveld & Branch, 2002).

What distinguishes migrations from nomadic relocations is the eventual return of individuals to their original point of departure in a predictable period of time, usually seasonally (Herrnkind, 1980). Evidence of long-distance movements is not always indicative of migration. For example, the majority of adult *Jasus edwardsii* have a very limited range of movement with 87% of the tagged lobsters being resighted within 5 km of their tagging site up to two years later (McKoy, 1983). However, 12% were found at distances from 5–100 km and 1% were further than 200 km from their initial tagging location. Kelly (2001) confirmed that this pattern was not just the result of haphazard recapture data by following 32 adults carrying acoustic tags and finding that 78% of individuals resighted (average time between sightings 3.58 days) remained within 0.1 km of their tagging site and that the maximum displacement over an entire year was less than 4 km for all 32 individuals.

Studies of lobster movement by tag–recapture methods may produce very different results depending on the type of tag used, the method of resighting the tag, the sampling frequency, catchability, and the geographic range resampled. For example, the homing studies discussed above involved a daily resampling of a small geographic area by divers directly searching for a few tagged individuals. This type of sampling is biased toward resighting those individuals that returned to a den they previously occupied while missing those individuals that departed the immediate search area. Other techniques, such as the use of ultrasonic telemetry, expand our ability to relocate individuals that have dispersed greater distances. Numerous studies have demonstrated that local foraging and meandering movements are typically less than 300 m/day (Fig. 3.7), but several studies demonstrate that lobsters undertake longer movements as well (Davis & Dodrill, 1980; Campbell, 1986; Gregory & Labinsky, 1986; Watson *et al.*, 1999; Kelly, 2001; Comeau & Savoie, 2002).

The value of these long-distance movements is speculative. One explanation that has some support is the larval-release hypothesis (Booth, 1997). Gravid females often migrate counter to the direction of the nearshore current leading them to upstream locations before they release their larvae to allow for retention or increased dispersal potential of offspring (McKoy, 1983; Booth, 1984; Moore & MacFarlane, 1984; Smith *et al.*, 2001; Groeneveld & Branch, 2002). If this behaviour confers an advantage in terms of larval survival, it is curious that such a small proportion of gravid females behave this way.

3.5.3 Migration

Both homarid and achelate lobsters are capable of annual migrations, usually from shallow, warm waters during the summer to deeper, more thermally stable waters during the winter (Fig. 3.6; Herrnkind *et al.*, 1973; Campbell, 1986; Pezzack & Duggan, 1986; Comeau & Savoie, 2002; Kelly & MacDiarmid, 2003). Depending on the species, the local topography and the environmental cues, this migration can be the result of a gradual increase in locomotory behaviour toward a particular direction over a period of several weeks such as seen in *Jasus edwarsdii* (MacDiarmid *et al.*, 1991; Kelly, 2001) and *Homarus americanus* (Estrella & Morrissey, 1997). In some species, such as *Panulirus argus*, seasonal migrations are cued by a sudden drop in temperature and increased turbidity associated with the first autumnal cold front (Kanciruk & Herrnkind, 1978) and results in a mass movement of individuals (Herrnkind *et al.*, 1973). These migrating masses often assemble into coordinated single file lines, or queues (Herrnkind & Cummings, 1964; Herrnkind, 1969). Migratory queues continue day and night allowing for a rapid crossing of habitats that lack suitable structures for diurnal resting. One functional benefit of queuing is drag reduction and thus, individuals in positions other than the lead may conserve as much as 50% of the energy required to maintain speeds of up to 35 cm/second (Bill & Herrnkind, 1976). However, individuals in queues may also benefit from a reduction in the probability of predation through a reduced time of exposure, a decreased probability

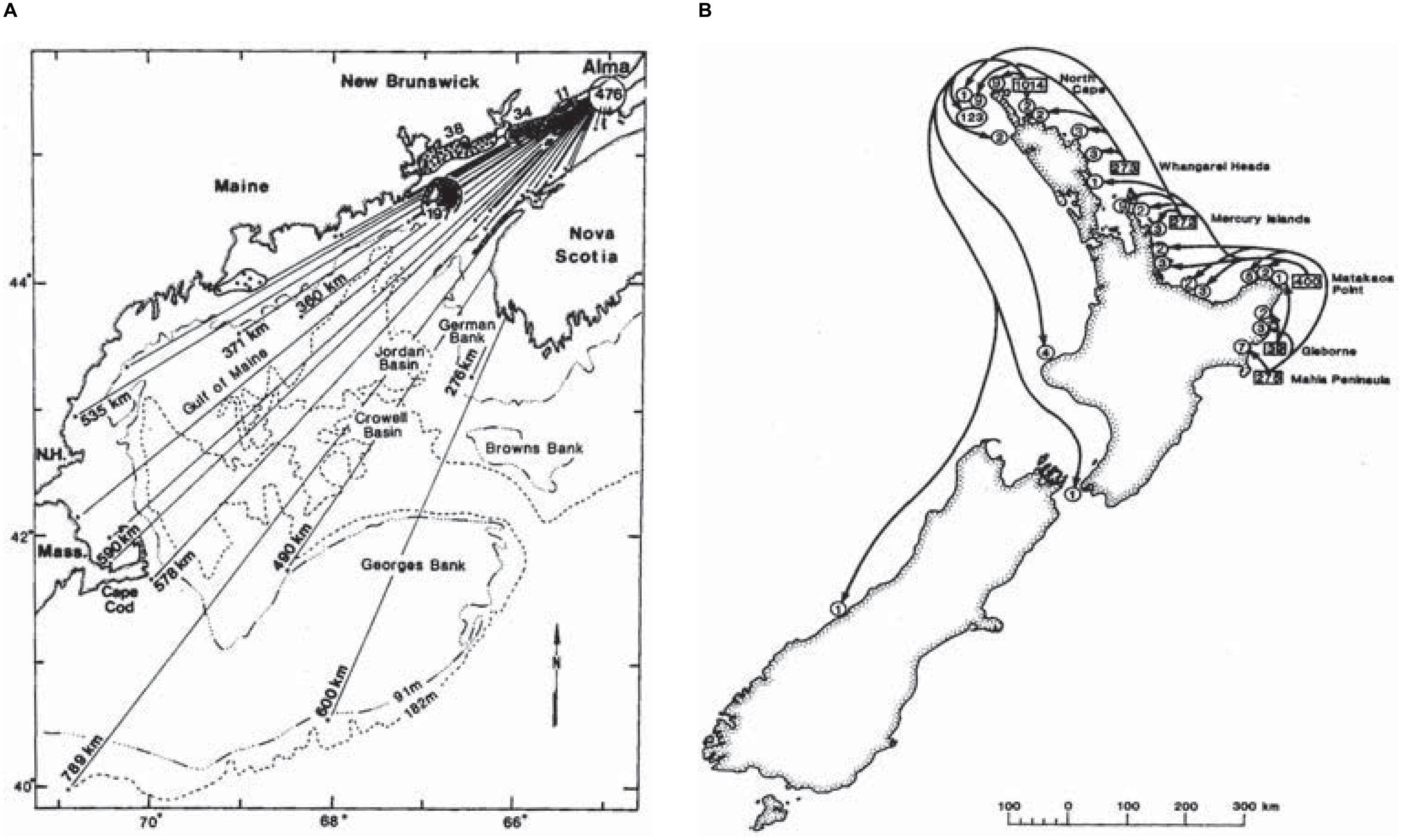

Fig. 3.7 A comparison of the long-distance movement of tagged and recaptured (A) homarid lobsters (*Homarus americanus*) in New England (adapted from Campbell & Stasko, 1986) and (B) achelate lobsters (*Sagmariasus verreauxii*) in New Zealand (adapted from Booth, 1997). In both studies, the majority of individuals were recaptured within 5 km of their tagging location, but a few individuals travelled more than 200 km.

of attack, an increased probability of cooperative group defence, or a decrease per capita risk of selection by the predator (i.e. the dilution effect), (Herrnkind *et al*., 2001). When queuing individuals rest, they circle into a tight spiral formation, or rosette (Kanciruk & Herrnkind, 1978). Studies in the field and in mesocosms have found that coordinated groups of *P. argus* are more efficient at defending themselves against attacking triggerfish (Herrnkind *et al*., 2001; Lavalli & Herrnkind, in preparation).

Both queuing and resting in coordinated groups in the open have been observed at times other than during a mass migration. For example, both *P. argus* and *P. marginatus* subadults have been observed moving in small queues of three to five individuals when moving out in the open (Berrill, 1975; MacDonald *et al*., 1984). Aggregations of lobsters resting in an outward-facing formation have also been observed for *Jasus edwardsii* on mussel beds or open sand habitats with no suitable structures to serve as diurnal shelters (McKoy & Leachman, 1982; Kelly *et al*., 1999). These observations suggest that the potential anti-predatory benefits of aggregation, when at rest or when moving, may be advantageous at times other than during mass migration. These observations support the group-defence hypothesis of lobster sociality, although a guide-effect benefit may also be realised if individuals can reduce the time they spend alone in the open by orienting toward conspecifics, resting in the presence of conspecifics, and/or coordinating movement with conspecifics.

It is unclear why some lobsters travel very long distances and others very little, and why in some areas a high percentage of animals move long distances and in other regions extensive movements are rare (Herrnkind, 1980; Estrella & Morrissey, 1997). Nonetheless, the analysis of movements and migrations has important management implications in terms of stock assessment, reserve design and location and control of fishing mortality. Further studies on the life-history-specific movements of male and female lobsters, before, during, and after they are reproductively mature may help reveal the factors that influence their movements and the subsequent impact on recruitment. Finally, the continued development of new technologies in behavioural research (e.g. telemetry, *in situ* monitoring, etc.) should allow for less invasive and longer field observations.

3.6 Mate choice and reproductive behaviour

Few behaviours have a more important role in determining the fitness of an individual than those associated with mating. The mating systems of homarid and achelate lobsters reveal much about the role of reproductive strategies in the development of lobster sociality (Aiken & Waddy, 1980; Atema & Cobb, 1980). The constraints imposed by the physiology of the reproductive cycle may be the single most important factor in the divergence of homarid and achelate lobsters (Quackenbush, 1994). In homarid lobsters, mating is usually associated with the female moult cycle (Atema & Voight, 1995) and insemination is internal, and thus limited by the capacity of the female's seminal receptacles (Waddy *et al*., 1995). In achelate lobsters, mating is independent of the female moult cycle and insemination is external (MacDiarmid & Kittaka, 2000). Furthermore, in some species of achelate lobsters, spermatophore deposition occurs many days before fertilisation, allowing sufficient time for interesting cryptic female choice and alternative male mating strategies associated with removal and replacement of spermatophores (MacDiarmid & Butler, 1999). Are these differences in reproductive physiology sufficient to explain the differences we see in the sociality of homarid and achelate lobsters?

3.6.1 Mate attraction and choice

Sexual selection has probably been an important force in shaping the sensory physiology and behaviours associated with mate recognition and mate choice in lobsters. Like most animals, the critical first step involves recognition of potential mates that are receptive to avoid wasting time, effort, injury or even predation. Both homarid and achelate lobsters use a combination of signals including environmental cues, urine-borne olfactory cues, and body-posture cues.

The role of chemical attractants is best known for homarid lobsters (Atema, 1995). Both male and female *Homarus americanus* are capable of detecting the sex of another individual from chemical cues in the water (Atema & Engstrom, 1971; Atema & Cowan, 1986; Cowan, 1991). The behavioural responses invoked depend on the sex and the moult stage of the sender and receiver (Atema & Engstrom, 1971; Tamm & Cobb, 1978; Bushmann & Atema, 2000) and previous experience (i.e. familiarity) between the sender and receiver (Karavanich & Atema, 1998b). Some component of this chemical signal is released in the urine as evidenced by a change in the behavioural response to catheterised signallers and antennule-ablated receivers (Cowan, 1991; Karavanich & Atema, 1998a). Although the identity of these substances is still unknown, they could be related to the breakdown products of peptide or steroid hormones that regulate the motivational and physiological state of the individual (Kravitz, 1988, 2000). Although less is known about the specific behavioural responses to chemical cues in the achelate lobsters, observations suggest that basic metabolites such as ATP and amino acids stimulate locomotion at levels only 2–8% above ambient environmental levels (Zimmer-Faust, 1987, 1991) and may be related to their aggregation with conspecifics and their ability to find crevice shelters (Zimmer-Faust *et al.*, 1985; Zimmer-Faust & Spanier, 1987; Nevitt *et al.*, 2000).

Assuming that male and female lobsters can and do assess the reproductive condition of prospective mates, how does this influence their choice of a particular mate? In homarid lobsters, females tend to be the searching sex and will visit the dens of several prospective males before entering one (Cowen & Atema, 1990). Females, but not males, are attracted to the odour cues of the opposite sex in Y-maze choice tests (Bushmann & Atema, 1997). This female choice is stronger in premoult females than in intermoult females and is lost when the resident males are catheterised to prevent urine release (Bushmann & Atema, 2000). Once a female reaches the den entrance of a male, the latency to enter may depend on additional cues beyond those provided in the urine, such as male body size, claw size, and dominance status (Bushmann & Atema, 2000; Debuse *et al.*, 2003).

In achelate lobsters, males appear to be the searching sex in *Panulirus argus* (Lipcius *et al.*, 1983) and females the searching sex in *Jasus edwardsii* (MacDiarmid *et al.*, 1991). This stark contrast is best explained by the relative timing between insemination and fertilisation. In both species, the male inseminates the female by transferring a sticky spermatophore to her sternum (Fig. 3.8). In *Panulirus,* this spermatophore develops a tough outer covering that protects the sperm and keeps them viable for many days until the sperm and eggs are mixed together. In *Jasus,* this spermatophore is not protected with an outer covering and rapidly degrades by exposure to seawater (MacDiarmid & Kittaka, 2000). Therefore, females must be ready to spawn eggs within a day or so of receiving the male's spermatophore. As a result, females increase their movement between dens from April to July corresponding to their moulting and ovarian maturation period, while the largest, most dominant males decrease their movement and tendency to share dens with other males (MacDiarmid *et al.*, 1991).

Size appears to be the one characteristic which is most important for female and male mate choice. Female size is correlated with fecundity (Aiken & Waddy, 1980) and male size is often correlated with dominance rank (Fielder, 1965; Scrivener, 1971), shelter quality (Atema *et al.*, 1979; MacDiarmid *et al.*, 1991) and spermatophore size (MacDiarmid & Butler, 1999; Gosselin *et al.*, 2003). Surprisingly, recent studies have shown that lobster reproductive output, as estimated by fertilised egg mass carried by females when mated to small males, is often limited by sperm availability in both homarid (Gosselin *et al.*, 2003) and achelate lobsters (MacDiarmid & Butler, 1999).

3.6.2 Copulation and spawning

Mating in lobsters involves a two-step process that is separated temporally: insemination and fertilisation. In homarid lobsters, females move into a den with a male and then moult (Karnofsky & Price, 1989; Cowan & Atema, 1990). The male initiates mating with the newly-moulted female by climbing onto her back and gently rolling her over with his pereiopods (Fig 3.8a). Mating usually occurs inside

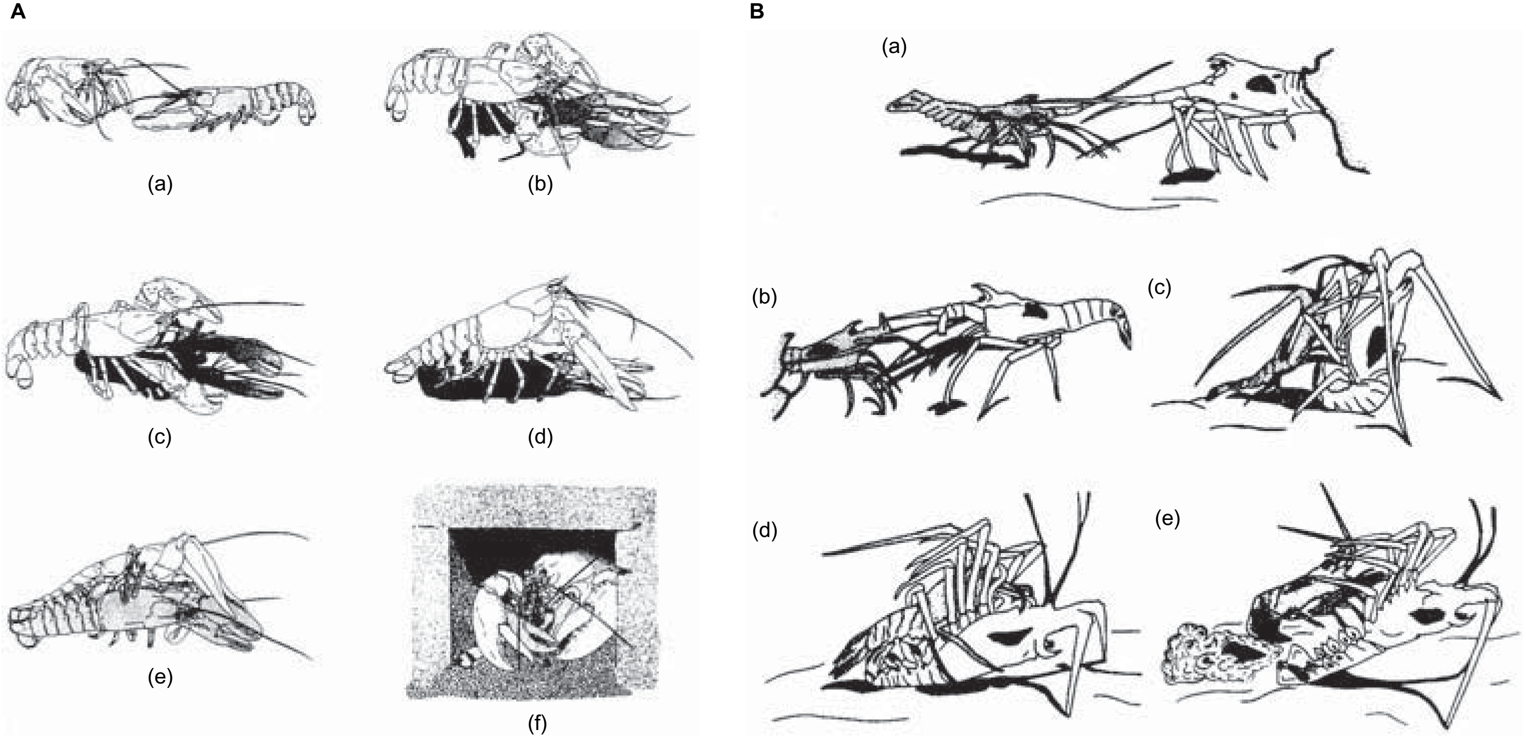

Fig. 3.8 A comparison of the mating behaviours of (A) a homarid lobster (*Homarus americanus*) (adapted from Atema *et al*., 1979) and (B) an achelate lobster (*Panulirus argus*) (adapted from Lipcius *et al*., 1983). The sequence of events is indicated by the order of the letters (a–f). Although both species mate ventral to ventral, the position of the sexes is reversed. Also, male homarid lobsters will typically guard the newly-moulted female until her exoskeleton hardens.

the den but not always (Debuse *et al*., 1999). Insemination occurs by insertion of the male gonopods in the female's gonopores and deposition of the spermatophore internally into the female's seminal receptacles (Aiken & Waddy, 1980). The spermatophore hardens into a sperm plug that potentially prevents future insemination until the next moult. After mating, the female usually remains in the den of the male for several days until her exoskeleton has hardened. The period of mate-guarding may be important to the survival of the female and prevention of additional inseminations from other males (Atema *et al*., 1979). Interestingly, in *Homarus americanus* it has recently been shown that even though insemination is internal, upon spawning, fertilisation is external as sperm leave the seminal receptacle via two grooves located posterior and lateral to the opening (Aiken *et al*., 2003).

In contrast, female achelate lobsters may mate at any stage in their moult cycle and either sex can initiate mating (MacDiarmid & Kittaka, 2000). After an initial approach and contact, males will rotate beneath or pull females up onto their ventral surface (Fig. 3.8b). The males lack a well developed organ of intromission and deposit their spermatophore externally on the ventral surface of the female's sternum (Lipcius *et al.,* 1983). As described above, this spermatophore is either short-lived or develops a hard protective cover protecting it until the time of fertilisation (MacDiarmid & Kittaka, 2000). In some *Panulirus* species, females may carry multiple spermatophores at the same time. Whether these spermatophores are from the same or different males and the degree to which some or all of the sperm will be used to fertilise the eggs is unknown, but a potentially important area of future research.

These observations suggest that homarid and achelate lobsters should differ widely in their potential for sperm competition and multiple paternity. If this is the case, then selection might favour very different behaviours associated with aggression, dominance-hierarchy structure, and den sharing among reproductive adults. In a recent study of *Homarus americanus,* 13% of females examined carried eggs fertilised by more than one male and multiple paternity appeared to be greater in the smaller females, than in the larger females (Gosselin *et al*., 2005). In another study, as many as 50% of female *Nephrops novegicus* have also been found to have multiple paternity (Gosselin *et al*., 2003). One potential explanation is that females may be mating with additional males during their intermoult period, as has been observed in *Homarus americanus* (Waddy & Aiken, 1990). In achelate lobsters, alternative male strategies include differential allocation of sperm, dependent on the size of the female, and the attempted removal of unwanted spermatophores before fertilisation by both males and females (MacDiarmid & Butler, 1999). These reproductive alternative strategies blur the distinctions between the typical mating system classifications and make generalisations about the role of sexual selection in the evolution of lobster sociality difficult at best. Future research should address how reproductive success and behavioural evolution are limited by genetic and physiological constraints as well as local and regional differences in sex ratio and size distribution. One particularly interesting attempt at evaluating mating system evolution found that operational sex ratio theory predicted a shift in female–female aggressive interactions in captive groups of *Homarus gammarus* (Debuse *et al*., 1999). Predicted differences in the behaviours of homarid and achelate lobsters based on their morphological and reproductive differences are summarised in Table 3.2.

3.7 Behaviour and fisheries management

Despite the wealth of knowledge regarding the biology of lobsters presented in this book and the volumes that came before it, we still cannot predict with certainty the future of lobster population densities or the impacts of current fisheries on their sustainability. One of the major reasons for this is that lobsters are highly variable in their behavioural strategies, making a number of our assumptions regarding population growth and limitation suspect. Only through the integration of alternative behavioural strategies into our population models, can we begin to understand their influence on our

Table 3.2 Predicted differences in the behaviours of homarid and achelate lobsters based on their morphological and reproductive differences.

Behaviour	Homarid lobsters	Achelate lobsters
Foraging and feeding	large prey items central-place foraging optimal prey selection	small prey items in-patch foraging optimal patch selection
Sheltering and den sharing	burrows and tunnels costly to maintain easy to defend not shared	crevices and holes costly to locate hard to defend shared with conspecifics
Ontogenetic habitat shifts	to avoid extreme conditions seasonal optional	to exploit new foods continuous obligatory
Anti-predator behaviours	strike with claws safer alone tail flip	strike with antennae safer in groups stand and fight
Shelter competition (residency–sociality)	intraspecific frequent intense	interspecific infrequent relaxed
Dominance hierarchies	present ritualised fighting individual recognition	absent gregariousness species recognition
Residency and homing	high den fidelity tight body : den size ratio homing by physical cues	low den fidelity loose body : den size ratio homing by conspecific cues
Nomadism	seasonal neg. density-dependence	permanent pos. density-dependence
Migration	infrequent alone	common in groups
Mate attraction and choice	female choice females come to male	male choice males come to female
Copulation and spawning	single matings mate guarding	multiple matings sperm competition

fisheries management models. Two areas of future research could provide critical insights into the role of behavioural variation in fisheries management: the behavioural basis of catchability and the influence of behaviour on the use and effectiveness of marine reserves.

3.7.1 *Behavioural basis of catchability*

Fishing gears used to capture lobsters are generally passive and rely upon species-specific behaviours for attraction and retention. The most commonly-used gear to collect mobile juveniles and adults is the trap, but even traps differ substantially between species in design, materials, and baits used (Miller, 1990). While some of the selectivity of fishing gear is by design (e.g. escape vents in traps to minimise retention of small lobsters), much of it is not, and the factors that influence behavioural selectivity are usually poorly understood (Cobb, 1995; Jury *et al.*, 2001). The factors influencing catchability include both abiotic (e.g. hydrodynamics of odour plume, trap design, temperature, density of traps, bait quantity and quality, time of day) as well as biotic factors (e.g. presence of conspecifics inside and outside the trap, size, sex, activity level, shelter affinity, gregariousness, agonistic interactions, olfactory ability, moult status, feeding motivation) (Heatwole *et al*., 1988; Miller, 1990; Cobb, 1995; Addison & Bell 1997; Fogarty & Addison, 1997; Jury *et al*., 2001). Several studies have reviewed the influence of lobster behaviour on catchability and how this influences the use of trap-derived data to estimate abundance (Hunt *et al*., 1985; Heatwole *et al*., 1988; Miller, 1990; Cobb, 1995; Jury *et al*., 2001).

Studies of the behavioural response of adult lobsters to traps have been done either in semi-natural settings in the laboratory (Karnofsky & Price, 1989; Miller & Addison, 1995), by divers in the field (Miller, 1990; Tremblay & Smith, 2001), by video monitoring (Bjordal, 1986, Jury *et al*., 2001) or by telemetry (Kelly, 1999). For gregarious species like *P. argus*, the presence of conspecifics in artificial shelters (casitas) or in traps as bait, have been shown to increase the catch over structures or traps that were empty (Heatwole *et al*., 1988; Briones-Fourzán *et al*., 2000). Studies *of H. americanus* indicate that only a small proportion of the lobsters that encounter a trap actually enter it and of those that enter, only a small percentage are subsequently caught (Karnofsky & Price, 1989; Jury *et al*., 2001). Morgan (1978) also found that because some spiny lobsters in the field were more catchable than others, trap surveys were underestimating the actual population by 40%. In another study, roughly 60% of spiny lobsters (*Panulirus*) that entered a trap were actually captured (Jernakoff & Phillips, 1988). A video study on the Norway lobster (*N. norvegicus*) in the field also showed that only 6% of lobsters that approached a trap were caught (Bjordal, 1986). The explanations put forth to explain the variability in approach and catch rate included: (1) temporal changes in feeding motivation, (2) difficulty in locating trap entrances, (3) frequent aggressive behaviour (small individuals chased off by larger ones), and (4) many individuals did not contact the trap at all. It is expected that similar processes are taking place when other lobster species interact with traps, but more work is required to understand the complex interactions in and around traps and passive fishing gears. For example, if behaviours such as conspecific attraction are being exploited to catch individuals more efficiently, are our fisheries influencing the level of sociality in future generations by intense artificial selection? There is very strong evidence that recreational fishing by divers is having substantial direct and indirect effects on spiny lobsters in the Florida Keys through injury to sublegal juveniles and correlated changes in conspecific attraction and den sharing behaviours (Eggleston *et al*., 2003; Parson & Eggleston, 2005).

Resource management agencies must rely on fishery-dependent or independent surveys for developing estimates of distribution and abundance of lobster populations. While independent methods for estimating abundance are often done via trawls, diver collection or video survey with remotely operated vehicles (ROVs), the spatial scale, or timing of these sampling techniques is often limited due to the cryptic nature and sheltering behaviours of lobsters, and often results in the use of traps even given their limitations as described above. Because of this and the effects of behaviour on growth, habitat limitation, reproduction and mortality, the interface of ecology, behaviour, and fisheries remains an important area of research (Cobb, 1995).

3.7.2 Movement and marine protected areas

Another management issue that has recently received extensive attention is the use of marine protected areas as a management tool for lobster fisheries (Childress, 1997). The effectiveness of marine reserves for lobsters depend on: (1) the size, number and spatial arrangement of reserves (Stockhausen & Lipcius, 2001; Acosta, 2002), (2) the type and arrangement of habitats included and their use by different life history stages (Acosta & Robertson, 2003; Lozano-Álvarez *et al*., 2003), (3) the relative movement of individuals into and out of the reserve (Rowe, 2001; Davidson *et al*., 2002; Kelly & MacDiarmid, 2003), (4) the proximity to deep water and/or strong oceanic currents (Lipcius *et al*., 1997, 2001), and (5) the rules regarding extraction and their relative enforcement (Acosta, 2001; Eggleston & Dahlgren, 2001). Effective marine reserve design requires close attention to the ontogenetic habitat requirements, seasonal movement patterns and overall habitat quality necessary to sustain lobsters.

3.8 Summary and future directions

Lobsters are extremely important model organisms in the study of the evolution of behaviour (Childress, 2006). The integration of laboratory and field studies will continue to be important in understanding the proximate and ultimate mechanisms leading to the expression of activity patterns, seasonal migrations, homing ability and use of habitat features as protective dens. The behavioural ecology of commercially important lobster species relative to their fisheries is an ongoing area of research as it relates to hatching locations, movements of ovigerous females, mating and moulting areas and times, and selection of habitats. Much of the work on lobster behaviour has been conducted in the laboratory on juvenile and adults and while this should continue, technological advances have enhanced our ability to study behaviour under the logistically difficult field situations increasingly allowing the study of multiple life history stages and populations in their natural environments. Our knowledge of the behaviour of the well-studied lobster species is continually expanding through the use of new and innovative technologies (e.g. telemetry, ROVs, *in situ* monitoring, remote sensing, molecular techniques, etc.) and the scope of multidisciplinary studies; however there are many areas of sensory biology, behaviour and ecology that remain to be explored in these species as well as in comparative studies with the less available deep water species (Cobb 1995; Lipcius and Eggleston, 2000). For example, given the increasing awareness and prevalence of lobster diseases, future research should address the role of behavioural processes in marine disease susceptibility and transmission (Berringer & Butler, 2006).

Despite the differences we have presented in morphology, life history and sociality, homarid and achelate lobsters also present an interesting study in convergent evolution (Chapter 8). Most commercially-important lobsters: (1) attain a very large body size (>1 kg), (2) occupy the same trophic niche as a generalist predator of benthic invertebrates, (3) traverse multiple benthic habitats from inshore to offshore with remarkable homing ability, (4) are nocturnally active and rely on sheltering behaviour to avoid diurnal predators, (5) have elaborate intra- and inter-specific interactions that often include a well developed and highly specific chemosensory component, and (6) have persisted in the face of intense human exploitation and anthropogenic modification of their ecological landscape. Those lobsters that deviate the most from these characteristics are usually those without an extensive commercial fishery and provide us with an interesting comparative glimpse at how behaviour has co-evolved with other aspects of morphology, life history and ecology.

So why are the social behaviours of homarid and achelate lobsters so different? The evidence reviewed here suggests that all three hypothesised mechanisms have contributed to the diversification of lobster sociality. First, the presence of the enlarged major chelae in the homarid lobsters, presumably an ancestral character inherited from their common ancestor with the crayfish, allowed them to excavate burrows and modify crevice shelters and better defend them against conspecifics. Thus, the behaviours associated with ritualised fighting, individual recognition, and female mate-choice may have been favoured by the resident-sociality hypothesis. Second, a fine tuning of the sensory structures to detect wave surge, pressure, temperature and salinity gradients, odours of conspecifics, and small changes in magnetic fields may have allowed the achelate lobsters the ability to travel long distances, find suitable crevice shelters in unfamiliar areas, and even return home to their exact point of departure. Thus, the behaviours associated with nomadism, migration, homing and aggregation may have been favoured by the guide-effect hypothesis. Finally, the development of sharp spines, long robust antennae, and, in some species, a stridulatory organ may have allowed the palinurid lobsters to better defend themselves when attacked by predators. Thus, the behaviours associated with group defence of a crevice shelter, stridulation, resting in formation when in the open, and even migratory queuing, may have been favoured by the group-defence hypothesis. Future research should continue to test the predictions of these and other hypotheses with particular attention to the conditions or scenarios where observed behaviours differ from these predictions. Only then will we have a better understanding of the historical constraints, proximate mechanism and current utility of lobster behaviours.

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Chapter 4

Phylogeny and Evolution

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4.1 Introduction

Our understanding of lobster phylogeny and evolution is at a turning point. While lobster taxonomy has remained fairly stable for many years, modern phylogenetic methods have not yet been systematically applied to the evolutionary relationships of lobsters. Thus, at this point in time, the strength of our understanding of lobster evolution is in the solid literature describing lobster taxa, primarily in the form of taxonomies, both in extant and fossil lobsters. With the advent of molecular techniques and new tools to combine different types of data (molecular and morphological; extant and fossil), new phylogenetic hypotheses are emerging and we are getting a fresh glimpse into lobster phylogeny. This chapter focuses on the recent literature surrounding the phylogeny of lobsters with particular emphasis on the different lines of evidence derived from extant and fossil morphology as well as from molecular data. Examination of morphological and molecular data provides a powerful framework for estimating divergence times in evolution of lobsters. We also discuss the evolutionary biogeography of lobsters, particularly in light of their global distribution and intriguing developmental stages. Our primary goal, throughout this chapter, is to provide a review of recent developments in lobster phylogeny and evolution, and to highlight promising directions and areas most needing research in this rapidly changing field.

4.2 Lobster phylogeny

What is a lobster? The term applies to several families of decapod crustaceans that do not form a monophyletic group (Scholtz & Richter, 1995; Schram, 2001; Dixon *et al.*, 2003) and share the general characteristic that they are the source of several major fishing industries. The organism that is called a 'lobster' also depends on the country in which one resides (Holthuis, 1991). Lobsters fall under the general category of shrimp ('ebi') in Japan, whereas clawed lobsters (homarid) and spiny lobsters (langouste) have entirely different names in France. In addition, among many other examples, spiny lobsters are often called crayfish/crawfish in the UK and South Africa rather than their clawed counterparts, which are indeed referred to as lobsters, while slipper lobsters are called 'bugs' in Australia. Common names aside, a discussion of lobster phylogeny necessarily involves a discussion of extinct or rare lobster families as well as many other crustaceans which fill in the gaps of the paraphyletic group of lobsters. Thus, we devote minimal time to addressing the taxonomy of lobsters and simply provide a quick reference (Table 4.1). We recognise that the taxonomic relationships of lobsters are still debated and attempt to address some of these uncertainties through our review of phylogenetic analyses. We begin this section by reviewing the phylogenetic relationships of lobsters to other decapod crustaceans, and then examine the relationships across the clawed lobsters, spiny lobsters and slipper lobsters.

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*These authors contributed equally and are listed in alphabetical order

Table 4.1 Taxonomy of major lobster families and geologic ranges of the families.

- Pleocyemata (suborder)
  - Astacidea (infraorder)
    - Glypheoidea
      - Glypheidae* – Triassic — Recent
      - Mecochiridae** – Triassic — Upper Cretaceous
      - Pemphicidae** – Middle Triassic
    - Nephropoidea
      - Erymidae** – Lower Triassic — Upper Cretaceous
      - Chimerastacidae** – Middle Triassic
      - Chilenophoberidae** – Middle Jurassic — Lower Cretaceous
      - **Nephropidae*** *clawed lobsters* – Lower Cretaceous — Recent
      - Thaumastochelidae – Recent
      - Enoplometopidae – Recent
    - Astacoidea
      - Cricoidoscelosidae** – Upper Jurassic
      - Cambaridae* – Upper Jurassic — Recent
      - **Astacidae*** – Lower Cretaceous — Recent
    - Parastacoidea
      - **Parastacidae*** – Oligocene — Recent
  - Palinura (infraorder) = Achelata
    - Eryonoidea
      - Tetrachelidae** – Upper Triassic
      - Eryonidae** – Upper Triassic — Lower Cretaceous
      - Coleiidae** – Upper Triassic — Lower Cretaceous
      - Polychelidae* – Middle Jurassic — Recent
    - Palinuroidea
      - Cancrinidae** – Upper Jurassic
      - **Palinuridae*** *spiny lobsters* – Upper Triassic — Recent
      - **Scyllaridae*** *slipper lobsters* – Lower Cretaceous — Recent
        - Arctidinae (subfamily)
        - Ibacinae (subfamily)
        - Scyllarinae (subfamily)
        - Theninae (subfamily)
      - Synaxidae *furry lobsters* – Recent

*indicates both fossil and extant information available. **indicates taxa represented by fossils only. **Bold** indicates substantial commercial lobster fisheries of at least one species within the family. (Adapted from Glaessner, 1969; Moore & McCormick, 1969; Holthuis, 1991; Taylor *et al.* 1999; Martin and Davis, 2001.)

4.2.1 Lobster–decapod relationships (Nephropidae, Scyllaridae and Palinuridae)

Morphological phylogenies of lobster–decapod relationships: fossil and extant taxa

Phylogenetic schemes for decapod crustaceans have traditionally been based upon the study of extant decapods. The characters used to define taxa, or clades, have been largely biased toward anatomical features that are not preserved in fossils (Fig. 4.1A, B, D), such as details of antennal architecture, structure of the maxillipeds, gill structure, and reproductive style and structures. The comparative anatomy of the carapace, abdomen, and appendages, which are far more likely to be preserved in the fossil record, either have been relegated to secondary significance or have been ignored altogether (Schweitzer & Feldmann, 2000). There is a reasonable basis for this approach, because the characters of gill architecture, reproductive structures, etc., are generally more conservative and tend to be less subject to the selective pressures of environment than are the hard, external elements of carapace, abdomen, and appendages.

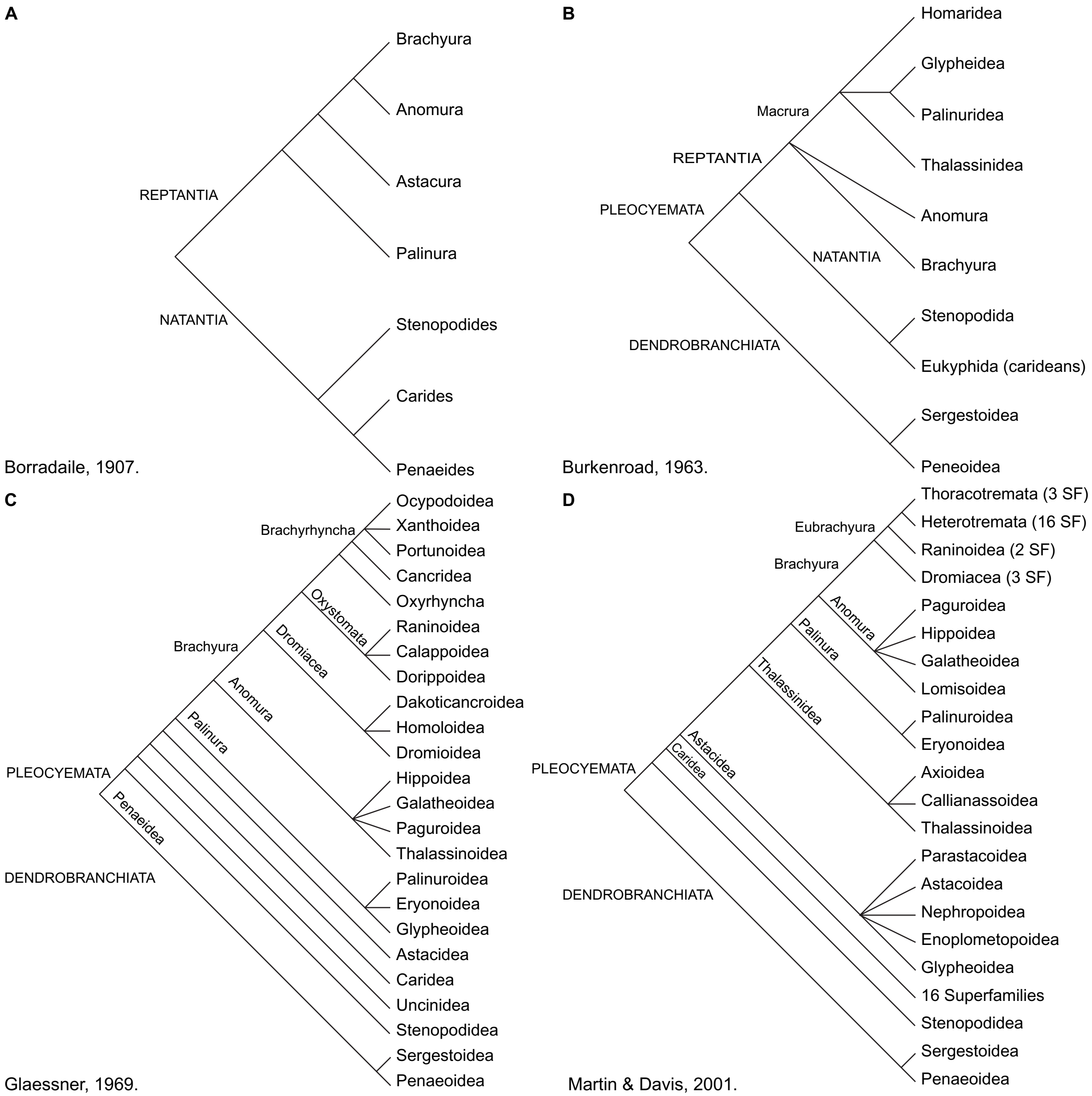


Fig. 4.1 Inferred phylogenetic relationships of lobster groups within the Decapoda, based upon classification schemes that are widely cited in the literature.

Upon development of a phylogeny based upon extant organisms, taxa recognised in the fossil record were fitted *a posteriori* into the existing phylogeny either by assigning the fossil taxon to a previously defined extant taxon or by defining a new taxon and allying it with extant taxa by comparison of the two using external morphological characters (Fig. 4.1C). The inevitable result of this approach has been that there were few bases for documentation of affinities between fossil and extant taxa and, even worse, coordinate taxa were frequently defined on totally different criteria. Thus, examination of the family and generic descriptors of the Decapoda within the *Treatise on Invertebrate Paleontology* (Glaessner, 1969) reveals manifold examples of taxonomic groups that cannot be compared to one another adequately because they are based upon totally different characters.

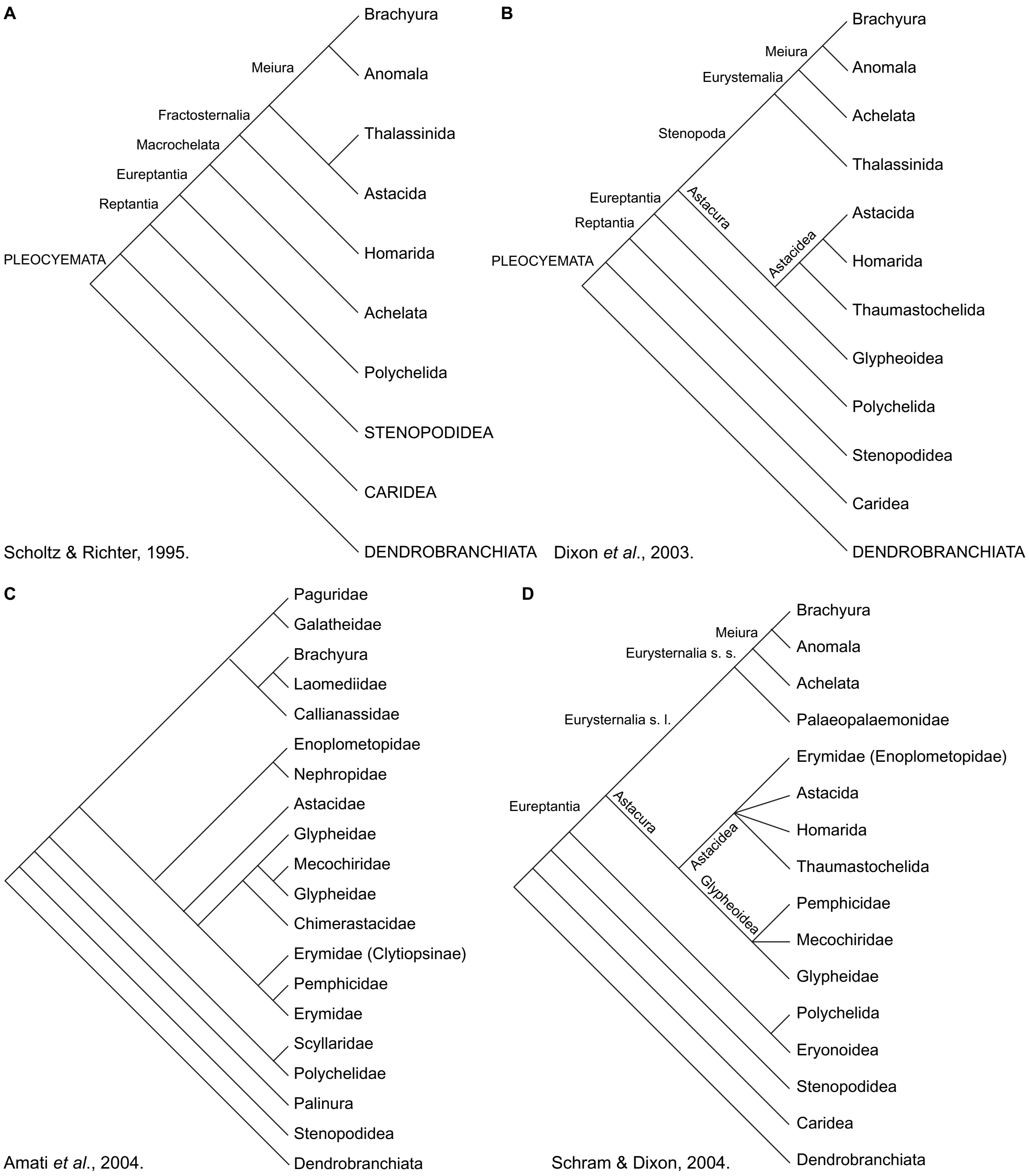
Another approach that has been taken recently is to ignore fossil evidence altogether and to consider, on an *ad hoc* basis, evidence from molecular, embryological, and reproductive studies as well as utilising morphological evidence (Martin & Davis, 2001) (Fig. 4.1D). The result is a non-phylogenetic classification that provides a useful framework for arranging organisms, but has not been tested either in whole or in part. Linking the fossil record to this classification must rely on definitions of the various taxa derived from independent sources and assignment of fossils to taxa within the scheme can only be done as described above.

Yet another approach has been to utilise morphological data matrices to develop hypotheses regarding decapod phylogeny. Several attempts, the most recent of which are discussed below, have been made to examine the entire order, or some subset of it, either utilising data solely from extant organisms or by incorporating data from the fossil record as well. This type of approach should ultimately result in a stable array of taxa upon which a classification can be based.

Scholtz and Richter (1995) applied non-computerised cladistic methods to the phylogenetic analysis of recent reptantian (crawling) Decapoda. Based on the morphology of not only typical hard parts and soft parts of taxa in adult form, but also larval morphology and scanning electron microscopy of previously unused features, they proposed that several of the traditional groupings were not demonstrable (Fig. 4.2A). They subdivided the Anomura into the Thalassinida and the Anomala, separated the Homarida from the Astacida, and placed the extant palinurids in a new clade, the Achelata, which they considered the sister group to the remainder of the reptants, the Macrochelata. One of the bases for these changes was the emphasis placed upon the presence or absence of fusion of the eighth thoracic sternite with the other sternites. They erected a new clade, the Fractosternalia, to embrace the Astacida, Thalassinida, Anomala, and Brachyura. Their initial work was subjected to a more formal, computerised, cladistic treatment by Schram (2001), and using characters similar to those employed by Scholtz and Richter, their arrangement was sustained. Subsequently, however, the Fractosternalia was determined to be a convergent feature and the marine lobsters and freshwater crayfish were united once again (Dixon *et al*., 2003).

Dixon *et al.* (2003) selected 70 external morphological characters and subjected 60 extant taxa of decapods to a cladistic analysis using the euphausid, *Euphausia superba*, as the out-group. This analysis (Fig. 4.2B) reconfirmed that the traditional groups, Palinura and Anomura, could not be sustained. In fact, the Palinuroidea were confidently placed in a new, highly-derived clade, the Achelata; the Glypheoidea were allied with the Astacidea, in the Astacura; and subsequent analyses utilising fossils as well as extant lobsters (Schram & Dixon, 2004) showed that the Eryonoidea were demonstrated to be the sister group of the Polychelida, basal to the other clades containing lobster-like forms. The significance of the separation of the eighth thoracic somite from the others was re-evaluated, because the condition is expressed in several clades. Dixon *et al.* (2003) concluded that the character was a primitive condition within the clade Eureptantia, and that fusion and subsequent loss of the character had occurred several times. The articulation of the eighth thoracic somite was interpreted as a feature facilitating burrowing. It was therefore inferred that the ancestral eureptants were burrowing forms and the more derived groups were less likely to burrow actively. The validity of the latter conclusion awaits verification.

Concomitant with this work, Amati *et al.* (2004) performed an independent cladistic analysis of 31 fossil and extant decapod genera, with primary emphasis on character selection using external features of the carapace and appendages; that is, those features that were judged to be most likely to be preserved in the fossil record. Curiously, the extinct Erymidae – widely believed to be primitive, based on morphology and stratigraphic occurrence – were resolved as the derived members of the large clade containing the crayfish. The rest of the analysis (Fig. 4.2C) produced results quite similar to those



Scholtz & Richter, 1995.

Dixon *et al*., 2003.

Amati *et al*., 2004.

Schram & Dixon, 2004.

Fig. 4.2 Phylogenetic relationships showing the position of lobster groups within the Decapoda, inferred from morphology-based cladistic analyses.

generated by Dixon *et al.* (2003), although, as discussed below, quite different characters were scored. The Palinura (= Achelata of Dixon *et al.*, 2003) were recognised as being quite separate from the remainder of the lobsters, but basal in this analysis; the glypheids were allied as a sister group to the astacideans; and the Scyllaridae were recognised as a sister group to the Polychelidae. Comparison of the two trees inspires confidence that fossil as well as extant forms can be incorporated successfully into a phylogenetic analysis because the results when fossil and extant forms are used closely parallel those derived by examination only of extant taxa.

Incorporation of fossil and extant taxa in a phylogenetic analysis has been approached in a manner different from that of Amati *et al.* (2004), with concordant results. Schram and Dixon (2004) built upon the phylogenetic hypothesis defined by Dixon *et al.* (2003) and inserted data from the fossil record to test whether or not the addition of fossil material, with the inevitable data loss resulting from the vagaries of preservation, would perturb the tree generated by using data solely from extant organisms. In order to perform the analysis, they reduced the number of characters from the original 70 to 44 by eliminating characters that were obscured by the carapace and, therefore, unlikely to be seen in the fossil record, and by adding one character that would have a high probability of being seen in fossils. They also eliminated some of the original extant forms from the analysis on the basis that they provided no new information. The result of the effort (Fig. 4.2D) was that when one or just a few fossil taxa were added to an analysis, the general framework of the tree was not disrupted and reasonable hypotheses regarding placement of the fossil taxa could be developed.

The most important observation to be drawn from these recent cladistic analyses (Scholtz & Richter, 1995; Schram, 2001; Dixon *et al.*, 2003; Amati *et al.*, 2004; Schram & Dixon, 2004) is that the general framework of the trees generated is largely the same despite the very different approaches. The palinurids emerge as a separate clade; the glypheids are allied with the astacurans, and the polychelids emerge as a relatively primitive group. Examination of some of the trees also indicates some significant, although not irresolvable, differences. For example, the palinurids occupy a basal position in the analysis of Amati *et al.* (2004), whereas they appear as highly derived forms in the other analyses. In all morphological studies, the taxon is widely separated from the other lobster groups. Another anomaly is the Palaeopalaemonidae, represented only by the Devonian genus *Palaeopalaemon*, which occupies a highly derived position in the analysis of Schram and Dixon (2004). This finding implies that nearly all of the differentiation of the major decapod clades would have occurred during or prior to the Devonian, which is not sustained by the fossil record. Thus, it is premature to conclude that the Palaeopalaemonidae occupy such a derived position on the tree and, until that group is studied further, they can reasonably be excluded from the arrangement. The position of the palinurids (= Achelata) is quite different in Amati *et al.* (2004) and Schram and Dixon (2004); however, it seems most reasonable to consider the group, including the families Scyllaridae, Synaxidae, and Palinuridae, to be derived, based upon the arguments presented by Schram and Dixon (2004). Finally, in all of the analyses, the astacidean clades emerge as among the least well resolved at this level of analysis. Amati *et al.* (2004) added a new, Middle Triassic family (Chimerastacidae) to the group and further analysis of that clade will be discussed below.

Molecular phylogenies of lobster–decapod relationships

In contrast to the plethora of morphology-based studies, molecular-based phylogenetic studies of decapod relationships are scarce, and the earliest molecular investigations of decapod lineages did not attempt to deal with relationships among the reptant groups (Kim & Abele, 1990; Abele, 1991). Several studies have used molecular data to infer relationships among the major decapod and/or reptant lineages (Crandall *et al.*, 2000; Porter *et al.*, 2005). Most recently, Ahyong and O'Meally (2004) used both molecules (16S, 18S, and 28S rRNA genes) and morphology in the first attempt at combining data types towards deciphering reptant relationships.

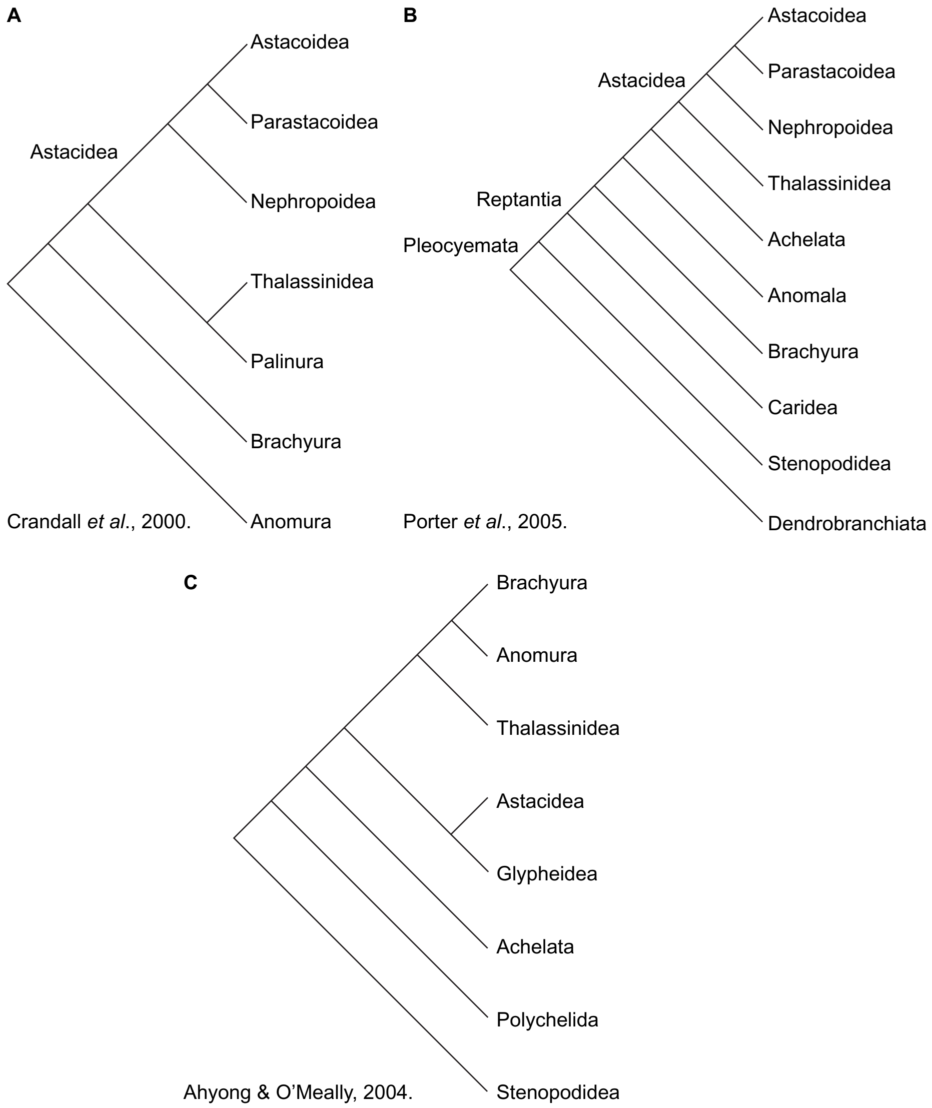


Fig. 4.3 Molecular phylogenetic hypotheses of lobster–decapod relationships from (A) Crandall *et al*., 2000; (B) Porter *et al*., 2005; and (C) Ahyong & O'Meally (2004).

At first glance, reconstructions using only molecular data produce inconsistent hypotheses of relationships within the Decapoda (Fig. 4.3); in fact, the topology of the molecular phylogeny of reptant lineages (Porter *et al*., 2005) (Fig. 4.3B) reverses presumed derived and ancestral taxa that were recovered in recent morphological (Dixon *et al*., 2003; Schram & Dixon, 2003) (Fig. 4.2B, D) and morphological/molecular combined (see Fig. 3 in Ahyong & O'Meally, 2004) phylogenies. These differences may be explained by polarisation of characters as well as the method of phylogenetic reconstruction (i.e. parsimony-based morphological and morphological/molecular combined analyses versus model of evolution-based (likelihood, Bayesian inference) molecular only analyses).

Nonetheless, a number of similarities are apparent. For example, the Nephropidae are monophyletic, nested within the Astacidea in studies using either molecules or extant and fossil morphology (Crandall *et al*., 2000; Dixon *et al*., 2003; Ahyong & O'Meally, 2004; Porter *et al*., 2005). Also similar is the molecular placement of the Palinura (= Achelata) near the Anomala and Brachyura clades, although it is a more basal clade in several molecular studies than in morphological phylogenies (Dixon *et al*., 2003).

As additional molecular data are generated towards the goal of understanding the relationships of the lobsters to the remaining decapods, sequences from representative species within the Polychelida, Enoplometopidae, Thaumastochelidae, and Glypheoidea will be particularly important. In the first study to incorporate representative sequences from these groups, Ahyong and O'Meally (2004) phylogenetically place the Polychelida as the basal reptant lineage distinct from the Achelata, the Thaumastochelidae and Enoplometopidae as affiliated with the Nephropidae, and the Glypheidae as sister to the Astacidea (Fig. 4.3). Recent advances in phylogenetic methodologies allow for the inclusion of all of the available data (fossil and extant morphology and molecules) into a single analysis (Ronquist & Huelsenbeck, 2003), and it will be particularly interesting to investigate decapod relationships in general and lobster relationships in particular, using these methods, and to further elucidate the conflicting evolutionary patterns produced by parsimony versus model-based methods of phylogeny reconstruction.

4.2.2 Clawed lobster families:(Nephropidae, Thaumastochelidae, Erymidae, Chilenophoberidae, Chimaerastacidae and Glypheidae)

Among marine biologists, the name 'clawed lobsters' usually indicates the family Nephropidae, including the familiar Maine lobster, *Homarus americanus*, and its clawed relatives with grossly similar anatomy (118 species arrayed in 18 genera; 67 species in 7 genera with a fossil record; listed in Tshudy, 2003). Biologists might also point out the much lesser-known family Thaumastochelidae, which consists of deep-sea lobsters with long, delicate claws (four recent species arrayed in 2 genera). Paleontologists, of course, recognise these clawed lobster families (which have fossil records traceable well into the Cretaceous Period) but also three additional families of clawed lobsters: Erymidae (Lower Triassic – Upper Cretaceous), Chilenophoberidae (Middle Jurassic – Lower Cretaceous; four genera) and Chimaerastacidae (one genus, Middle Triassic) (Table 4.1). The glypheids (Triassic – Recent) were traditionally placed in the Infraorder Palinura (spiny lobsters) but more recently, have been allied with the clawed lobsters (e.g. Forest & de Saint Laurent, 1989).

Morphological phylogenies of fossil and extant clawed lobsters

Biologists and, especially, paleontologists have long hypothesised about the evolutionary relationships of clawed lobsters. Beginning in the late 1800s, workers began proposing evolutionary lineages connecting extinct and extant genera. Fritsch and Kafka (1887), for example, erected the Cretaceous *Paraclytia* and concluded that it was morphologically intermediate between the extinct *Hoploparia* and extant *Nephrops* (the latter including what is now *Metanephrops*). Since then, biologists and paleontologists too numerous to list here have contributed. Williams (1995) provided a good review of the non-cladistic work that specialists such as Mertin (1941), Glaessner (1960, 1969), Secretan (1960a, b, 1964), Förster (1966, 1967), Holthuis (1974) and others have published. Much of the morphology-based cladistic work that we do today is rooted in these traditional systematic morphologic studies. The pattern of carapace grooves, more than any other feature, has been the basis for non-cladistic interpretations of clawed lobster phylogeny, and it remains important in cladistic analyses.

Mertin (1941) was the first to broadly interpret the phylogeny of the clawed lobsters. He arranged all then-known nephropid genera into three subfamilies, and considered one of them, the Phoberinae, (see Tshudy, 1993 for discussion), to be derived from the Erymidae and to be the probable stem group of the Nephropidae. Mertin hypothesised that the Phoberinae is the ancestral sister clade to *Hoploparia* which, in turn, is a sister clade to other nephropids, including *Homarus* and *Oncopareia–Thaumastocheles*. Secretan (1964) and Glaessner (1969) agreed (as we still do today) with Mertin that the fossil clawed lobster, *Hoploparia*, was probably ancestral to some or most extant nephropid genera. Glaessner (1969) maintained, with minor modifications, Mertin's three-fold (subfamily) division of the Nephropidae and expanded the phylogeny to include more erymids and also the freshwater crayfish. Holthuis (1974), in a monograph on recent, western Atlantic clawed lobsters, elevated nephropids to superfamily level (as Nephropoidea), divided the superfamily into two families, Nephropidae and Thaumastochelidae, and divided the Nephropidae into three subfamilies.

Freshwater crayfish (Superfamilies Astacoidea and Parastacoidea, Table 4.1) have been considered to be a sister group to the extant Nephropidae in particular (Crandall *et al.*, 2000; Dixon *et al.*, 2003; Porter *et al.*, 2005) or a part of a larger sister group (to the Nephropidae) including the Thalassinida, Anomala and Brachyura (Scholtz & Richter, 1995). Rode and Babcock (2003) noted, however, that extinct lobster groups could not be considered in the molecular analysis of Crandall *et al.* (2000) and were not considered in the morphologic analysis of Scholtz and Richter (1995) (nor were they in Dixon *et al.*, 2003). Rode and Babcock (2003), who incorporated fossil taxa in a morphologic analysis, determined that the sister taxon to the crayfish is the extinct, marine Chilenophoberidae. Tshudy and Babcock (1997) considered the Chilenophoberidae to be an evolutionary-intermediate between the extinct Erymidae and extant Nephropidae, as supported by both cladistic analysis and non-cladistic judgments on morphology, especially carapace groove pattern, and also by stratigraphic occurrence. This is contradicted by the cladistic results of Rode and Babcock (2003), which showed the Chilenophoberidae to be more derived than the Nephropidae. Rode and Babcock (2003) did not address this difference in their paper. Nonetheless, they recognise the Chilenophoberidae as a monophyletic group, as a family, and as an apparent sister group to the freshwater crayfish.

Amati *et al.* (2004) examined the relationships between crayfish (freshwater) and clawed lobsters (marine) (Fig. 4.2C). In determining the phylogenetic position of *Chimaerastacus pacifluvialis*, a new fossil genus and species of Triassic decapod bearing small claws on the first pereiopods, they found that the Nephropidae, as represented by the extant *Homarus*, extinct *Hoploparia*, and extant *Nephrops*, form a sister group with *Enoplometopus*. These, in turn, form a sister group to a much larger clade that includes, among others, the freshwater crayfish (Family Astacidae), Glypheidae, and Erymidae. The Triassic form in question resolves within this larger clade as a sister group to the Glypheioidea. Amati *et al.* (2004) erected the Family Chimaerastacidae to accommodate this Triassic form.

Dixon *et al.* (2003) found the Homarida (Bate, 1888) as traditionally defined (i.e. typical-looking nephropid lobsters plus *Thaumastocheles*) to be paraphyletic, in that *Thaumastocheles* is resolved as a sister group to other 'clawed lobsters' (including *Enoplometopus*) plus the freshwater crayfish (Astacidae). Their cladograms (Fig. 4.2B) show *Homarus* and *Nephropsis* to be more closely related to freshwater crayfish than to *Thaumastocheles.* The reunited 'Astacidea' clade (Homarida + Thaumastochelida + Astacida) of Dixon *et al.* (2003) is supported by two synapomorphies: (1) a deep transverse groove on the carapace (an unambiguous synapomorphy) and (2) a diaeresis on the exopods of the uropods (an ambiguous synapomorphy also occurring in many other taxa).

Schram and Dixon's (2004) best assessments about clawed lobster relationships (Fig. 4.2D) suggest that the Erymida (possibly including *Enoplometopus*), Astacida, Homarida, and Thaumastochelida should be united under the Astacidea, and that the Glypheoidea is a sister group to the Astacidea. The Astacidea and Glypheoidea are sister groups united as the Astacura. The alliance between *Eryma* and *Enoplometopus* was based, in part, on a controversial feature, the median carapace plate that is well documented in the fossil *Eryma* and newly recognised in the recent *Enoplometopus*. There are other characters, which support the alliance of *Eryma* and *Enoplometopus*, and none that argue against it. Schram and Dixon (2004) state that the fossil Erymidae and recent Enoplometopidae 'are at least within the same superfamily clade, if not within the same family'.

The Glypheidae were traditionally known only from the fossil record and placed in the Infraorder Palinura (Glaessner, 1969), but Forest and de Saint Laurent (1989), based on the discovery of the 'living fossil' *Neoglyphea*, moved them to the Infraorder Astacidea. Dixon *et al.* (2003) found the Glypheidae to plot out differently in their ordered and unordered cladograms. In their unordered cladogram, *Neoglyphea* is resolved as a sister group to the Astacidea, but in their ordered cladogram, *Neoglyphea* is resolved as a sister group to the Palinura. Favouring the unordered analysis, Dixon *et al.* (2003) noted that the combined Glypheoidea and Astacidea (as 'Astacura') are united by three synapomorphies: (1) telson spines (except on *Thaumastocheles*), (2) presence of a long process emanating from the ischium of the first pereiopod that articulates with the coxa of the first pereiopod, and (3) a horizontal position of the first pereiopod.

The Nephropidae and Chilenophoberidae were resolved by Tshudy (1993) – the first study to apply cladistic methods to clawed lobster phylogeny by examining the relationships of all genera within the Nephropidae. This work was later slightly modified and published by Tshudy and Babcock (1997) as the only formal, taxonomically comprehensive analysis of nephropid phylogeny. They analysed a 21 taxon (plus one outgroup genus, *Eryma*) · 41 character data matrix. Thirty-one of the 41 characters were cladistically informative; the others were invariant or were unique to individual taxa and were therefore not phylogenetically informative. Two main clades, the new family Chilenophoberidae and revised Nephropidae, were resolved in their cladogram (Fig. 4.4). The Chilenophoberidae embraces four genera: *Palaeophoberus*, *Chilenophoberus*, *Pseudastacus* from the Jurassic and *Tillocheles* from the Lower Cretaceous. The revised Nephropidae includes 18 genera, 13 extant and 5 known only from the fossil record. Cladistic results were consistent with Tshudy's non-cladistic interpretation that erymid lobsters gave rise to chilenophoberids, which, in turn, gave rise to nephropids. The non-cladistic interpretation was based on morphology, particularly of the carapace groove pattern, but was corroborated by stratigraphic occurrence. The Erymidae, overall, pre-date the Chilenophoberidae which in turn pre-date the Nephropidae.

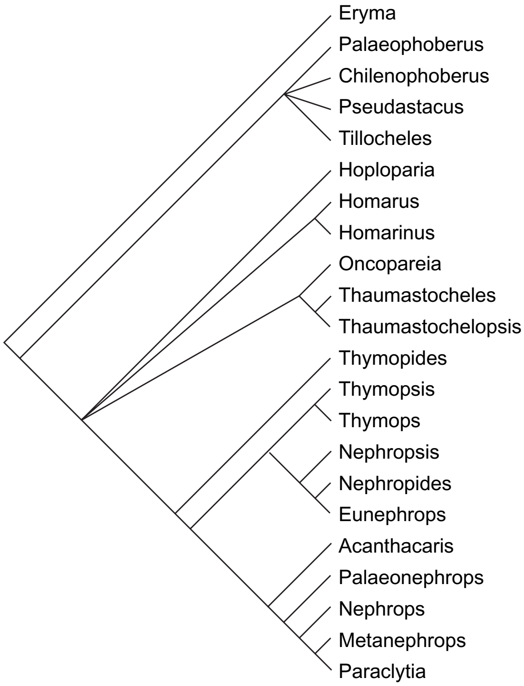


Fig. 4.4 Morphological phylogeny of the clawed lobsters based on a majority-rule consensus of the 2000 most parsimonious trees determined using heuristic search (Tshudy & Babcock, 1997).

Among the chilenophoberids and nephropids, homoplasy (convergence) is rampant in aspects of groove pattern, ornamentation, and the appendages. Nonetheless, multiple (12) unambiguous synapomorphies define clades; some of these are given below. The presence/absence of a fusiform dorsomedian plate, as well as variation in carapace groove pattern, provide phylogenetically informative characters for resolving the erymid, chilenophoberid and nephropid clades. The Chilenophoberidae plus Nephropidae clade is defined by the derived absence of the fusiform dorsomedian plate. The Chilenophoberidae are united by a single unambiguous synapomorphy – a postcervical groove that begins near (not on) the dorsome-

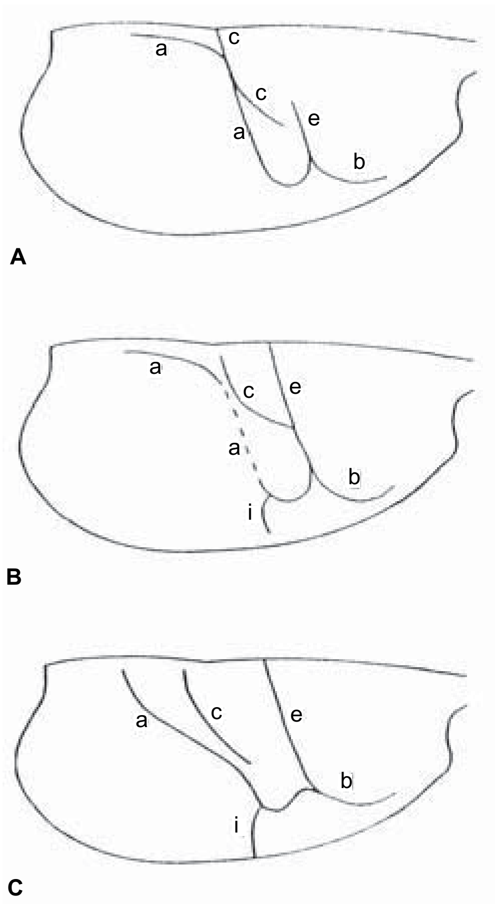


Fig. 4.5 Generalised carapace groove patterns of clawed lobster families. (A) Nephropidae; (B) Chilenophoberidae; (C) Erymidae. Abbreviations: a, branchiocardiac groove; b, antennal groove; c, postcervical groove; e, cervical groove; i, inferior groove (adapted from Tshudy & Babcock, 1997).

dian and extends anteroventrally to the cervical groove. The Nephropidae are likewise united by a single unambiguous synapomophy – a cervical groove that extends ventrally from the level of the orbit to the antennal groove (the cervical groove extends from the dorsal midline in the Erymidae and Chilenophoberidae).

Based on its similarities with the erymid pattern, the long-held view (Glaessner, 1932, 1969; Chong and Förster, 1976) that the chilenophoberid groove pattern was primitive was supported by Tshudy and Babcock (1997) (Fig. 4.5). Their results suggest that evolution of the Chilenophoberidae from the Erymidae involved the following modifications of the erymid groove pattern: (1) extension of the postcervical groove anteriorly to meet the cervical groove (but without the postcervical groove being joined by the branchiocardiac groove), and (2) change in the orientation of the branchiocardiac groove dorsally, from transverse to longitudinal. In contrast, the evolution of the Nephropidae from a chilenophoberid involved: (1) shortening of the upper end of the cervical groove, so that it terminates well below the dorsomedian, (2) extension of the upper end of the postcervical groove to meet the dorsomedian, and (3) loss of the posteriorly-situated inferior groove. One nephropid genus, the recent *Thymops*, exhibits a posteriorly-situated inferior groove but, as predicted intuitively, the cladogram indicates that this is a homoplastic feature.

The thaumastochelid and nephropid lobsters seem to be well established as monophyletic groups. The only question in recent years, has been whether or not the thaumastochelid group deserves family-level status. Holthuis (1974), in his still widely-used, traditional systematic works on extant nephropid and thaumastochelid genera, erected the Thaumastochelidae to embrace (at the time) two species of *Thaumastocheles*. Tshudy and Babcock (1997) found that the *Oncopareia–Thaumastocheles–Thaumastochelopsis* clade, despite some very distinctive synapomorphies (especially in claw form), was unresolved from *Hoploparia*, *Homarus*, and *Homarinus* and, therefore, the Thaumastochelidae were considered paraphyletic and moved into the Nephropidae (Fig. 4.4). However, more recent morphology-based studies on higher decapod groups find the Thaumastochelidae resolved from the Nephropidae (Dixon *et al.*, 2003; Ahyong & O'Meally, 2004; Schram & Dixon, 2004) (Figs. 4.2, 4.3).

The thaumastochelid clade has a fossil record traceable back to the Upper Cretaceous. Mertin (1941) and Tshudy (1993) interpreted the fossil *Oncopareia* as a morphological and evolutionary intermediate link between fossil *Hoploparia* and recent *Thaumastocheles*, mainly based on groove pattern. In cladistic analysis (Tshudy and Babcock, 1997), the clade formed by *Oncopareia*–

Thaumastocheles–Thaumastochelopsis is united by two distinctive, unambiguous synapomorphies: (1) abdominal pleura that are quadrate and wider than long and (2) a major claw consisting of a short, bulbous palm and very elongate fingers equipped with acicular denticles. *Thaumastocheles/Thaumastochelopsis* are further united by: (1) a telson that is quadrate and wider than long, and (2) a chelate fifth pereiopod.

Holthuis' (1974) division of the Nephropidae into three subfamilies is not supported by the cladogram in Tshudy and Babcock (1997), which indicates that two of the subfamilies, Nephropinae and Thymopinae, are paraphyletic. The third of Holthuis' three subfamilies, the Neophoberinae, is monospecific. However, Tshudy and Babcock's cladistic analysis supports Holthuis' conclusion that *Thymops*, *Thymopsis*, *Nephropsis*, and *Nephropides* are closely related (Fig. 4.4). Tshudy and Sorhannus (2000a) described a new genus and species of fossil (Upper Cretaceous) lobster, *Jagtia kunradensis*, and found that *Jagtia* is part of a clade that includes *Thymops* and *Thymopsis*, making it the first fossil form to be closely allied with these deep-water genera. The three genera are synapomorphic for the presence of a parabranchial groove. *Thymops* and *Thymopsis* are synapomorphic for the absence of an exopod on maxilliped two; this character is indeterminate on the fossil *Jagtia*.

Relationships among the *Hoploparia*, *Homarus* and *Homarinus* species have also been examined. Based on the fossil record, *Hoploparia* was probably ancestral to not only *Oncopareia*, but also *Homarus* and most or all other nephropid genera (e.g., Mertin, 1941; Secretan, 1964; Glaessner, 1969; Tshudy, 1993), although it was recently suggested that *Hoploparia* is an artificial, 'wastebasket' genus (Tshudy & Sorhannus, 2003). The evolution of *Homarus* from *Hoploparia* was characterised by a general reduction in groove pattern and ornamentation (Glaessner, 1969; Tshudy, 1993). The fossil records of both *Hoploparia* and *Homarus* begin in the Lower Cretaceous, indicating that divergence occurred early in nephropid history.

Within the Nephropinae, the informally defined 'nephrops' clade (*Palaeonephrops*, *Nephrops*, *Metanephrops* and *Paraclytia*) is united by three synapomorphies, including: (1) an intermediate carina with a spine at the anterior end, (2) an inferior groove that curves under the mandibular insertion (not *Palaeonephrops*), and (3) a cervical spine (not *Paraclytia*). *Metanephrops* and *Paraclytia* are further united by two synapomorphies, a long and prominent supraorbital carina and a branchial carina (Tshudy & Babcock, 1997).

At present, a collaborative effort is underway to expand the morphologic analysis of Tshudy and Babcock (1997) and also to test that morphology-based tree with molecular evidence.

Molecular phylogenies of clawed lobsters

Until very recently, little nucleotide sequencing had been done on the clawed lobsters as a whole. Only the commercially important genera, *Homarus* and to a lesser extent, *Nephrops*, had received much attention. The National Institute of Health's genetic sequence database, GenBank, shows, at the time of this writing, nucleotide sequences for just five clawed lobster genera (*Homarus*, *Homarinus*, *Metanephrops*, *Nephrops*, *Nephropsis*) (Table 4.2). This includes at least partial 12S or 16S mitochondrial rRNA sequences for these five genera. Both the 12S and 16S mt rRNA gene seem to be useful in phylogenetic work at the generic level (see discussion about useful molecular genes in Sections 4.3, 4.5).

Kornfield *et al.* (1995) used morphologic and molecular evidence (16S mt rRNA gene sequences) in distinguishing *Homarinus* n. gen. (new genus) from *Homarus*. Tam and Kornfield (1998) used partial sequences of the 16S mt rRNA gene (450 nucleotides; 350 used in the cladistic analysis) to study the phylogenetic relationships of five nephropid genera, including *Homarus*, *Homarinus*, *Metanephrops*, *Nephrops*, and *Nephropsis*. The hermit crab, *Pagurus pollicaris*, was used as an outgroup. Tam and Kornfield's (1998) molecular results are at odds with the traditional, morphologic perspective, and indicate that what seem to be homologous similarities may instead be convergent features. In their cladogram, *Homarus* (two species) and *Nephrops* form a clade that is a sister group to *Homarinus*, despite the morphological similarity between *Homarus* and *Homarinus*. It is

Table 4.2 A list of the published nuclear genes isolated from lobsters available as potential targets for screening genetic variation. Sequences obtained from GenBank (http://www.ncbi.nlm.nih.gov/). The species each gene has been isolated from are indicated as: Nn = *Nephrops norvegicus*; Ha = *Homarus americanus*; Hg = *Homarus gammarus*; Je = *Jasus edwardsii*; Pe = *Palinurus elephas (vulgaris)*; Pa = *Panulirus argus*; Pi = *Panulirus interruptus*; Ps = *Panulirus stimpsoni*.

Gene	GenBank Accession No.	Sequence length (bp)	Reference
1. Alpha actin$^{\mathrm{Ha}}$	AF399872	1386	Koenders *et al*. (2002)
2. Arginine kinase$^{\mathrm{Hg}}$	X68703	1403	Dumas & Camonis (1993)
3. CoA reductase$^{\mathrm{Ha}}$	AY292877	3125	Li *et al*. (2004)
4. CUB-serine protease$^{\mathrm{Pa}}$	AF357226	1801	Levine *et al*. (2001)
5. Cysteine proteinases$^{\mathrm{Nn,Ha}}$	X80989	1093	Le Boulay & Van Wormhoudt (1995)
	X63569	1147	Laycock *et al*. (1989)
6. Cytochrome P450$^{\mathrm{Ha,Pa}}$	AF065892	1581	Snyder (1998)
	U44826	1601	James *et al*. (1993)
7. Dopamine beta hydroxylase$^{\mathrm{Ha}}$	AY098944	1242	Hollins *et al*. (2003)
8. Eyestalk peptide$^{\mathrm{Je}}$	AF112986	568	Khoo & Sin (2001)
9. Fast muscle P75-like$^{\mathrm{Ha}}$	AY302591	766	Medler & Mykles (2003)
10. Frequenin$^{\mathrm{Pi}}$	AF260780	586	Jeromin *et al*. (1999)
11. G-protein alpha subunits$^{\mathrm{Ha}}$	AF010292	1466	Xu *et al*. (1997)
	U89139	1451	McClintock *et al*. (1997)
	S47614	1307	McClintock *et al*. (1992)
	AF201328	1700	Munger *et al*. (2000)
12. GABA receptor beta subunit$^{\mathrm{Ha}}$	AY098945	2645	Hollins & McClintock (2000)
13. Gelsolin-related protein$^{\mathrm{Ha}}$	Z29534	3221	Luck *et al*. (1995)
14. Glutamine synthetase$^{\mathrm{Pa}}$	M96798	2045	Trapido-Rosenthal *et al*. (1993)
15. Gonad inhibiting hormone$^{\mathrm{Nn,Ha}}$	AF163771	1359	Edomi *et al*. (2002)
	X87192	2165	de Kleijn *et al*. (1994)
16. Haemocyanins$^{\mathrm{Ha,Pe}}$	AJ272095	2266	Kusche & Burmester (2001)
	AJ516004	2298	Kusche *et al*. (2003)
	AJ344361	2286	Kusche *et al*. (2003)
	AJ132141	2497	Burmester (1999)
17. Hyperglycemic hormone$^{\mathrm{Nn,Ha}}$	AY285782	1874	Mettulio *et al*. (2004)
	X54842	218	Tensen *et al*. (1991)
	S76846	1183	de Kleijn *et al*. (1995)
18. Inositol 1,4,5-triphosphate receptor$^{\mathrm{Pa}}$	AF055079	8647	Munger *et al*. (2000)
19. Ionotropic glutamate receptor$^{\mathrm{Ha}}$	AY098942	3514	Hollins *et al*. (2003)
20. Metallothionein$^{\mathrm{Ha,Je}}$	AJ401298	824	Valls *et al*. (2001)
	AF091369	960	Khoo & Sin (1999)
21. Muscle-specific calpain$^{\mathrm{Ha}}$	AY124009	1977	(Yu & Mykles (2003)
22. Myosin heavy chain$^{\mathrm{Ha,Hg}}$	AY232598	1795	Medler *et al*. (2004)
	AF515799	2645	Magnay *et al*. (2003)
	AF474969	483	Holmes *et al*. (2002)
	U03091	1529	Cotton & Mykles (1993)
23. Phospholipids phospholipase C$^{\mathrm{Ha}}$	AF128539	3351	Xu & McClintock (1999)
24. Potassium channel proteins$^{\mathrm{Pi}}$	AF375605	1827	Baro *et al*. (2001)
	AF017137	301	Kim *et al*. (1998)
	L33868	1072	Baro *et al*. (1994)
	L49135	1641	Baro *et al*. (1996)
25. Preprotachyinkin$^{\mathrm{Pi}}$	AB113379	1997	Yasuda-Kamatani & Yasuda (2004)
26. Serotonin receptors$^{\mathrm{Pi}}$	AY550910	2187	Clark *et al*. (2004)
	AY528822	1308	Sosa *et al*. (2004)
27. Superoxide dismutase$^{\mathrm{Pe}}$	X64063	432	Smith & Doolittle (1992)
28. Tropomyosin$^{\mathrm{Ha,Ps}}$	AF034953	2223	Mykles *et al*. (1998)
	AF030063	822	Leung *et al*. (1998)
29. Tubulins$^{\mathrm{Ha}}$	AF405439	2247	Hollins *et al*. (2003)
	U41810	1543	Demers *et al*. (1996)
30. Ubiquitin$^{\mathrm{Ha}}$	L22645	360	Shean and Mykles (1995)
31. Vacuolar H (+)-ATPase$^{\mathrm{Nn}}$	S40059	918	Finbow *et al*. (1992)

also interesting that, in their molecular cladogram, *Metanephrops* is resolved as being distant from *Nephrops*, whereas these genera seem morphologically similar both by inspection and by cladistic analysis (Tshudy & Babcock, 1997). Both *Nephrops* and *Metanephrops* exhibit ridges on the carapace, abdomen, and claws that are absent on *Homarus*.

At present, at least two laboratories are sequencing nephropid and other 'clawed lobster' genera (12S, 16S, and COI genes) with the purpose of producing a molecular phylogeny for the nephropids. These molecular phylogenies ultimately will be compared to new improved morphologic phylogenies.

4.2.3 Palinuridae and Synaxidae

Morphological phylogenies of extant palinurid and synaxid lobsters

The spiny lobsters, Palinuridae, are defined by elongated, spiny antennae, prominent horns over their eyes, and absence of a rostrum and presence of a small claw on the fifth pereiopod of females. The latter two characteristics are shared with the Scyllaridae (slipper lobsters). The features typically used to describe the Synaxidae (coral or furry lobsters) are not found exclusively in these taxa, and include the presence of a rostrum, lack of chelae on the first pereiopods, and extensive hairy covering of the carapace. The extant palinurid family contains approximately 47 species and eight genera, and the Synaxidae contains one genus and two species. The placement of *Palibythus magnificus* in the Palinuridae will be discussed below.

The phylogenetic relationships within the Palinuridae and Synaxidae have been examined using adult and larval morphology. George and Main (1967) were among the first to propose an evolutionary tree of palinurid lobsters based on adult morphology and using non-cladistic methodology. Their analysis was based primarily on characters associated with a sound-producing mechanism, supraorbital processes (horns over the eyes), eye position and pleopodal endopods. In line with previous work (Parker, 1883), George and Main (1967) divided palinurid genera into Silentes and Stridentes groupings based on the absence/presence of a sound-producing structure located on the antennular plate in some fossil and extant taxa. Specifically, they proposed that the non-sound-producing genera (Silentes), *Jasus* and *Projasus*, form a sister clade to sound-producing (stridulating) genera (Stridentes), *Linuparus*, *Puerulus*, *Palinustus*, *Justitia*, *Palinurus*, and *Panulirus*.

The separations of the Palinuridae and Synaxidae, as well as the Stridentes and Silentes, were called into question by the intriguing discovery of a stridulating lobster, *Palibythus magnificus*, which exhibits a fully-developed stridulation apparatus that very closely resembles those of the Stridentes in the Palinuridae (Davie, 1990). However, *Palibythus* otherwise appears highly similar to the non-stridulating *Palinurellus* species belonging to the Synaxidae family. Given that the stridulation apparatus is nearly identical with that of members of the Stridentes in the Palinuridae, it seems unlikely that the stridulation mechanism of *Palibythus* is convergent with the Stridentes and instead is more likely to be a shared-derived character with the Stridentes (Davie, 1990; S. Patek, personal observation). Thus, Davie (1990) and Patek and Oakley (2003) suggested that both *Palinurellus* and *Palibythus* should be placed within the family Palinuridae.

Two morphology-based studies since Davie's (1990) discovery have tackled the evolutionary relationships among and across palinurids and synaxids. Baisre (1994) used larval and adult characters from 50 species belonging to the Palinuroidea to construct a phenogram using non-cladistic cluster analyses. Baisre found support for two separate clades within the palinurids following the same Silentes and Stridentes groupings proposed by George and Main (1967). The synaxid genus, *Palinurellus*, emerged both within and adjacent to the palinurid clade, depending on the data and taxa used. Baisre (1994) did not have access to *Palibythus* and thus did not include it in his analysis.

In the only study to date that used cladistic methods to analyse palinurid morphological systematics, Patek and Oakley (2003) constructed both morphological and molecular phylogenies of the Palinuridae and Synaxidae and included *Palibythus magnificus* in the analyses (Fig. 4.6). They found support for placement of *Palibythus magnifi-*

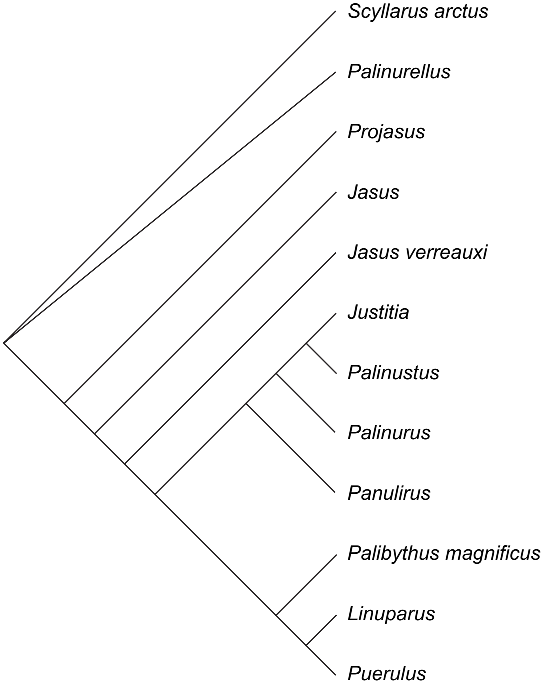


Fig. 4.6 Genus-level morphological phylogeny of the Palinuridae based on Patek & Oakley's (2003) species-level phylogeny. *Scyllarus arctus* is the outgroup. *Jasus (Sagmariasus) verreauxi* is the only species that does not fall within a monophyletic genus.

cus within the Palinuridae, with some support for its placement as a sister taxon to *Linuparus* and *Puerulus* species. *Palinurellus* species fell outside the palinurid clade, thus providing some support for a synaxid clade. As in the morphological studies described above, external adult morphology did not clearly define the generic relationships within the Palinuridae, although the Stridentes and Silentes groupings were supported and *Palibythus* was located in the Stridentes.

The substantial morphological variation of the stridulation apparatus provides phylogenetically informative characters for resolving palinurid relationships (Patek, 2002; Patek & Oakley, 2003) as do several other interesting morphological characters. Antennular morphology varies noticeably across palinurid genera, with potential implications for understanding the evolution of olfaction in marine environments (Goldman & Patek, 2002). Also related to sensory systems, fine scale variation was noted at the level of the chemo-mechanosensory hooded sensilla morphology across lobsters (Cate & Derby, 2002). McWilliam (1995) identified phylogenetically informative traits when comparing phyllosoma and puerulus larvae across *Panulirus* spp. (Palinuridae) and found four subgroups of *Panulirus* spp., consistent with adult morphology and habitat previously identified by George and Main (1967).

Reproductive traits also have provided interesting insights into evolutionary relationships. For example, Berry and Heydorn (1970) examined vas deferens morphology and spermatophoric masses across five palinurid genera; three types of spermatophores were identified as well as interesting morphological differences in the vas deferens. Tudge *et al.* (1998) found potentially informative characters in the ultrastructure of spermatozoa. In addition, George (2005a) analysed the intriguing variation in adult reproductive structures across the genus *Panulirus*.

Morphological phylogenies of fossil palinurid and synaxid lobsters

To our knowledge, there have been no phylogenetic studies on palinurids that have been based upon fossil taxa or that have incorporated fossil taxa into studies of extant forms. The fossil record of the palinurids is quite robust and the possibility exists to develop data sets that could be used in cladistic analyses. The record of the Palinuridae extends from the Upper Triassic to the Recent (Glaessner, 1969; Garassino *et al.*, 1996) and the Scyllaridae are known from the Lower Cretaceous to the Recent (Glaessner, 1969) (Table 4.1). The Synaxidae have no known fossil record. Fossils are not uniformly distributed throughout these groups. For example, an excellent record of eryonids is available from specimens from the Solnhofen Limestone, a Middle Jurassic lithographic limestone in Germany (Fig. 4.7); however, most other species within the superfamily Eryonoidea are far rarer. Fossil records of palinurid crustacean phyllosoma larvae also have been found in the Solnhofen limestone (Polz, 1984, 1986, 1987, 1995, 1996). Among the Palinuroidea, the palinurid genus *Linuparus* is

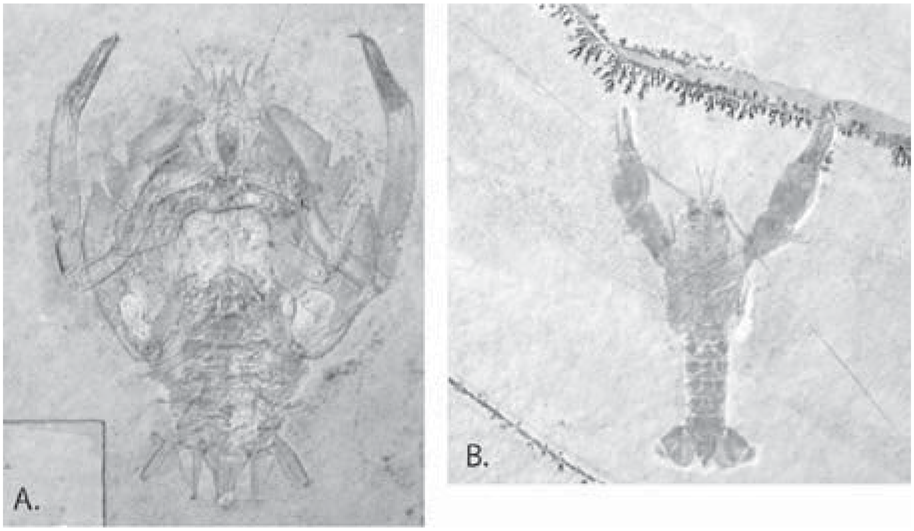


Fig. 4.7 Fossil eryonid lobsters from the Solnhofen. (A) *Eryma modestiformis* Schlotheim, 1822. Dorsal view of specimen from Upper Jurassic Solnhofen Plattenkalk, Eichstatt, Germany. Carapace length, 22.9 mm. Inv.-Nr. 1995.4, Paläontologisches Museum, Museum fur Naturkunde Berlin. (B) *Eryon propinquus* (Schlotheim). Ventral view of specimen from Upper Jurassic Solnhofen Plattenkalk, Solnhofen, Germany. Carapace length, 60.0 mm. CM 34359, Department of Invertebrate Fossils, Carnegie Museum.

extremely well represented from the Upper Cretaceous to the Recent and would form the single most important genus upon which phylogenetic analyses could be based (Glaessner, 1969; Feldmann & Bearlin, 1988). Any analysis of the palinurids must embrace the eryonids as well. Examination of Figure 4.2 shows that the relationships between the Eryonidae, Polychelidae, and Palinuridae are vastly different in the various analyses.

Selection of characters for a phylogenetic analysis must include elements that are preservable in the fossil record; however, this condition can be met easily. Because the Eryonoidea are generally characterised by a broad, flattened cephalothorax, they tend to be preserved with the upper surface parallel to bedding. Thus, preparations of both the dorsal and ventral surfaces of fossils can be readily accomplished. Definition of the members of the Eryonoidea is based upon outline and nature of the margin of the cephalothorax, presence or absence of axial keels, degree of development of the cervical and other carapace grooves, morphology of the abdomen and presence or absence of a diaeresis on the uropods.

In a similar fashion, the palinurids tend to be preserved with the dorsal surface parallel to the bedding planes, owing to the broadened sternum and the broad splay of their pereiopods. Palinuroidea are distinguished on the basis of the shape of the carapace, presence or absence of a rostrum, form of the antennae, development of keels on the cephalothorax, ornamentation of the abdomen and nature of the telson. These features can be readily observed on many palinuroid fossils. With regard to antennal structure, as noted above, George and Main (1967) based a phylogenetic study of the extant Palinuridae on the presence or absence of stridulation devices. Stridulation devices have been found in fossil *Linuparus* from New Zealand (Feldmann & Bearlin, 1998) and preliminary examination of other fossil palinurids suggests that the structure could be present on other specimens, if properly prepared.

Molecular phylogenies of palinurid and synaxid lobsters

Molecular data have been used to examine phylogenetic relationships both within and between palinurid genera. Generic relationships between the palinurids and synaxids were tested using nuclear (18S and 28S) and mitochondrial (16S) genes and analysed using parsimony, maximum likelihood, and Bayesian methods (Patek & Oakley, 2003). These analyses yielded several well-supported clades within the palinurids, including the monophyletic *Jasus* spp. + *Projasus* sp. However, *Jasus verreauxi* consistently fell outside the clade formed by the other *Jasus* spp. (also observed in Ovenden *et al.* (1997) using 16S and cytochrome oxidase subunit I (COI)). The observed genetic and morphologic divergence of *Jasus verreauxi* from the other *Jasus* spp., has led to a widely adopted suggestion that this taxon should be given a separate generic or subgeneric designation, *Sagmariasus verreauxi* (for discussion, see Chapter 10 in this volume).

In the 18S and 16S datasets, there was some support for placing *Palinurellus* at the base of the *Jasus* + *Projasus* clade, and, therefore, within the Palinuridae. The three tree topologies suggest a possible loss of the stridulation apparatus within the Palinuridae; however, statistical tests did not favour a loss or single gain of the stridulation apparatus, given the uncertainties of the tree topology (S. Patek, unpublished data; Patek & Oakley, 2003). Extremely long branch-lengths of several *Panulirus* species in the 18S dataset probably yielded problematic tree arrangements, while the 16S and 28S datasets supported a monophyletic *Panulirus* genus. *Palibythus magnificus* fell within the Palinuridae in all datasets. Overall, the tree topologies were not consistent across these three genes, and trees based on a combination of the three datasets did not provide additional resolution (Patek & Oakley, 2003). In order to resolve the genus-level relationships within the Palinuridae and Synaxidae, alternative genes need to be explored and tested for their ability to resolve relationships at the multiple timescales represented in the Palinuridae.

Several studies have examined the relationships within palinurid genera. For example, species relationships within *Jasus* were analysed using mitochondrial DNA (Brasher *et al.*, 1992a, b) with one cladistic study based on 16S ribosomal RNA (rRNA) and cytochrome oxidase subunit I (COI) (Ovenden *et al.*, 1997). They found that *J. caveorum* was more closely related to *J. tristani* and *J. paulensis* than to *J. frontalis* (Fig. 4.8), even though both *J. frontalis* and *J. caveorum* are the only *Jasus* species found in the eastern South Pacific. Three studies have examined *Panulirus* species relationships using 16S, 18S and, COI (Ptacek *et al.*, 2001; Patek & Oakley, 2003; Ravago & Juinio-Meñez, 2002). Ptacek *et al.* (2001) conducted the most intensive analysis of *Panulirus* evolution and found two monophyletic groupings within the genus that were robust across both 16S and COI datasets (Fig. 4.9). Interestingly, these two groups correspond with the morphology-based groups I + II and III + IV described in George and Main (1967) and McWilliam (1995), although none of the individual four groups is monophyletic. Sequence divergences were higher in group I + II than in group III + IV, which suggested that group I + II radiated earlier than group III + IV. Within Group I + II, another monophyletic clade persisted across all datasets, consisting of *P. cygnus* + *P. longipes* + *P. marginatus* + *P. pascuensis*, all of which are found in the Indo-West Pacific.

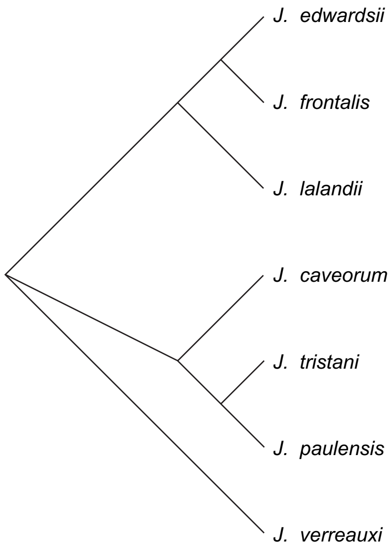


Fig. 4.8 Molecular phylogeny of species within the genus *Jasus* based on COI and 16S genes (Ovenden *et al.*, 1997). As discussed in the text, *Jasus verreauxi* is now widely accepted as a separate genus or subgenus, *Sagmariasus*.

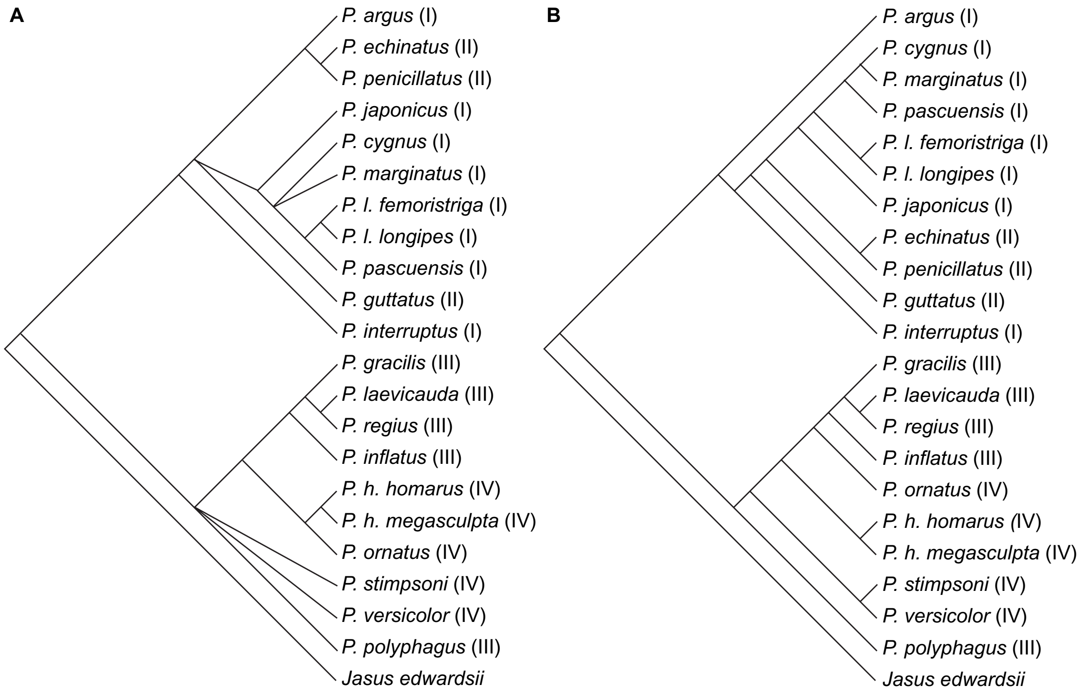


Fig. 4.9 Molecular phylogenies, based on combined 16S and COI genes, of species in the genus *Panulirus* (Ptacek *et al.*, 2001). Roman numerals indicate the four groupings proposed by George & Main (1967). *Jasus edwarsii* is the outgroup. (A) Results of a maximum parsimony analysis in the form of a strict consensus tree. (B) Results of a maximum likelihood analysis.

Molecular analyses have also been used for identifying and differentiating *Panulirus* species, including a study of the population genetic structure across *Panulirus argus* populations (Silberman *et al.*, 1994), as well as analyses of subspecies designations in several *Panulirus* species, (e.g., Sarver *et al.*, 1998; Ravago & Juinio-Meñez, 2002). A region of 28S rDNA has been suggested for use in molecular identifications of *Panulirus* larvae, which otherwise have been difficult to identify to the species level (Silberman & Walsh, 1992). At larger phylogenetic scales, cDNA sequences of *Palinurus elephas* haemocyanin (Kusche *et al.*, 2003) and the complete mitochondrial genome for *Panulirus japonicus* (Yamauchi *et al.*, 2002) have been used in phylogenetic studies of decapod relationships.

4.2.4 Scyllaridae

The scyllarids are defined by their short, broad and flattened antennal flagella. Many other aspects of their morphology are similar to the palinurid lobsters. The family consists of four extant subfamilies (Arctidinae, Ibacinae, Scyllarinae, Theninae) (Holthuis, 1991). The Scyllarinae recently was revised from one genus, *Scyllarus*, to include 13 genera (Holthuis, 2002). Remarkably, we were unable to find any morphological or molecular cladistic analyses of scyllarid species relationships. Baisre (1994) conducted the most extensive study to date on the evolutionary relationships of scyllarids and constructed a phenogram based on both larval and adult characters. Among the seven measured genera, *Ibacus* and *Evibacus* were most closely related, as were *Scyllarides* and *Arctides*. Because these trees were constructed using non-cladistic methods, it is difficult to assess the robustness of these relationships. Nonetheless, the combination of adult and larval characters provides important insights into the scyllarid tree. Several molecular phylogenetic studies have included sequence data from single scyllarid species, as outgroups or decapod representatives (e.g. Tam &

Kornfield, 1998; Ptacek *et al.*, 2001; Tudge & Cunningham, 2002; Patek & Oakley, 2003), so it may soon be possible to construct a molecular phylogeny of this family.

Relatively few fossil scyllarids have been described and although some are extremely well preserved, to our knowledge no attempts at phylogenetic analysis of the family have been attempted. As with the other palinuroids, scyllarids tend to be preserved with the dorsal surface parallel to the bedding planes so that they are ideally oriented to yield detailed information on the carapace, abdomen, and antennae.

4.3 Divergence time estimates

Estimates of divergence times in lobsters have been made using vastly different types of data. The fossil record is always the baseline for investigating the evolutionary history of a group. However, large gaps exist in the fossil record of most decapod lineages, with many groups having little or no representation. Therefore, particularly for estimates of more recent divergences, many researchers have used biogeography/palaeoceanography to constrain evolutionary events within lobster groups. Genetic data, (allozymes, restriction fragment length polymorphisms (RFLPs), sequences), have also been employed by calculating levels of divergence and using molecular clock techniques (Chan & Chu, 1996; Ovenden *et al.*, 1997; Ravago & Juinio-Meñez, 2002; Kusche *et al.*, 2003). However, most genetic data fail to meet the assumptions of clock-like evolution and rates are often taken from distantly related groups. More recently, multiple types of data have been combined into single analyses resulting in more robust estimates. Morphology-based phylogenetic studies incorporating both extant and fossil taxa are helping to elucidate the evolutionary sequence of events in lobster clades (Tshudy & Babcock, 1997; Rode & Babcock, 2003; Tshudy & Sorhannus, 2003; Amati *et al.*, 2004) and the newest divergence time estimation methods are able to combine multi-locus sequence data with multiple calibration dates based on either fossils, biogeography or geologic events, while relaxing the assumption of a molecular clock (Thorne & Kishino, 2002; Yang & Yoder, 2003). In the following section we will discuss the current hypotheses regarding nephropoid and palinuroid divergence times, highlighting the similarities and/or differences resulting from the various methods used. Consequently, the need for further studies investigating divergence times in lobsters will be apparent.

Most divergence time estimates in nephropoid lobsters are based on the fossil record; very little work has been done using either biogeography or molecular data. Fossils suggest that the Nephropoidea date from the Lower Triassic (e.g. the Erymidae), with the chilenophoberid lineage emerging in the Middle Jurassic and the nephropid lineage emerging in the Early Cretaceous (Tshudy & Babcock, 1997). Many of the major extant lineages appear to have diverged early in nephropid history from *Hoploparia*, with most fossil-based schemes placing the divergence from *Hoploparia* of the *Homarus* lineage, the *Oncopareia–Thaumastocheles–Thaumastochelopsis* lineage, and the remaining nephropids in the Cretaceous (Mertin, 1941; Secretan, 1964; Glaessner, 1969; Tshudy & Babcock, 1997). Using genetic data, Stamatis *et al.* (2004) proposed post-Pleistocene divergences for Atlantic and Mediterranean populations of *Nephrops norvegicus*. Similarly, based on allozyme data, Williams (1995) speculated that *Homarus gammarus* and *H. americanus* were isolated during the Pleistocene. Unfortunately, no other molecular studies could be found in which nephropoid divergence times were investigated.

Within palinuroids, the most commonly investigated genera with respect to divergence time estimates are *Panulirus* and *Jasus*. In general, *Jasus* is considered the older lineage, based on the fossil of *J. flemingi* from the early Miocene (Glaessner, 1960). Furthermore, George and Main (1967) hypothesised that *Jasus* split from an ancestral pemphicid stock during the Cretaceous based on their morphological assessment of lobster evolution and fossil data. Based on palaeoceanography, Pollock (1990) proposed the existence of an ancestral *Jasus* as early as the Paleocene (~60 mya) and George (1997) the emergence of the subgenus *Jasus* before the late Eocene (37 mya). A large gap exists, however, between estimates of the emergence of *Jasus* and speciation events within the genus. Based on calculations from mitochondrial RFLP data, Brasher *et al.* (1992a) proposed that *Jasus verreauxi* split from *J. edwardsii*, *J. lalandii*, and *J. tristani* (the 'lalandii' group) ~8 mya, and that the 'lalandii' species split 2–4 mya. However, these times were calculated using a primate mtDNA rate of evolution, and are not concordant with either fossil or biogeographical evidence (Brasher *et al.*, 1992a). In even 'younger' taxa, Ovenden *et al.* (1997) used sequence data to estimate the divergence of populations within *J. edwardsii* and between *J. tristani* and *J. paulensis* as ~0.5 mya. This estimate supports Pollock's (1990) hypothesis that the *J. tristani* and *J. paulensis* divergence occurred relatively recently (<700 000 years ago).

In the more recently evolved *Panulirus* genus, investigations of the evolution of the haemocyanin gene estimate the split between *Palinurus elephas* and *Panulirus interruptus* at ~100 mya (Kusche *et al.*, 2003). Although this estimate is considerably larger than divergence times estimated based on the fossil record (George and Main, 1967), Kusche *et al.* (2003) hypothesise that the divergence of these genera could be related to the formation of the Atlantic Ocean in the Cretaceous. Within the genus, George and Main (1967) erected four species groups and the divergence times among these four main species groups have been debated in the literature (George & Main, 1967; Baisre & Ruiz de Quevedo, 1982; Pollock, 1992; Pollock, 1993; McWilliam, 1995; Sekiguchi, 1995; George, 1997). However, it is generally agreed that the subtropical groups I + II represent an earlier radiation than the tropical groups III + IV based on adult morphology (George & Main, 1967), larva and puerulus morphology (McWilliam, 1995), biogeography (Pollock, 1992; George, 1997), and allozyme and sequence data (Chan & Chu, 1996; Ptacek *et al.*, 2001). Pollock (1992) proposed that *Panulirus* radiation occurred after the late Pliocene, with speciation from a common Pacific ancestral type related to Pleistocene events. However, other studies point to a much earlier origin and radiation within the *Panulirus*. As a result of the formation of new habitats after collisions of the Indian/Australian plate with the Eurasian plate, George (1997) argued for speciation of group I + II as early as the late Miocene and for group IV during the early Pliocene. This hypothesis is based on biogeography for estimates of *P. versicolor* emergence in combination with allozyme-based estimates for seven Philippine and Japanese species (J. Macaranas, personal communication as cited in George, 1997), resulting in divergence times estimated as: *P. japonicus* and *P. l.* 'shirahige' (group I, 8.9 mya), *P. l. longipes* and *P. penicillatus* (group I and II respectively, 8.5 mya), *P. ornatus* and *P. h. homarus* (group IV, 3.4 mya), *P. versicolor* (2 mya). Additional allozyme studies support this hypothesis, with an estimated divergence time of 4.6 mya between *P. l. longipes*, *P. femoristriga*, and *P. japonicus* (Chan & Chu, 1996). At shallower taxonomic levels, Ravago and Juinio-Meñez (2002) used sequence data to estimate that *P. longipes longipes* and *P. longipes bispinosus* diverged less than 1 mya.

Most lobster divergence time estimations have focused on speciation events within genera, and not on the deeper-level splits of the original palinuroid and nephropoid lineages. Schram (2001) used a morphology-based phylogeny in conjunction with the fossil record to provide a stratigraphic context for the evolution of the Decapoda. Although there are large areas of uncertainty ('ghost lineages') due to gaps in the fossil record, this provides a hypothesis for emergence of both the nephropoid and palinuroid lineages from decapod stock in the Devonian. Furthermore, this method suggests a divergence between *Palinurus* and *Scyllarus* in the Jurassic and a late Jurassic/early Cretaceous radiation of the nephropid genera. Methods incorporating multiple fossils as calibration points for estimating divergence times from sequence data produce similar times, with the *Panulirus*/*Scyllarus* divergence occurring in the Jurassic (201 ± 34 mya) and the radiation of the extant nephropid genera near the Jurassic/Cretaceous boundary (140 ± 35 mya) (Porter *et al.*, 2005). However, the molecular methods differ slightly from previously discussed hypotheses in estimating the *Homarus*/*Nephrops* divergence in the late Paleocene (55 ± 22 mya) and in placing the emergence of *Jasus edwardsii* in the Triassic (239 ± 35 mya). The molecular estimates of palinuroid and nephropoid emergence (341 ± 25 mya and 278 ± 24 mya, respectively) are also later than hypothesised by Schram (2001).

4.4 Evolutionary biogeography

Estimates of divergence times provide the information necessary to reconstruct lobster diversification in the context of tectonic plate movements, ocean currents and depth changes over the past 250 million years. Many of the important questions about palinurid lobster evolutionary biogeography were laid out in George and Main (1967), which was published before tectonic plate movements were incorporated into studies of evolutionary biogeography. Since the publication of that paper, several studies have addressed the evolutionary biogeography of lobsters, focusing primarily on palinurid lobsters.

Since the first appearances of lobsters in the fossil record (Fig. 4.10), there have been dramatic changes in continental positions, currents, and sea levels (Newman, 1991; Windley, 1995; Wright & Rothery, 1998). Sea levels dropped to low levels in the late Permian and Triassic (~210–230 mya) when there is evidence of considerable diversification of lobster taxa and the formation of most of the major lobster lineages (Fig. 4.10). Sea levels gradually rose to a peak in the Cretaceous (~80 mya), and, on average, have been decreasing ever since. In the Jurassic, (~150–210 mya), the earth was dominated by Pangea, the large land mass formed by Gondwana and Eurasia, surrounded by the Panthalassa Ocean and Tethys Sea. By the Cretaceous (100 mya), Gondwana had started to break apart, forming new ocean pathways from the Tethys Sea into regions that eventually formed the Atlantic Ocean. It is in this time period that fossil evidence suggests substantial radiation of palinurid lobsters and the origin of the nephropid lineage. In the Eocene (50 mya), the Tethys Sea was diminished in size, the Indian subcontinent had moved close to Eurasia, and the Australian plate had moved further from Antarctica to allow the formation of the Antarctic circumpolar current. Another important factor was the gradual cooling of ocean waters at higher latitudes, starting in the Tertiary (65 mya) until about 30 mya. At this time, the tropics began to warm to higher temperatures, while at the same time, the deep, cold Antarctic circumpolar current was established. These phenomena have been proposed to explain the amphitropical distributions and southern hemisphere endemism of many marine taxa (Newman, 1991). The opening and widening of Drake's Passage in the late Oligocene also probably contributed to the splitting of *Jasus lalandii* subgroups into *J. edwarsii* (George, 1997).

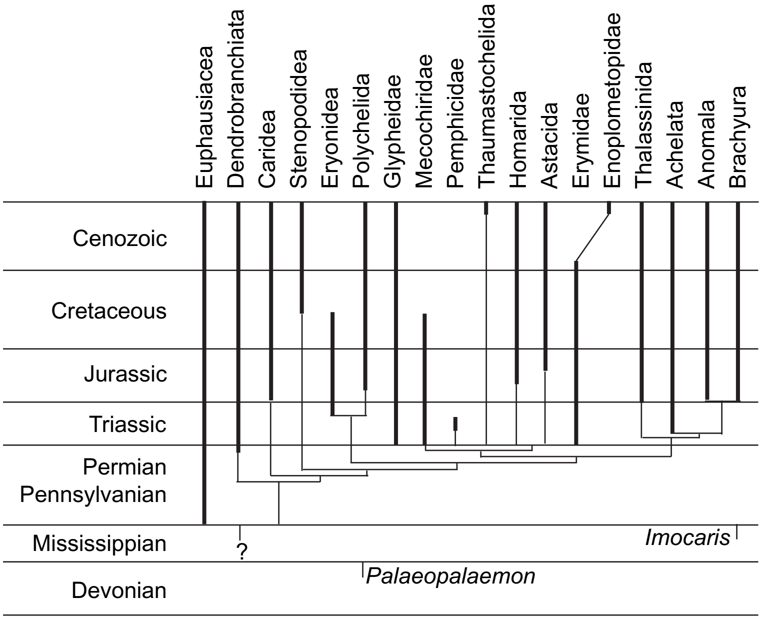


Fig. 4.10 Phylogenetic scheme of Schram & Dixon (2004) scaled to reflect the geological occurrence of clades. The geological ranges indicated are taken from Glaessner (1969), Garassino *et al.* (1996), and Schram & Dixon (2004). The inferred times of origins of clades has been scaled without considering the implications of the occurrences of *Palaeopalaemon* and *Imocaris*. Broad lines denote confirmed ranges; narrow vertical lines denote ghost ranges.

The wide geographic range of spiny lobster genera is impressive and holds some potentially interesting evolutionary patterns. While the speciose genus *Panulirus* is found in the Indo-Pacific and Atlantic, the much smaller genus *Palinurus* is restricted to south-east Africa and the north-eastern Atlantic (Chapters 11, 12). Newman (1991) suggested that the distribution of *Palinurus* may be due to reliction, based on his observations of similar patterns in some gastropod molluscs. Another genus with few extant species, *Linuparus*, only is found at the boundary of the Indian and Pacific Oceans, with one species located off south-eastern Africa (Holthuis, 1991). Both genera are thought to be relicts from previous widespread distributions, especially given the pervasive fossil remains of *Linuparus*, which are found abundantly in both hemispheres from mid to high latitudes during the Upper Cretaceous to Eocene – in marked contrast to today's limited distribution (Newman, 1991).

As discussed in Section 4.3, the evolutionary significance of present-day distributions of *Jasus* and *Panulirus* species has received considerable attention. Species of *Jasus* are found only in the Southern Hemisphere, off the southern coasts of South America, Africa, Australia and several islands in that region (Chapter 10). Origins of the genus *Jasus* are still uncertain, with estimates ranging from 2 mya (Brasher *et al.*, 1992a) to 60 mya (Pollock, 1990). One extant species, *Jasus* (*Sagmariasus*) *verreauxi*, is morphologically similar to the fossil *J.* (*Sagmariasus*) *flemingi*, which occupied the warmer waters of either the Oligocene or Miocene, before the warm currents moved northward and probably left isolated *J.* (*S.*) *flemingi* populations in the north Tasman Sea (Pollock, 1990, 1995; George, 1997). Based on similar distributions in other marine taxa, Newman (1991) proposed that *Jasus* species are relicts of an amphitropical distribution, or perhaps a Tethys Sea distribution. Another hypothesis suggests that speciation could have been caused by local changes in ocean circulation patterns, due to changes in sea level and formation/collapse of sea ridges, islands and seamounts (Pollock, 1990). Phylogenetic studies show a substantial genetic divergence between *J.* (*S.*) *verreauxi* and other species of *Jasus*; some correspondence exists between biogeography and phylogeny, although *J. caveorum* is not more closely related to its geographically closest neighbours and *J. edwarsii* shows surprisingly little population variation across its 4600 km distribution (Brasher *et al.*, 1992a, b; Ovenden *et al.*, 1992; Ovenden *et al.*, 1997).

The more widespread and speciose genus, *Panulirus*, offers an interesting study of evolutionary biogeography. *Panulirus* species are found in tropical and subtropical areas around the world, with their geographical distribution to some extent reflected in their phylogeny. As discussed in Section 4.3, molecular evidence supports a divergence of *Panulirus* into two groups, both from an original Indo-Pacific ancestor (Fig. 4.9). Ptacek *et al.* (2001) suggested that Group I + II species radiated from an '*argus*-like ancestor', with separate *P. argus* and *P. interruptus* lineages splitting within this group. In the late Miocene, westward-flowing ocean currents probably promoted the radiation of Group I species found in the Indo-West Pacific (Ptacek *et al.*, 2001). Allopatric speciation due to vicariance events in the Indo-West Pacific, such as weather changes and current directions due to the uplifts of the Himalayas and New Guinea ranges, respectively, are cited as likely factors in the speciation of Group III + IV species (George & Main, 1967; George, 1997; Ptacek *et al.*, 2001).

In contrast to nephropid lobsters, palinurids have exceptionally long-lived planktonic larvae (up to 12 months), which finally metamorphose to a postlarva (puerulus), which can control the time and location of settlement. This long planktonic larval phase has drawn attention, not only because of the potentially interesting implications for nephropid and palinurid evolutionary biogeography, but also because of palinurid lobsters' ability to choose their settlement sites while limited to vertical migrations between ocean currents (Cobb, 1997). This combination of factors may result in little genetic variation of populations, or a lot, depending on the relative role of settlement choice and currents. Large and small-scale ocean currents, larval swimming behaviour during diurnal migrations, and population genetic architecture all have the potential to play a role in short-term and long-term patterns of lobster biogeography (Katz *et al.*, 1994; Hill *et al.*, 1996; Griffin *et al.*, 2001;

Perez-Enriquez *et al.*, 2001; Yeung & Lee, 2002; George, 2005b).

The numerous factors influencing speciation are difficult to resolve at these tremendous timescales, yet biologists are making rapid progress in developing analytical tools to quantitatively test correlations between divergences and physical factors (Palumbi, 1994). With accurate divergence estimates based on morphologic and genetic data, we will ultimately be able to identify correlations between historical oceanic events and periods of major lobster diversification. An understanding of the effects of historical changes in water temperature and circulation patterns may also yield important insights into the effects of present day shifts in oceanic environments on lobster populations.

4.5 Conclusions and future directions

4.5.1 Strategies for future phylogenies

Morphological challenges and strategies

As Schram and Dixon (2004) explained well: 'Systematists working with the decapods of course would like a single, stable, useful, widely accepted, (ideally true) classification that can be used for extinct and extant forms alike – the 'holy grail' of carcinology. The only way to achieve this would be to include both extinct and extant taxa in the process of building the tree and resultant classification'. Previous workers also have urged this perspective. For example, Donoghue *et al.* (1989) showed that intermediate character combinations of extinct groups might alter tree topology and provide further resolution when incorporated into cladistic analysis. Recent phylogenetic works examining clawed lobsters have included both fossil and recent taxa (Williams, 1995; Tshudy & Babcock, 1997; Tshudy & Sorhannus, 2000a, b; Rode & Babcock, 2003; Amati *et al.*, 2004; Schram & Dixon, 2004) and more studies are in progress. In fact, synthetic studies on clawed lobster phylogeny that include both extant and extinct taxa, and which also use both morphologic and molecular (on extant taxa) evidence, are now underway.

The key challenge in constructing morphological data matrices is to determine synapomorphies for both fossil and extant taxa. Decapod systematists are challenged by the rampant homoplasy present across all taxonomic levels as well as the difficulties in defining synapomorphies that often are context dependent (determined by the particular taxa, characters, codings, cladistic procedures) and thus affect the resulting tree topologies. This has become apparent through phylogenetic analyses at both the high and low taxonomic levels. Tshudy and Sorhannus (2000b) found that, among the decapod crustaceans, long slender chelipeds armed with pectinate (comblike) denticles have evolved independently in at least four lineages in three families in three decapod infraorders: once in the Polychelidae, once in the Ctenochelidae, and twice in the Nephropidae. Tshudy and Babcock (1997) found that among the Nephropidae, convergence at the generic level is widespread in aspects of groove pattern, ornamentation, and the appendages.

Ultimately, we have not come close to exhausting morphology as evidence. Future studies should not only consider expanding morphological data sets (e.g. larval morphology and scanning electron micrographs), but also focus on choosing characters that permit incorporation of fossils into the phylogenetic studies. Given that at least some lobsters tend to fossilise with their carapace parallel to the bedding plane, considerable information is available about exoskeletal grooves, spines and ornamentation, as well as antennal and claw morphology. With a rich foundation of lobster research, we are challenged to use new cladistic tools and new morphological characters to tackle these longstanding and interesting questions about lobster and decapod phylogeny.

Molecular challenges and strategies

With the advent of molecular techniques, our ability to generate sequence data to address wide-ranging questions, including phylogeny, conservation and biogeography, has increased at an astounding rate. However, molecular data are not yet widely used in studies of lobster phylogeny and evolution, and are particularly rare within the

Nephropoidea. In lobster studies, molecular data have been used mostly to address questions of species relationships (Brasher *et al*., 1992a; Ovenden *et al*., 1997; Tam & Kornfield, 1998; Ptacek *et al*., 2001; Ravago & Juinio-Meñez, 2002; Patek & Oakley, 2003), although at least a few studies have focused on identifying microsatellite markers useful for population genetics (Streiff *et al*., 2001; Jones *et al*., 2003; Diniz *et al*., 2004). Currently, the most commonly used molecular data for palinurid and nephropid species-level studies include the mitochondrial 16S and COI genes, and the nuclear 18S and 28S rDNA. An investigation of the available sequence data for these markers from the National Center for Biotechnology Information (NCBI) GenBank sequence database (http://www.ncbi.nlm.nih.gov/) illustrates the paucity of molecular phylogenetic studies in lobsters. However, even given the low numbers of representative sequences in some groups, estimates of sequence divergence at different taxonomic levels provides a preliminary guide to the genetic variation present in each marker (Table 4.3).

Although not yet common, there are a number of resources available which will make the use of molecular data in lobster research more tenable. With the availability of the complete mitochondrial genome of *Panulirus japonicus* (Yamauchi *et al*.,

Table 4.3 Estimates of nucleotide diversity (pi) (Tajima, 1983) were estimated for the four most common nephropoid and palinuroid molecular markers. Sequences were downloaded from the GenBank sequence database (http://www.ncbi.nlm.nih.gov/) and aligned in ClustalX (Thompson *et al.*, 1997). Palinuroid 28S estimates were based on gene fragments sequenced in Patek & Oakley (2003) and COI estimates were calculated from two different gene fragments, indicated by the amino acid numbering of the complete sequence of *Panulirus japonicus*. — indicates that not enough sequences were present for estimation.

	Sequence Divergence (%) (No. families/No. genera/No. species/No. sequences)				
Taxa	16S	COI		18S	28S
		AA21–241	AA246–430		
Palinuroidea	19.1 (3/12/38/47)	—	18.4 (2/2/9/19)	4.7 (3/13/24/25)	9.8 (2/13/20/20)
Palinuridae	18.6 (2/8/34/42)	20.0 (1/2/26/32)	—	5.1 (2/8/19/20)	10.6 (1/10/17/17)
Panulirus	16.3 (1/1/21/25)	19.5 (1/1/19/22)	17.7 (1/1/8/18)	8.3 (1/1/7/7)	7.3 (1/1/3/3)
P. longipes	—	—	4.2 (1/1/1/6)	—	—
Jasus	4.3 (1/1/7/11)	8.4 (1/1/7/10)	—	1.0 (1/1/5/5)	0.7 (1/1/3/3)
J. edwardsii	0.55 (1/1/1/5)	0.9 (1/1/1/4)	—	—	—
Scyllaridae	12.8 (1/2/2/3)	—	—	1.4 (1/3/3/4)	3.8 (1/2/2/2)
Nephropoidea	9.2 (1/4/7/14)	—	—	0.8 (1/4/5/7)	8.6 (1/4/5/6)
Homarus	3.1 (1/1/3/8)	—	—	0.1 (1/1/2/3)	1.5 (1/1/2/3)
H. gammarus	1.3 (1/1/1/4)	—	—	—	—

2002) and at least one study devoted to identifying conserved primer sites for amplifying entire nephropoid mitochondrial genomes (Katsares *et al.*, 2003), the investigation of genetic variation at additional mitochondrial markers in lobsters is guaranteed. Comparing these data with the five other complete decapod mitochondrial genomes will help identify additional conserved areas to target for primer design not only for lobsters, but also for decapods in general.

While mitochondrial genes are useful for studies of genetic variation, population subdivision, and systematics, these genes are inherited as a single (linked) locus and in general have faster rates of evolution relative to the nuclear genome. By sampling the nuclear genome, one can increase the number of independent loci examined and investigate the power of slower evolving genes for resolving relationships at deeper levels. The histone H3 and U2 snRNA nuclear loci have already been used to investigate decapod and arthropod phylogeny (Colgan *et al.*, 1998; Giribet *et al.*, 2001; Porter *et al.*, 2005), and may be informative for studies of lobster evolution. Furthermore, in a search of the NCBI GenBank sequence database, a large number of nuclear genes characterised from lobster species were found (Table 4.2). Although the genetic variation of most of these genes has yet to be assessed for information content relative to systematic studies, these loci represent an unexploited resource. Particularly promising for use in lobster evolutionary studies are the haemocyanin genes, which have been the subject of a number of studies in both nephropoid and palinurid lobsters (Burmester, 1999; Kusche & Burmester, 2001; Kusche *et al.*, 2003), and the myosin heavy chain nuclear gene, which has been investigated as a marker for population and phylogenetic studies in the decapod shrimp *Alpheus lottini*, using primers partially designed from the *H. americanus* sequence (Williams *et al.*, 2002).

To a large extent, molecular phylogenetics in lobsters is a wide-open field of study, with relatively few molecular studies having been conducted on the global diversity of species. Much work is waiting to be done using both well-characterised and novel genetic markers. As sequence data accumulate for multiple genetic markers from larger numbers of palinurid and nephropid species, additional phylogenetic resolution will be gained across different levels of taxonomic classification. Studies of the congruence between molecular and morphological data can be assessed towards the goal of developing new classifications that better reflect the evolutionary history of all of the available data.

4.5.2 Conclusions

Perhaps the most important conclusion of this review is that lobster phylogeny has been studied unevenly and with noticeably different approaches depending on the particular group. While the Scyllaridae remain virtually unstudied, many clawed lobsters (Nephropidae) have been subjects of an impressive array of phylogenetic analyses based on fossil and extant morphological characters. In contrast, while the molecular phylogeny of clawed lobsters has not been studied extensively, the molecular phylogeny of the Palinuridae has been tackled to a reasonable extent. Although there is a solid fossil record of palinurids and eryonids, fossil evidence has yet to be incorporated into any palinurid phylogeny. Even with molecular, fossil and extant morphological data, the lobster–decapod relationships continue to require extensive study.

While many aspects of lobster phylogeny and evolution require more research, we can draw some solid conclusions based on the above literature review. In studies of lobster–decapod relationships, palinurids are consistently a monophyletic clade, glypheids are most closely related to astacurans and polychelids are a relatively ancient group. The nephropids are also monophyletic and are nested within the Astacidea. In studies of clawed lobsters, marine lobsters (e.g. nephropids) are closely related to freshwater crayfish, although the details of these relationships and the extinct Chilenophoberidae remain unsettled. Within the Palinuridae, it appears that *Palibythus* should be included in this family, and that *Panulirus* species form two monophyletic groups within the genus. The geologic record of lobsters has been examined by applying cladistic methodology, which has resulted in the recognition of several new families of fossil lobsters as well as in the extension of geologic ranges for some of the groups.

The combination of molecular, fossil and extant morphological data is essential, not only for resolving phylogenies, but also for understanding the divergence times and evolutionary biogeography of lobsters. Tables 4.2 and 4.3 provide important clues for which genes to target in future studies, and the extent of nucleotide diversity in particular genes. As the results of ongoing molecular analyses are accumulated, we will soon be able to pinpoint divergence times at short and long timescales, which ultimately can be used to resolve the finer-scale divergence times and the paleo-oceanographic factors underlying the intriguing fossil-based timescale presented in Figure 4.10. Not only are these new initiatives important for understanding lobster evolution, they are also important for understanding global distribution and the effects of historical environmental changes. By examining the phylogeny and biogeography of lobsters over evolutionary time, we may be better able to understand the impact of ongoing environmental changes on the future of lobsters.

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Chapter 5

Pathogens, Parasites and Other Symbionts

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> ‘The lobster is no exception to the rule that all living things are subject to disease, and that each appears to have its own group of afflictions.’ – J.E. Stewart, 1980

5.1 Introduction

Given that lobsters support valuable fisheries around the world, it is surprising what little is known of their diseases and parasites. This is in part due to the fact that the industries are largely based on fishing for, and not the culture of, these marine delicacies. Nonetheless, fishers handle millions of lobsters per year and overt signs of disease are rarely reported. However, with the advent of increased fishing pressures and the development of live-holding facilities, and an emphasis on short- and long-term aquaculture, the situation has changed, as disease is no longer a curiosity but a threat to profitability. For example, recent morbidities and mortalities of clawed lobsters in the New England states (Tall *et al.*, 2003; Mullen *et al.*, 2004), continuing outbreaks of a protozoan in Scotland’s Norway lobster industry (Field *et al.*, 1992; Stentiford *et al.*, 2001a) and the emergence of a virus in the Caribbean spiny lobster (Shields & Behringer, 2004) highlight both the overt and more subtle damage caused by diseases.

We present a review of the microbial diseases, parasites, and symbionts of the clawed lobsters, *Homarus* spp. and *Nephrops norvegicus*, and the spiny lobsters, *Panulirus* spp., *Palinurus* spp., and *Jasus* spp. Previous reviews have provided synopses of the disease agents occurring in lobsters in general (Evans & Brock, 1994; Evans *et al.*, 2000) or an excellent synthesis of specific agents such as gaffkaemia in *Homarus americanus* (Stewart, 1980). In addition, several overviews and syntheses of crustacean diseases are available (Couch, 1983; Johnson, 1983; Overstreet, 1983; Brock & Lightner, 1990; Meyers, 1990; Sindermann, 1990), and these are important references for the study of diseases in Crustacea, not only for their guide to the earlier literature, but for their syntheses of the ecological aspects of infectious diseases.

The first reported diseases of the American lobster, *Homarus americanus*, were shell disease (Hess, 1937) and gaffkaemia (Snieszko & Taylor, 1947), but a few symbionts (e.g. *Histriobdella homari*, *Nicothoe astaci*, *Stichocotyle nephropis*) had been described prior to 1900. Nephropid (clawed) lobsters are now known to be infected by a specialised, yet disparate fauna comprised of bacteria, fungi, protozoans, helminths, and even other crustaceans (Table 5.1). Fewer symbionts are known from palinurid lobsters, but they include a virus, bacteria, protozoans and helminths. Disease is a normal part of any host population. Environmental stressors (stimuli that cause stress) such as pollution, high temperature, overcrowding, pesticides and even fishing stress have long been known to push the host–parasite equation toward the fulmination of an epidemic outbreak. We do not, however, review the effects of environmental or anthropogenic stressors on lobsters; for that, see Mercaldo-Allen & Kuropat (1994).

Recently, several pathogens (*Panulirus argus* virus 1, *Vibrio fluvialis*, *Hematodinium* sp.,

Table 5.1 Diseases, parasites and symbionts from different species of lobsters, the tissues in which they reside, and key references selected by the authors.

Parasite	Host	Tissue	Key reference
Virus			
PaV1	*P. argus*	Connective tissues, haemocytes	Shields & Behringer (2004)
Bacteria			
Aerococcus viridans	*H. americanus,* *H. gammarus,* *P. argus*	Systemic	Snieszko & Taylor (1947), Rabin (1965), Stewart *et al.* (1966), Stewart (1980), Bobes *et al.* (1988)
Vibrio harveyi	*J. edwardsii*	Systemic, phyllosoma	Diggles *et al.* (2000)
V. alginolyticus	*P. homarus*	Systemic	Hameed (1994), Abraham *et al.* (1996)
Vibrio fluvialis-like	*H. americanus*	Systemic	Tall *et al.* (2003)
Vibrio spp.	All	Shell disease	Hess (1937), Castro & Angell (2000)
Leucothrix mucor	All	Carapace, eggs	Nilson *et al.* (1975), Steenbergen & Schapiro (1976), Harper & Talbot (1984)
Fungi[1]			
Haliphthoros milfordensis	*H. americanus,* *H. gammarus*	Postlarval juveniles	Fisher *et al.* (1975)
Haliphthoros sp.	*Sagmariasus verreauxi*	Pueruli, small juveniles	Diggles (2001)
Lagenidium sp.	*H. americanus*	Larval forms	Nilson *et al.* (1976), Fisher *et al.* (1978)
Fusarium solani	*H. americanus*	Carapace, gills	Lightner & Fontaine (1975), Fisher *et al.* (1978)
Didymaria palinuri	*Palinurus elephas*	Gills	Sordi (1958)
Ramularia branchiales	*H. gammarus*	Gills	Sordi (1958)
Protozoans			
Anophryoides haemophila	*H. americanus*	Haemolymph	Aiken *et al.* (1973), Cawthorn *et al.* (1996)
Ephelota gemmipara	*H. gammarus*	Eggs	Dannevig (1928, 1937)
Porospora gigantea	*H. gammarus,* *H. americanus*	Digestive tract	Hatt (1928), Boghen (1978)
Porospora nephropis	*N. norvegicus*	Digestive tract	Leger & Duboscq (1915), Tuzet & Ormières (1961)
Hematodinium sp.	*N. norvegicus*	Systemic, hepatopancreas	Field *et al.* (1992), Field & Appleton (1995)
Paramoeba sp.	*H. americanus*	Nervous tissues, systemic	Mullen *et al.* (2004)
Microsporidia	*P. argus,* *P. cygnus,* *P. ornatus*	Muscle tissues	Bach & Beardsley (1976), Dennis & Munday (1994)
Helminths			
Turbellaria	*Panulirus* spp.	On mouthparts	Shields (unpub. data)
Thulakiotrema genitale	*P. cygnus*	Gonad	Deblock *et al.* (1991)
Cymatocarpus solearis	*P. argus*	Abdominal muscle	Gomez del Prado-Rosas *et al.* (2003)

Table 5.1 *continued*

Parasite	Host	Tissue	Key reference
Stichocotyle nephropis	*N. norvegicus,* *H. americanus*	Gut wall	Cunningham (1887), Nickerson (1894), MacKenzie (1963)
Tetraphyllid cestode	*Panulirus* spp.	Foregut	Shields (unpub. data)
Carcinonemertes wickhami	*P. interruptus*	Eggs	Shields & Kuris (1990)
Carcinonemertes australiensis	*P. cygnus*	Eggs	Campbell *et al.* (1989)
Pseudo-carcinonemertes homari	*H. americanus*	Eggs	Fleming & Gibson (1981), Uhazy *et al.* (1985)
Polymorphus botulis	*H. americanus*	Gut wall, muscles	Montreuil (1954), Brattey & Campbell (1985a)
Ascarophis sp.	*H. americanus*	Rectal wall	Uzmann (1967b)
Hysterothylacium sp.	*H. americanus*	Foregut wall	Brattey & Campbell (1985a)
Histriobdella homari	*H. gammarus,* *H. americanus,* *N. norvegicus*	Carapace, eggs	Sund (1914), Uzmann (1967a), Briggs *et al.* (1997)
Crustaceans			
Nicothoe astaci	*H. gammarus*	Gills	Mason (1959)
Nicothoe analata	*N. sinensis*	Gills	Kabata (1966)
Nicothoe brucei	*N. sagamiensis,* *N. andamanicus*	Gills	Kabata (1967)
Nicothoe simplex	*N. japonicus*	Gills	Kabata (1967)
Choniomyzon panuliri	*Panulirus* spp.	Eggs	Pillai (1962)
Unicaleuthes sp.	*H. americanus*	Carapace	Sindermann (1990)
Paramphiascopsis sp.	*J. edwardsii,* *S. verreauxi*	Gills	Booth (pers. comm.)
Parapleustes commensalis	*P. interruptus*	Eggs	Shoemaker (1952)
Gitanopsis iseebi	*P. japonicus*	Branchial chamber	Yamato (1993)
Isaea elmhirsti	*H. gammarus*	Mouthparts	McGrath (1981)
Octolasmis spp.	*T. orientalis*	Gills, carapace	Jeffries *et al.* (1984)

1. We use the term Fungi to include the fungus-like Phycomycetes and other classical forms that are now placed in a separate Kingdom.

Paramoeba sp.) have shown the capacity to severely damage regional fisheries for different lobster species. The fact that in every case the causative agents were unknown until an outbreak occurred underscores the rather low value placed on the study of disease agents in these industries. No doubt this will change as these diseases continue to affect their respective host populations. Furthermore, with the opening of international markets, other problems have also arisen, namely post-harvest management of lobsters in short-term culture systems with shipment over long distances (Evans & Jones, 1999).

The study of parasitology and pathobiology is fraught with specific jargon that can be confusing, even to those trained in these fields. Several parasitological terms have been defined by Margolis *et al.* (1982) and updated by Bush *et al.* (1997). Briefly, 'prevalence' is the number of infected hosts divided by the total number of hosts examined. 'Intensity' is the number of parasites infecting a host, with mean intensity representing the mean number of parasites per *infected* host. 'Density' refers to the number of parasites per unit of measure (area, volume, or weight). 'An epizootic' is an epidemic or outbreak of a pathogen in an animal as opposed to human population. A disease is considered 'enzootic', or native, if it is consistently present in the affected host population. We also use the term 'symbiont' in the broader sense, two animals, a host and a symbiont that simply live together, and not necessarily in a mutualistic relationship. A 'parasite' lives on or in another organism and has a negative effect on the physiology or metabolism of the host.

5.2 Viral diseases

5.2.1 Panulirus argus *Virus 1 (PaV1)*

Recently, the first naturally occurring pathogenic virus was reported from a lobster. The virus infects *Panulirus argus* and has an affinity for certain haemocytes (hyalinocytes and semi-granulocytes), soft connective tissue cells, some haematopoietic tissues, and fixed phagocytes (Shields & Behringer, 2004). It is an unclassified, unenveloped, icosahedral, DNA virus with a nucleocapsid approximately 182 nm in size (Fig. 5.1). Lobsters in late stages of the disease are moribund and their normally clear haemolymph is diagnostically milky white from cellular debris and exudates. Lobsters apparently die from metabolic wasting because reserve inclusion cells in the hepatopancreas and epidermis are devoid of glycogen inclusions, which are important energy reserves, (Shields & Behringer, 2004) and the hepatopancreatic tubules often show atrophy. Lobsters inoculated with infected haemolymph die from the viral infection within 30–90 days, but some appear to survive the infection, particularly larger animals.

The virus is widespread in the juvenile habitats of the Florida Keys and Florida Bay. In surveys conducted at 12 sites in 1999, 2000 and 2001, prevalence was as high as 30%, but overall prevalence was lower: 7% (Shields & Behringer, 2004). The disease is most prevalent (mean = 16%) among the smallest crevice-dwelling juveniles (<20 mm CL). In contrast, less than 1% of the 1548 adults sampled along the Florida Keys in 2001 presented gross signs of infection. In experimental trials, 90% of the lobsters inoculated with infected haemolymph acquired the infection. In feeding trials, 42% of the lobsters acquired infections when fed infected tissues (Behringer, Shields & Butler, unpublished data). In contact-transmission trials with juvenile lobsters, 63% of the smallest individuals (<25 mm CL), 33% of those 30–40 mm CL, and 11% of the large juveniles (40–50 mm CL) became infected after 80 days of continual contact with infected individuals (Behringer, 2003). Thus, the virus appears to be transmitted by direct contact and shows a distinct predilection for very small juveniles.

PaV1 appears to be widespread and highly pathogenic to spiny lobsters. Given the notoriety of shrimp viruses and their global spread (see WSSV below), emphasis should be placed on development of good diagnostic tools for PaV1. Monitoring programmes should be developed for baseline data on prevalence in nursery populations and further studies should be directed at the natural history and biology of the virus in the Caribbean Sea.

5.2.2 White spot syndrome virus

Until the discovery of PaV1, naturally-occurring viral infections were unknown in lobsters. However, the host range and pathology of an important shrimp virus, white spot syndrome virus (WSSV), has been examined in experimentally infected spiny lobsters. Chang *et al.*, (1998) used a DNA probe specific to WSSV to detect the virus in the gills, stomach, cuticular epidermis and hepatopancreas of *Panulirus versicolor* and *P. penicillatus.* They did not assess the consequences of infection, but lobsters survived infection for at least 70 days without clinical signs of disease. Wang *et al.* (1998) used polymerase chain reaction (PCR) to detect WSSV in the lobsters *P. versicolor*, *P. penicillatus*, *P. ornatus* and *P. longipes* that had been experimentally exposed through ingestion of infected shrimp. WSSV was detectable at low levels in all of the lobsters, but none developed signs of disease. These hosts are not naturally infected with the virus. However, several crustaceans, including three species of *Panulirus*, could serve as experimental reservoir hosts for WSSV (Supamattaya *et al.*, 1998; Rajendran *et al.*, 1999).

Despite the paucity of viruses in lobsters, pathogenic viruses are notoriously common in other decapod crustaceans. At least 20 pathogenic viruses are known from penaeid shrimps (Lightner & Redman, 1998) and at least four are known from

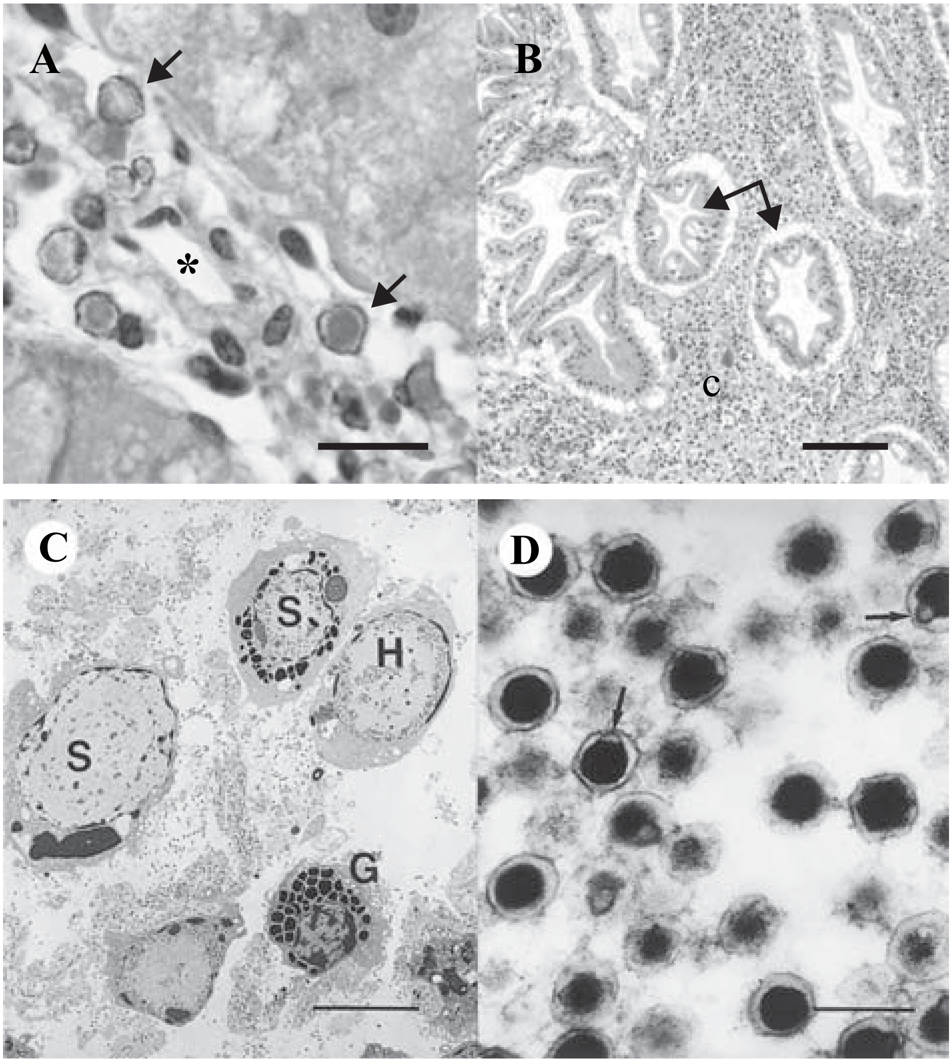

Fig. 5.1 *Panulirus argus* virus 1 (PaV1) in the Caribbean spiny lobster *Panulirus argus* from the Florida Keys. (A) Infected connective tissue cells (arrows) showing Cowdry-like inclusions and emarginated chromatin. Arteriole (*) with few fixed phagocytes remaining. H&E, bar = 20 μm. (B) Atrophied hepatopancreatic tubules (arrows) surrounded by proliferating soft connective tissues (C) that are infected with the virus. H&E, bar = 100 μm. (C) Lobster haemolymph with infected hyalinocyte (H) and semi-granulocyte (S). The granulocyte (G) is not infected. TEM, bar = 10 μm. (D) Icosahedral virions of PaV1 showing the distinct toroid (arrow). TEM, bar = 3 μm. (C and D modified from Shields & Behringer, 2004.)

blue crabs, (Shields & Overstreet, in press). Several shrimp viruses (infectious hypodermal and haematopoetic necrosis virus (IHHNV), white spot syndrome virus (WSSV), yellowhead virus (YHV), taura syndrome virus (TSV)) have severely hindered aquaculture of penaeid shrimp and pandemics of WSSV, IHHNV and TSV have spread rapidly through the Americas and Asia with catastrophic results for shrimp aquaculture and fisheries industries (Flegel, 1997; Lightner & Redman, 1998). Although viruses infect many crustaceans, few outside the shrimp viruses have been well characterised. No doubt more viruses will be found from lobsters.

5.3 Bacteria

5.3.1 Gaffkaemia – Aerococcus viridans

Biology

Gaffkaemia, or red-tail disease, is one of the most damaging diseases known to the clawed lobster industry. It is primarily a disease of confined lobsters with outbreaks occurring regularly in holding facilities; however, it also occurs in natural populations (Stewart *et al.*, 1966; Keith *et al.*, 1992; Lavallée *et al.*, 2001). It has been reported in *Homarus americanus* throughout much of the Canadian Atlantic (Stewart *et al.*, 1966) including the Gulf of St Lawrence (Menard & Myrand, 1987) and into the Gulf of Maine (Vachon *et al.*, 1981), and in *H. gammarus* from the Orkney Islands (Nilsen *et al.*, 2002) and Norway (Wiik *et al.*, 1987). It is probably established in every fished population of these host species, albeit in some cases it is present at extremely low levels, e.g. 0.13% in Norway in 1981 and zero in 1982–1984 (Wiik *et al.*, 1987). It has also been reported in lobster-holding facilities in Norway (Nilsen *et al.*, 2002; Mortensen, 2002) and in fact, it is thought to have been introduced to Europe via the shipment of diseased *H. americanus* to Norway (Alderman, 1996; Jørstad *et al.*, 1999a, b), but there is some controversy about its occurrence there (Egidius, 1972) and whether it has become established in natural populations. Gaffkaemia may also have been the causative agent for a lobster mortality in 1893 described by Herrick (1909), but the culprit was not well described.

Gaffkaemia is caused by *Aerococcus viridans*, a facultatively parasitic, non-motile, microaerophilic, encapsulated, tetrad-forming, gram-positive coccus (Fig. 5.2). Originally described as *Gaffkya homari* by Hitchner & Snieszko (1947), but due to various systematic constraints reviewed in Stewart (1980), it is now firmly established as *Aerococcus viridans* var. *homari*. Gaffkaemia is the best studied disease of any lobster species and Stewart's 30-year span of research on it represents a model approach for understanding diseases of Crustacea (e.g. Stewart *et al.*, 1966; Stewart & Cornick, 1972; Stewart, 1980 for review; Stewart *et al.*, 2004; and many others).

Fig. 5.2 *Aerococcus viridans* in a wet smear of the haemolymph of *Homarus americanus*. Note the formation of tetrads. Phase contrast, 1000x. (Photograph courtesy of Andrea Battison.)

Lobsters with gaffkaemia are lethargic, anorexic and often exhibit a pink ventral abdomen, hence the name 'redtail disease'. Moribund lobsters often lie on their side in distress and easily autotomise appendages. Mortality can be high, especially in summer months when water temperatures increase (Snieszko & Taylor, 1947). Temperature is an extremely important factor in mortalities as the time between infection and death can be as little as 2 days at 20°C but more than 60 days at 3°C and even longer at lower temperatures (Fig. 5.3) (Stewart *et al.*, 1969a, b). Temperature also plays a role in the pathology of the disease (Stewart *et al.*, 1972; Stewart, 1980). Stewart *et al.* (2004) demonstrated that strains of the pathogen could vary in virulence depending upon the presence of a capsule, with mean time to death ranging from 8.8 days at 15°C in virulent strains with a capsule to 23.8 days at 15°C in avirulent strains without a capsule. The presence of a capsule is a virulence factor in several other bacteria, particularly in *Streptococcus* spp.

Virulent strains of *Aerococcus viridans* var. *homari* have a capsule and are not agglutinated by lobster haemolymph serum (Stewart *et al.*, 2004). Virulence was lost after prolonged passage on trypticase soy agar and trypticase soy broth but was eventually restored after growth in lobster haemo-

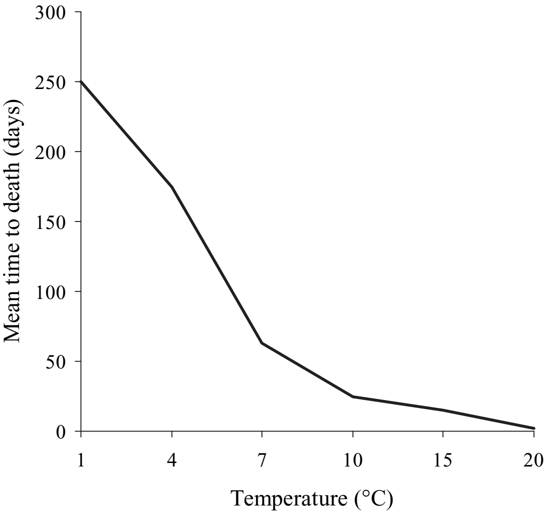

Fig. 5.3 Mean time to death for *Homarus americanus* infected with *Aerococcus viridans*. Infected lobsters held at 1°C did not die but remained infected. (Data from Stewart & Rabin, 1970).

lymph serum. The factor in lobster haemolymph serum responsible for restoring virulence is heat labile (Stewart *et al.*, 2004).

Lobsters obtain infections through damage to their exoskeletons as the pathogen cannot penetrate intact cuticle nor survive contact with gastric fluid (Stewart *et al.*, 1969c). The minimum infectious dose is extremely low; as few as five bacteria can result in clinical disease because the immune system of the lobster can be ineffective in controlling the rapid growth of virulent strains of the bacterium (Cornick & Stewart, 1968). The bacterium naturally infects only lobsters and can be found in sediments from lobster habitats. It can remain viable in mud and detritus for several months and can thus be a significant reservoir of infection in lobster pounds and other holding facilities (Stewart, 1984).

Upon entry to the host, bacteria colonise the hepatopancreas and heart, and multiply rapidly, particularly in the hepatopancreas, with its rich glycogen reserves (Stewart & Arie, 1973). Although bacteria are phagocytosed by haemocytes that then form aggregations, the pathogen thrives within haemocytes, using the cytoplasm of the haemocytes as a source of nutrients (Johnson *et al.*, 1981). Total haemocyte numbers decline as infections become septicaemic (Battison *et al.*, 2004), further impairing the clotting ability of the haemolymph. Eventually the haemolymph turns a pink colour, contains few haemocytes, has a prolonged clotting time and low viscosity (Snieszko & Taylor, 1947; Stewart, 1984). In heavy infections, the oxygen binding capacity of the haemocyanin becomes reduced by as much as 50% (Rittenburg *et al.*, 1979). Glycogen stores in the tissues become depleted, as do the levels of glucose and lactic acid in haemolymph and adenosine triphosphate in muscle (Stewart & Arie, 1973). The depletion of metabolic reserves occurs rapidly at temperatures above 10°C (Stewart *et al.*, 1969a, b, d, 1972).

Diagnostics

Diagnosis of gaffkaemia is generally done by culturing haemolymph aliquots directly in phenylethyl alcohol (PEA) broth (Stewart *et al.*, 1966; Lavallée *et al.*, 2001; Battison *et al.*, 2004). Positive cultures result in a colour change from purple to yellow over 96 hours, and characteristic Gram-positive tetrad-forming cocci are diagnostic for the pathogen. An indirect fluorescent antibody technique (IFAT) has been developed for the detection of *A. viridans* in lobster haemolymph (Marks *et al.*, 1992). The method reduced detection time from the normal four-day culture period to two hours for heavy infections or two days when cultures needed enrichment. Cross-reactions with *Staphylococcus aureus* occurred but were overcome with a pre-treatment using a papain digestion. PCR-based tests have also been used to characterise different strains of *Aerococcus viridans* (Greenwood *et al.*, 2005).

Epidemiology

Whereas the disease is primarily one of clawed lobsters, *Homarus* spp., natural infections have occurred in *Panulirus argus* from the Caribbean region (Bobes *et al.*, 1988). Further, the aetiological agent *Aerococcus viridans* var. *homari* was isolated from two sites adjacent to a lobster-holding facility in Anaheim Bay, California, indicating a rather high potential for spread due to transportation of contaminated or diseased individuals over wide areas (Kellog *et al.*, 1974). Disease was experimentally induced in the Californian spiny lobster *Panulirus interruptus*, but the lethal dose ($LD_{50} = 3.0 \cdot 10^5$ bacteria per ml) was considerably higher than that for *H. americanus* (Schapiro *et al.*, 1974; Steenbergen & Schapiro, 1974). Nonetheless, these results and the possible spread of the disease into European waters indicate that caution must be used when moving lobsters between regions or oceans.

Experimental infections have been examined in a number of crustaceans other than the American lobster (Stewart, 1980). Briefly, several crab hosts including *Cancer borealis*, *C. irroratus*, *C. magister*, *Libinia emarginata*, *Chionoecetes opilio*, *Chaceon quinquedens*, and a shrimp host, *Pandalus platyceros*, developed septicaemia after inoculation, with only a few individuals dying from the pathogen and only after prolonged periods (Bell & Hoskins, 1966, cited in Stewart, 1980; Cornick & Stewart, 1968, 1975; Rabin, 1968; Rabin & Hughes, 1968). Interestingly, the agent was reisolated at low levels from *C. quinquedens* and *C. opilio* after up to 100 days, and upon reinoculation into *H. americanus*, it was still highly virulent to lobsters (Cornick & Stewart, 1968, 1975).

Aerococcus viridans is not a natural part of the microflora of lobsters (Stewart, 1975). While it is a facultative parasite, and has been isolated from within and adjacent to lobster-holding facilities (Goggins & Hurst, 1960, cited in Stewart, 1980; Kellog *et al.*, 1974), its presence is indicative of diseased or previously gaffkaemic lobsters (Stewart, 1980).

The prevalence of gaffkaemia in wild lobsters is generally low but there have been reports of prevalences of up to 40% (Rabin, 1965; Stewart *et al.*, 1966). In 1997, a prevalence of 6.3% was detected in a random assessment of lobsters off Prince Edward Island (Lavallée *et al.*, 2001). Studies based on trapping are likely to underestimate the prevalence of infection because anorexic, lethargic lobsters are thought to be less likely to enter traps (Lavallée *et al.*, 2001). Gaffkaemia also occurs periodically in lobster-holding facilities. In 1982, an outbreak in a holding facility in Iles de le Madeleine, Quebec, Canada, resulted in the loss of over 40 000 lobsters (Menard & Myrand, 1987). It was feared that the outbreak would expand into the wild stocks of the lobster, but prevalence in the wild stock was only 2% in 1983 and was zero in 1984.

Control and treatment

Methods of controlling the disease in impoundments include prevention of damage to the exoskeleton of the lobsters, decreasing stocking density, reduction of water temperature, and attention to hygiene and water quality management (Bower & McGladdery, 2004). The practice of pegging a lobster's claws to immobilise the chelae created a portal of entry for the bacteria and is no longer used by the industry.

There have been a number of studies of antibiotics against gaffkaemia and absorption of antibiotics in lobsters (Bayer *et al.*, 1983; Bayer & Daniel, 1987; Huang & Bayer, 1989). Oxytetracycline is effective in the treatment of infected lobsters in post-harvest storage facilities (Bayer *et al.*, 2000; Speare *et al.*, 1996), and terramycin, a formulation of oxytetracycline, is the only FDA-approved drug available for use in *H. americanus*. It is sold as medicated feed in a pelleted form and it is considered efficacious against gaffkaemia (FDA, 1994). In fact, terramycin is the only medication qualified for use in the USA for treating a disease in invertebrates. The duration of treatment for terramycin is 5 days at 1 g/0.4536 kg of medicated feed and the withdrawal time is 30 days for lobster. Standardised tests have been developed for testing for the presence of the antibiotic in the tissues of treated lobsters (Bayer & Daniel, 1987; Anderson & Bayer, 1991).

Although experimental in nature, palinurid lobsters are either immune to, or show a high degree of resistance to, natural infections of gaffkaemia (Schapiro & Steenbergen, 1974; Schapiro *et al.*, 1974). That, coupled with the finding that vancomycin provided additional protection to clawed lobsters inoculated with *A. viridans* (Stewart & Arie, 1974) led Stewart and Zwicker (1974) to examine the stimulation of immune resistance in lobsters. Using formalin-killed bacteria (bacterin) with and without vancomycin, several studies have shown that immune resistance can be conferred to vaccinated lobsters (Stewart & Zwicker, 1974;

Mori & Stewart, 1978; Keith *et al.*, 1992) though the mechanism behind this resistance is not yet understood. In laboratory and field trials, resistance to infection was shown to develop 6 to 11 days after vaccination, with protection lasting at least 93 days, but not 123 days (Keith *et al.*, 1992). Lobsters showed resistance to *A. viridans* when vaccinated with the bacterin both with and without vancomycin. Inoculation provided better protection than bath immersion, but the latter still provided an enhanced (13% increase) survival to challenge. Interestingly, while there is a patent for a vaccine against gaffkaemia (Rittenburg & Bayer, 1980), the delivery of the vaccine and its relatively short-term efficacy has limited its development. Nonetheless, this is probably the first vaccine developed for a marine invertebrate.

5.3.2 Shell disease

Biology

Bacterial shell disease was first described from *Homarus americanus* (Hess, 1937). It is typically a non-fatal, external syndrome caused by a suite of chitinoclastic bacteria on crustaceans that have been subjected to stress. Fungal infections of crustaceans also cause shell lesions (e.g., crayfish plague caused by *Aphanomyces astaci*), but bacteria are most frequently isolated from the shell lesions (Rosen, 1967; but see Alderman, 1973).

Classical 'shell disease syndrome' is defined as 'progressive chitinolysis and necrosis of the exoskeleton of aquatic crustaceans' (Rosen, 1970). The syndrome affects species of Crustacea worldwide and begins as small 'burn' spots in the cuticle before merging to form continuous eroded lesions (Plate 5.1) (Rosen, 1970; Getchell, 1989; Noga *et al.*, 1994). More recently, an epizootic form of the syndrome has emerged wherein there is a more rapid spread of the lesions (Hsu & Smolowitz, 2003; Smolowitz *et al.*, 2005), but it has not been well contrasted with the classical form of the disease. In tagging studies, the presumptive epizootic form of the syndrome can apparently develop rapidly (Castro *et al.*, 2000). This presumptive form occurs primarily off Rhode Island and southern Massachusetts (Estrella, 1991), but more data are needed to validate the distribution of the syndrome and to separate it from the classical syndrome. With both forms, the unattractive appearance of affected lobsters, and their increased morbidity and mortality results in significant economic losses when lobsters are held in pounds or other holding facilities for days or weeks prior to sale.

Factors associated with shell disease in Crustacea include injuries sustained from high stocking densities, long-term confinement, and moulting (Rosen, 1967; Iversen and Beardsley, 1976; Overstreet, 1978; Johnson, 1983; Getchell, 1989; Sindermann, 1989; Smolowitz *et al.*, 1992). Pollutants (i.e. sewage sludge, dredge spoils, heavy metals, organic debris) are also known to be associated with the syndrome (Gopalan & Young, 1975; Young & Pearce, 1975; Couch, 1983; Morado *et al.*, 1988; Gemperline *et al.*, 1992; Weinstein *et al.*, 1992; Ziskowski *et al.*, 1996), and in at least two cases, heavy metals, and not chitinoclastic bacteria, have been implicated in the aetiology of a similar syndrome in crustaceans (Doughtie *et al.*, 1983; Andersen *et al.*, 2000).

Gram-negative, chitinoclastic, rod-shaped bacteria are the primary agents of shell disease on lobsters. The most commonly isolated bacteria are *Vibrio vulnificus*, *V. parahaemolyticus*, *V. alginolyticus*, unidentified species of *Vibrio*, *Shewanella* spp. and *Aeromonas hydrophila* (Reuter *et al.*, 1999; Porter *et al.*, 2001; Geddes *et al.*, 2003). Using classical microbiology, Roald *et al.* (1981) identified *V. anguillarum*, *Pseudomonas* and *Aeromonas* from lesions on *H. gammarus*. Abraham *et al.* (1996) isolated *V. alginolyticus* and a *V. harveyi*-like form from the haemolymph and lesions in *Panulirus homarus* reared under controlled conditions. Using a molecular approach, Porter *et al.* (2001) examined the bacterial fauna of *P. argus* with and without shell disease. While *Vibrio*, *Pseudoalteromonas*, *Pseudomonas* and *Shewanella* were all identified by DNA fingerprinting, of the 16S and 23S rRNA intergene regions, none of the isolates or fingerprints were specific to a unique aetiological agent. That is, the normal fauna were implicated in the aetiology of the shell disease lesions from spiny lobsters.

Grading systems for evaluating shell disease usually categorise the initial lesions as pits or erosions and more advanced stages as ulcers (Estrella, 1991; Smolowitz *et al.*, 1992). Classical shell disease begins as small, brown puncture-like craters on the sternum or legs (Rosen, 1967; Johnson, 1983). As the underlying chitin is exposed, it becomes colonised by chitinoclastic bacteria. The syndrome progresses into broad, irregular lesions with deep necrotic centres (Rosen, 1967) that occasionally penetrate through the shell (Overstreet, 1978; Johnson, 1983). Interestingly, the lesions tend to expand outward into the cuticle rather than through it. The weakened cuticle is often friable and becomes discoloured from the deposition of melanin (Johnson, 1983; Smolowitz *et al.*, 1992). In advanced cases, the lesion penetrates into the non-calcified membranous layer, essentially providing a portal of entry for other microorganisms or developing into a lesion that becomes fatal during moulting. The host response to infection ranges from cellular infiltration, epicuticle deposition, and melanisation to pseudomembrane formation (Smolowitz *et al.*, 1992).

In most cases, individuals overcome the disease by moulting (Rosen, 1967; Castro & Angell, 2000), therefore larger (older) lobsters, which moult less frequently, particularly ovigerous females, are most affected by it (Estrella, 1991; Castro & Angell, 2000). There is also a strong seasonal component to the presumptive epizootic form of shell disease with increased prevalences in the autumn (Estrella, 1991; Castro & Angell, 2000).

Shell disease arises primarily from mechanical abrasion of the epicuticle, which is a thin layer of lipoproteins and polyphenols. Experimental abrasion of the exoskeleton is a prerequisite for the development of classical shell disease in *H. americanus* and resistance to infection is influenced both by temperature and stage of ecdysis (Malloy, 1978). Similarly, experiments in blue crabs indicate that abrasion is an important feature of shell disease (Cook & Lofton, 1973) with lesions developing over 4 to 10 days in crabs abraded and held in polluted areas (McKenna *et al.*, 1990). Diet may also be an important factor as lobsters fed on an experimental diet had significantly less shell disease than those fed a normal fish diet (7.73% versus 10.39%, respectively, Prince *et al.*, 1995). Furthermore, diet is critical to the resistance of shell disease in captive juvenile lobsters (Fisher *et al.*, 1976a).

American lobsters with shell disease have significantly different biochemical characteristics compared with those of unaffected lobsters (Floreto *et al.*, 2000). Some of the differences in shell-diseased lobsters include low protein content of haemolymph, higher ash content in haemolymph and hepatopancreas and lower moisture and lipid content of the hepatopancreas. These and other alterations to normal biochemical parameters suggest that the immune system, mineral transport and deposition, moulting and other metabolic processes are likely to be dysfunctional in lobsters with shell disease. Whether some of these changes are normal and involved in wound repair remains to be determined.

Epidemiology

Shell disease is normally found at low (<1%) levels in healthy wild populations. For example, Hess (1937) reported three cases out of 5000 lobsters examined. However, several studies place prevalences at 1–10%. Roald *et al.* (1981) reported 12% prevalence in *H. gammarus* from the Oslofjord, Norway. Ziskowski *et al.* (1996) reported a significant association between offshore sewage sludge sites and shell disease, with prevalences ranging from 6–10% in areas adjacent to dump sites. However, Wilk *et al.* (1996) found a low prevalence (<2%) of shell disease in *H. americanus* sampled during a broad-scale monitoring programme of commercial trawl and pot fisheries from the Gulf of Maine south to Virginia.

There has been a documented increase in presumptive epizootic shell disease off Rhode Island and Massachusetts. From 1995 to 1999, the prevalence of shell disease rose from zero to over 20% with more than 50% of ovigerous females having the syndrome (Castro & Angell, 2000). The increase was higher in inshore waters than in offshore waters and was associated with a fall peak in prevalence. In 1989, off Massachusetts, shell disease was high in the more confined embayments, Buzzards Bay (51.1%) and Cape Cod Bay (42.8%), but the overall prevalence, including other inshore sites, was lower at 33.3% (Estrella, 1991).

The site of lesions varies by host species. In spiny lobsters, *Panulirus argus*, *P. cygnus* and *Jasus edwardsii*, the shell lesions are most frequently reported on the uropod and telson, and the condition has been described as 'tail fan necrosis' (Plate 5.2) (Porter *et al.*, 2001; Geddes *et al.*, 2003). In *H. americanus*, the lesions are more frequently seen on the ventral side of the claws, tail and carapace (Estrella, 1991). Large necrotic lesions on the chelae have also been reported from *H. gammarus* from Norway (Roald *et al.*, 1981).

Treatments are available against shell disease but they are not applicable to animals destined for the dinner plate. Malachite green has been used to treat juvenile lobsters (Fisher *et al.*, 1978), malachite green and formalin, and antibiotic baths (penicillin–streptomycin, Furanace, erythromycin, oxolinic acid) have been used for shrimp (Tareen, 1982; El-Gamal *et al.*, 1986). The FDA or other national regulatory agencies have not approved any of these for use with lobsters primarily because many of these are known or suspected carcinogens. Aquaria can be disinfected with bleach solutions. Animals with severe lesions should be destroyed to prevent further spread in impoundments.

Anecdotal evidence suggests that the prevalence of shell disease is increasing in wild populations of lobsters where water quality is deteriorating as a result of increased levels of sewage, heavy metals and suspended solids (Getchell, 1989; Ziskowski *et al.*, 1996; Porter *et al.*, 2001). In some instances, anoxia, high stocking densities of lobsters, abrasions of the exoskeleton, poor nutrition and high or low water temperatures have been associated with a high prevalence of shell disease in lobsters in holding facilities (Getchell, 1987; Geddes *et al.*, 2003). While there has to date been little experimental evidence demonstrating a significant correlation between shell disease and environmental conditions in lobsters, shell disease in blue crabs is clearly associated with deteriorating water quality, (McKenna *et al.*, 1990; Gemperline *et al.*, 1992; Weinstein *et al.*, 1992) and crabs from polluted sites show significantly less callinectin, an antibacterial peptide, in the plasma and haemocytes than crabs from more pristine areas (Noga *et al.*, 1994; Khoo *et al.*, 1996; Noga *et al.*, 1996). Whether lobsters also show changes in defensive peptides remains to be determined.

Finally, given the nature of the presumptive epizootic form, its relatively rapid development, and its distribution in anthropogenically-altered habitats, research should focus on determining the underlying aetiology of the syndrome, its potential relationship with pollutants, and its potential for spread in host populations.

5.3.3 Vibriosis

Lobsters are exposed to a large number of salt-tolerant environmental bacteria including many species of *Vibrio*. These ubiquitous bacteria form a large part of the natural bacterial flora of invertebrates such as *Panulirus argus* (Porter *et al.*, 2001). *Vibrio alginolyticus*, *Vibrio harveyi*, *Vibrio parahaemolyticus* and *Listonella* (*Vibrio*) *anguillarum* are opportunistic pathogens that have caused disease in adult lobsters that were stressed, immuno-compromised or injured (Brinkley *et al.*, 1976; Bowser *et al.*, 1981; Jawahar *et al.*, 1996). Vibrios can be important human pathogens; they can be transmitted to humans from contaminated surfaces and undercooked foods. They can also be transported in seafood products including lobsters (Wong *et al.*, 1999). Therefore, we recommend that all lobsters be properly cooked prior to eating, and that all surfaces used in preparing lobsters be suitably cleaned and disinfected.

An outbreak of the luminescent *V. harveyi* was reported from phyllosoma larvae of *Sagmariasus verreauxi* reared in a culture facility in New Zealand (Diggles *et al.*, 2000). Mortalities reached 75% of the larvae over a four-week period. Gross signs included opaque larvae with small red spots distributed throughout the body. Histologically, the hepatopancreatic tubules were atrophied and filled with bacterial plaques (Plate 5.3). Koch's postulates were fulfilled, as the bacterium was isolated in pure culture, which was used to infect healthy larvae in bath exposures. Furthermore, injured larvae were more susceptible to infection than uninjured ones, so the bacterium is more likely to be a secondary pathogen. Sulfadimidine and trimethoprim significantly improved survival of both infected and uninfected larvae (Diggles *et al.*, 2000).

Panulirus argus and *P. laevicauda* sampled from commercial landings at two locations in Brazil were infected with *V. alginolyticus* (prevalence = 45.7%), *V. parahaemolyticus* (8.6%) and *V. anguillarum* (2.8%) (Silva dos Fernandes Vieria *et al.*, 1987). *Vibrio alginolyticus* and a *V. harveyi*-like bacterium have been reported from juvenile and adult *Panulirus homarus* from India (Hameed, 1994; Abraham *et al.*, 1996). Isolates were cultured from shell disease-like lesions (see above) and from the haemolymph. Inoculations of vibrios induced similar lesions on larvae of *Penaeus indicus* and *Panulirus homarus* (Hameed, 1994). Interestingly, histopathological changes were observed in the hepatopancreas, gut and muscle of infected animals indicating that the infection had become systemic. Abraham *et al.* (1996) induced 100% mortality in lobsters inoculated with 10^8 bacterial cells, but no mortality in lobsters inoculated with 10^7 bacterial cells.

The scarcity of published reports of outbreaks of disease associated with *Vibrio* bacteria in lobster-holding facilities in temperate and tropical areas most likely under-represents the real impact of this group of bacteria on lobster health when environmental conditions are less than ideal. This group of bacteria is frequently isolated from the haemolymph of lobsters affected by other health problems such as shell disease and is likely to cause an end-stage septicaemia following significant injury, disease, other stressor, or immune or metabolic dysfunction.

5.3.4 Limp lobster disease

Tall *et al.* (2003) described a systemic disease called 'limp lobster disease' in *H. americanus* caused by a *Vibrio fluvialis*-like bacterium. The disease emerged in 1997 in Maine, USA resulting in losses exceeding US$2.5 million dollars to the lobster industry. The bacteria accumulate in the heart, midgut and haemolymph resulting in rapid onset of weakness, lethargy and slow responses to sensory stimuli. Strains with a plasmid were more pathogenic than those without. There is evidence that the pathogen produces several toxins including an enterotoxin. Lobsters were more susceptible to the disease when they were stressed by overcrowding, high water temperatures, poor water quality or damage to the exoskeleton (Tall *et al.*, 2003).

5.3.5 Fouling bacteria

Leucothrix mucor is a common filamentous bacterium that often fouls the eggs of crustaceans (Johnson *et al.*, 1971; Bland & Brock, 1973). It has been reported from cultured larvae of the American lobster where it is thought to be a nuisance species (Nilson *et al.*, 1975; Dale & Blom, 1988). Nilson *et al.* (1975) note that fouling with this and other commensals gradually decreases in postlarvae, presumably because they established effective preening activity. *Leucothrix mucor* and other fouling agents are common problems in larval culture (e.g. Kittaka, 1997) as they are ubiquitous in seawater systems and are saprophytes of algae. Preventing their access to aquaculture facilities is difficult because of their ubiquitous nature. Control methods include careful site selection and system design and careful attention to larval nutrition and water quality. Antibiotics have been used to control outbreaks of *L. mucor* on crustaceans including the eggs of lobsters (Fisher & Nelson, 1977; Sadusky & Bullis, 1994).

5.4 Water moulds and fungi

Historically, the Kingdom Fungi comprised several polyphyletic classes including members of the Oomycetes, Phycomycetes and Deuteromycetes, several of which infect crabs and lobsters. Advanced molecular techniques, refined biochemical studies and transmission electron microscopy (TEM) studies of zoospores have resolved several systematic problems in the 'Fungi' resulting in the erection of a new Kingdom, the Chromista (Cavalier-Smith, 1993). That is, the Oomycetes and Phycomycetes are now considered the Oomycota after Margulis *et al.* (1990) and the 'higher' fungi, including the Deuteromycetes, are now firmly in the Kingdom Fungi. For the sake of simplicity, we refer to the Oomycetes and other 'lower' fungi as water moulds.

Unestam (1973), Alderman (1976), Lightner (1981), and Johnson (1983) have reviewed diseases of crustaceans that are caused by water moulds and fungi. In culture conditions, water mould infections, primarily those caused by *Lagenidium callinectes*, *Haliphthoros milfordensis*, and *Fusarium solani*, are relatively common in crustacean embryos, including those of the American lobster, *H. americanus*. They can, however, impose significant threats to the culture of these crustaceans (Lightner, 1981).

5.4.1 Atkinsiella

Members of the genus *Atkinsiella* infect invertebrates. The oomycete *Atkinsiella panulirata* was isolated and described from phyllosoma of *P. japonicus* in Japan (Kitancharoen & Hatai, 1995).

5.4.2 Lagenidium

Species of *Lagenidium* are holocarpic, oomycete fungus-like protists that attack and kill crustacean embryos. Mortalities caused by *Lagenidium* spp. have been reported in larvae of *Homarus americanus* (Nilson *et al.*, 1975, 1976; Fisher *et al.*, 1976b). Other filamentous commensal organisms were associated with the infestation but only *Lagenidium* spp. penetrated the host tissues. Infections occur naturally in the embryos of the blue crab (Sandoz *et al.*, 1944; Rogers-Talbert, 1948), the barnacle, *Chelonibia patula* (Johnson & Bonner, 1960), the zoea of *Cancer magister* (Armstrong *et al.*, 1976), and algae (Fuller *et al.*, 1964; Gotelli, 1974a, b). *Lagenidium* spp. is considered to be a significant problem to crustacean aquaculture because of their predilection for embryos and larval stages (Lightner & Fontaine, 1973; Nilson *et al.*, 1975).

The mould thallus consists of intra-matrical hyphae within an embryo or larva, and extra-matrical hyphae that function in sporogenesis and spore discharge. The life cycle of *L. callinectes* was elucidated by Bland & Amerson (1973) with additional work on an algal isolate by Gotelli (1974a, b). Sporangia discharge zoospores after 12 to 15 hours in sterile seawater, with continued release extending over 48 hours. Zoospores encyst and the cyst germinates a single germ tube that penetrates into the tissues. Young hyphae have few septa (Gotelli, 1974a, b). From 20 to 200 zoospores are produced by a single sporangium. Zoospores swim to, encyst on, and infect new embryos or larvae, but extramatrical hyphae can also grow between embryos to infect new ones.

Several strains of *L. callinectes* have been isolated from decapod embryos and algae. Biochemical and morphological criteria have been used to separate strains (for details see Bahnweg & Bland, 1980; Crisp *et al.*, 1989). Most strains are obligate marine forms, but isolates from the American lobster and the Dungeness crab, *Cancer magister*, do not require NaCl (Bahnweg & Gotelli, 1980).

Lobster larvae die quickly when infected with *Lagenidium* sp., typically within 1–2 days (Nilson *et al.*, 1976). Hyphae can be observed in the dead and dying larvae. Embryos can be infected, too; they display similar characteristics to infections in the embryos of blue crabs (Fisher *et al.*, 1978). On the blue crab, the mould appears as brown or grey patches on the periphery of the clutches of infected females (Couch, 1942; Rogers-Talbert, 1948). It rarely penetrates more than 3 mm into the clutch of eggs. Diseased eggs die before hatching. In larvae, infections become established in the organs, and then spread throughout the body (Armstrong *et al.*, 1976, Nilson *et al.*, 1976). The thicker cuticle of postlarval juvenile lobster is thought to provide resistance to infection (Fisher *et al.*, 1978). In larval specimens of *C. magister*, the fungus was highly pathogenic, with 40% mortality over 7 days (Armstrong *et al.*, 1976).

The embryos of *H. americanus* exhibit some resistance to infection by *L. callinectes.* Apparently, a Gram-negative, penicillin-sensitive *Alteromonas* bacterium isolated from embryos releases 4-hydroxyphenethyl alcohol, or tyrosol, a known antifungal compound (Gil-Turnes *et al.*, 1989; Gil-Turnes & Fenical, 1992). The presence of a similar 2,3-indolinedione from bacteria growing on the eggs of *Palaemonetes macrodactylus* was sufficient to inhibit mortality in embryos exposed to the mould.

5.4.3 Haliphthoros

The oomycete *Haliphthoros mildfordensis* is a halophilic, holocarpic water mould that is a frequent cause of death of postlarval spiny and clawed lobsters in aquaculture facilities around the world (Fisher *et al.*, 1975, 1978; Nilson *et al.*, 1975). In a recent outbreak, *Haliphthoros* sp. was isolated and identified as the aetiological agent of a fungal disease in pueruli and juveniles of *J. edwardsii* reared in experimental growout facilities in New Zealand (Diggles, 2001). Gross signs included lethargy, loss of appetite, and brown necrotic lesions in the gills. Hyphae were observed in wet smears and histological preparations of the gills, with penetration into the adjacent skeletal muscles. Melanisation of the necrotic areas and infiltration of haemocytes occurred within the affected areas. Notably, lobsters over 30mm CL did not become infected. Malachite green and formalin prevented the spread of disease. As with many microbial infections, the disease was related to poor hygiene of the culture system (Diggles, 2001).

Invasion of the host is likely through a portal of entry such as a wound, or in the lightly cuticularised regions of the axillae or apodemes of the limbs or the branchial chamber (Fisher *et al.*, 1975). Blackened spots within the tissues of the host are a result of the host's melanisation response to invasion of the mould (Fisher *et al.*, 1978). Affected animals often die before or during moulting. Moulting can be impaired by the adherence of lesions to the carapace.

Sporulation is rapid, occurring over 24–48 hours and zoospores are released from an extramatrical discharge tube (Tharp & Bland, 1977). Zoospores form cysts from which germination tubes arise to initiate infection. Hyphal fragments have been implicated in infections in lobster postlarvae (Fisher *et al.*, 1975). Maintaining animals in conditions of excellent water quality is the preferred method of controlling the condition. The antifungal compound 'Furanace' as well as malachite green have shown some efficacy in treating infected systems (Abrahams & Brown, 1977; Fisher *et al.*, 1978), but again, these drugs are not approved for use in aquaculture in most countries.

5.4.4 Fusarium

Fusarium solani is a deuteromycete fungus that has been reported from cultured crustaceans worldwide. Infections by *Fusarium* cause black lesions on the exoskeleton, mainly on the abdominal plates, telson and uropods (Plate 5.4). *Fusarium solani* has been implicated as the cause of shell lesions in adult lobster on more than one occasion. In 1979, an outbreak of shell lesions occurred in the western rock lobster, *Panulirus cygnus*, in Western Australia. The lesions were granulomatous and up to 40mm in diameter on the abdomen, uropod, telson and pereiopods (McAleer & Baxter, 1983). *Fusarium solani* was isolated from the lesions and also from some samples of seawater from areas with diseased lobsters. The disease has not recurred and environmental factors that might have pre-disposed lobsters to developing the disease were not identified.

Other isolations of the same or a similar fungus have been made from *H. gammarus* (= *H. vulgaris*) (Alderman, 1981) and *H. americanus* (Lightner & Fontaine, 1975). In both instances these lobsters were held in aquaculture facilities and lesions appeared on the exoskeleton or gills. The fungus has not been reported from larval lobsters (Fisher *et al.*, 1978). Two other deuteromycetes, *Didymaria palinuri* and *F.* (*Ramularia) brachialis*, were reported from the gills of moribund lobsters, *P. elephas* and *H. gammarus*, from the Mediterranean Sea (Sordi, 1958).

Fusarium causes lesions to occur on the cuticle and in the tissues, and these are often melanised in response to the infection (Lightner & Fontaine, 1975; Fisher *et al.*, 1978). Intense haemocyte aggregations, necrotic tissue, and fungal hyphae can be seen in histology. Hyphae produce micro- and macro-conidia, the latter of which are diagnostic for *Fusarium* (Lightner & Fontaine, 1975). In culture, the fungus produces a dark brown/purple pigment, which is soluble in water and diffuses into the surrounding isolation media. The pigment seen in histology sections of lesions is more likely to be melanin resulting from the lobster's immune defence mechanisms than pigment produced by the fungus (Lightner & Fontaine, 1975). Fisher *et al.* (1978) warn that this fungus represents a significant threat, as there are no effective control measures for it and it has been a problem in shrimp culture.

5.5 Protozoa

5.5.1 Ciliata – Anophryoides haemophila

Anophyroides haemophila is an orchitophyrid scutiociliate that causes 'bumper car disease' in *H. americanus*. The disease was first recognised as *Anophrys* sp. by Aiken *et al.* (1973), and was variously identified as a 'parasitic ciliate' or '*Paranophrys*' by Loughlin *et al.* (1993, 1994), or *Mugardia* (Sherburne & Bean, 1991) until being properly described by Cawthorn *et al.* (1996). The disease gets its common name, 'bumper car disease', after the appearance and energetic motility of the ciliate even at low temperatures (Plate 5.5) (Cawthorn *et al.*, 1996). In the early 1990s, increasing numbers of epizootics of 'bumper car disease' in lobster impoundments in eastern Canada and the USA resulted in significant research effort being applied to understanding the epidemiology of this disease (Cawthorn *et al.*, 1996).

In 1971–1972, the prevalence of the ciliate was 20% in lobsters held in winter impoundments in Nova Scotia (Aiken *et al.*, 1973). It was also observed in the following winter in wild stocks from Nova Scotia and Prince Edward Island. Aiken and Waddy (1986) reported it in lobsters collected in later years during winter sampling. Brattey and Campbell (1985a) did not find the ciliate, but they were not examining the haemolymph of lobsters. Sherburne and Bean (1991) reported an epizootic in 1990 with 100% prevalence. They also showed the presence of the ciliate in earlier studies from two impoundments in Maine as well as from nearby embayments. The parasite was more prevalent in the hepatopancreas than the haemolymph of the lobster hosts. The rock crab, *Cancer irroratus*, may serve as a reservoir host (Sherburne & Bean, 1991), but this needs further confirmation.

More recently, Lavallée *et al.* (2001) surveyed freshly-captured lobsters from around Prince Edward Island, Canada, using an indirect fluorescent antibody method. Only one out of 254 lobsters was positive, a prevalence far below the 17.8% reported by Cawthorn *et al.* (1996). The lower prevalence is no doubt an underestimate of the true prevalence as Lavallée *et al.* (2001) sampled in June and September, and the pathogen appears to have a winter peak in abundance (Aiken & Waddy, 1986). Furthermore, as discussed by Lavallée *et al.* (2001), the seasonal conditions and bias resulting from the method of capturing lobsters are factors that need to be considered in any study of the prevalence of clinically-diseased lobsters in wild populations and probably account for some of the variation between results of different surveys.

Infected lobsters have white, milky haemolymph with marked haemocytopenia and loss of clotting (Sherburne & Bean, 1991; Cawthorn, 1997). Diseased animals often have a 'spread-eagled' appearance, are usually fouled, and are less likely to survive the stresses of handling and transport (Cawthorn, 1997). Athanassopoulou *et al.* (2004) studied the pathology of lobsters experimentally infected with *Anophryoides haemophila*. The onset of lesions was dose-dependent with granulomas developing over five to nine weeks post-infection when inoculated with 2000 ciliates, or four weeks when inoculated with 500 000 ciliates. The first lesions to appear were small haemocytic encapsulations in the gills. Encapsulation and granuloma formation were the main host defence mechanisms observed in the infected lobsters, but phagocytosis and melanisation responses were not evident. The parasites appear to prefer oxygen-rich areas such as the gills and epipodites near the gills, but also infect the connective tissue of the hepatopancreas, intestine, antennal gland and testis during later stages of infection. Most lobsters tend to die nine to eleven weeks post-infection. The ciliates appear to feed on reserve inclusion cells and derive their nutrient requirements from the host (Athanassopoulou *et al.*, 2004).

Epidemics of bumper car disease often occur when water temperatures are in the range of 1–5°C, when lobster stocking density is high and water quality less than optimal (Cawthorn, 1997). Transmission probably occurs through breaks in the cuticle. Cannibalism, a route of transmission for some pathogens of crustaceans, is an unlikely route of infection because gastric fluids are a barrier to transmission of the ciliate (Loughlin *et al.*, 1998). The parasite, therefore, is more likely to enter the host through damaged cuticle (cf. gaffkaemia) or through a soft ecdysial exoskeleton.

At least three methods are used to diagnose bumper car disease in lobsters. Haemolymph smears can be useful, but they can drastically underestimate the prevalence of the tissue-dwelling parasite (Sherburne & Bean, 1991). Histological methods are useful, particularly at moderate to heavy infections, and when coupled with an indirect fluorescent antibody technique, give excellent results (Lavallée *et al.* 2001). The Scuticociliata, the order to which *A. haemophila* belongs, have a conserved DNA sequence in the small sub-unit (SSU) and internal transcribed spacer (ITS) regions and therefore polymerase chain reaction (PCR)-based primers are quite specific and useful to diagnose the species (Ragan *et al.*, 1996; Goggin & Murphy, 2000).

Formalin baths, freshwater dips and chloramine have been shown to kill the ciliate *in vitro* (Speare *et al.*, 1996). In bath trials, 200 mg/L formalin or 10 mg/L chloramine for one hour were tolerated by healthy lobsters with no change in several biochemical parameters in the haemolymph. Low salinity (8 psu) baths were also tolerated by healthy lobsters, but they showed altered behaviours and haemolymph chemistry for one week following treatment. Speare *et al.* (1996) indicate that these treatments may be effective for control of the transmissive stages but will not be efficacious for diseased animals. Novotny *et al.* (1996) used a cell-culture system to test the efficacy of several antibiotic treatments against the ciliate. Monensin, formaldehyde and pyrimethamine with sulphaquinoxaline were shown to reduce the motility of the ciliate and cause lysis. Oxytetracycline and amprolium had little to no effect on the ciliate motility. Cribb *et al.* (1999) developed an *in vitro* tetrazolium-blue formazan assay for testing the efficacy of various antibiotics against *A. haemophila*. They found that 100 M lasalocid or pyrimethamine was cytotoxic to the ciliate over 24 hours.

From a commercial viewpoint, infected lobsters result in economic losses because they are often downgraded because of reduced muscle mass, poor muscle quality and an unpleasant flavour (Cawthorn, 1997). Therefore, reducing parasite numbers in impoundments should reduce the incidence of disease. This may be achieved by treatment of water in lobster impoundments with formalin or chloramine-T (Speare *et al.*, 1996).

Given the potential damage that this parasite can cause to the industry, it is surprising that there are so few epidemiological studies documenting its distribution, abundance, and use of reservoir hosts, as well as studies detailing environmental and host factors important to its spread. This should be given a high priority by the industry.

Internal infections of ciliates are typically rare in crustaceans. With the exception of *Anophryoides haemophila*, internal infections in lobsters have not been reported. However, a presumably facultative *Mesanophrys*-like ciliate was recently reported from *Nephrops norvegicus* (Small *et al.*, 2005a, b). The parasite secretes strong proteases that probably facilitate its parasitic life style.

5.5.2 Peritrich ciliates

Peritrich and suctorian ciliates are common epibionts on the gills, carapace, eggs, and other external surfaces of crustaceans. Most are commensals, but at high intensities, they either indicate the presence of a predisposing disease, or they become a burden themselves. They usually do not cause health problems unless lobsters are held in aquaculture facilities or are affected by some other primary health problem. Under these conditions, the number of organisms can dramatically increase resulting in respiratory distress or possibly damage to the exoskeleton. Species of sessile peritrichs in the genera *Vorticella* and *Zoothamnium*, the suctorian ciliates *Acineta* and *Ephelota*, and several cyanobacteria and diatoms are commonly responsible for fouling of lobsters and lobster embryos (Dannevig, 1928, 1937; Nilson *et al.*, 1975; Harper & Talbot, 1984; Dale & Blom, 1987). Heavy growth of the sessile ciliate *Zoothamnium* sp. was reported to have caused mortalities of *Nephrops novegicus* larvae, presumably by interfering with respiration (Anderson & Conroy, 1968). Phyllosomal larvae of *Jasus edwardsii* were fouled by several organisms including *Vorticella*, *Navicula*, *Leucothrix mucor* and others (Kittaka, 1997). Fouled larvae eventually died, but determination of the causative agent was hindered by the presence of numerous fouling agents, including the mould, *Saprolegnia*. Recent evidence indicates that freshwater crabs develop microscopic lesions due to the peritrich ciliates and experience significantly greater oxygen consumption while resting (Schuwerack *et al.*, 2001). Experimental work with another gill symbiont, the stalked barnacle *Octolasmis muelleri* on blue crabs indicates that heavily-infested crabs are in a functional state of heavy exercise (Gannon & Wheatly, 1992, 1995). Heavy infestations of ciliates may cause a similar condition. Wescodyne and malachite green have been used against *Vorticella*, and while intensities were lowered, neither was completely successful in ridding lobsters of the fouling ciliates (Boghen, 1982).

5.5.3 **Hematodinium** *spp. infections in* **Nephrops norvegicus**

The genus Hematodinium is comprised of a number of poorly-described dinoflagellates that are internal parasites of crustaceans. They live in the haemolymph and are highly pathogenic, in most cases killing their hosts. Two species have been described, *H. perezi* and *H. australis*, but several forms warrant species status, including that from the Norway lobster, *N. norvegicus*. The same or similar species of dinoflagellates cause a similar clinical disease in a number of crab species in Europe (see Stentiford & Shields, 2005).

Members of the Order Syndinida, which includes species of *Hematodinium*, have complex life cycles consisting of at least three stages: a multinucleate plasmodial stage, a vegetative phase (trophont, produced via merogony) and an asexual reproductive phase (sporont produced via sporogony). Sporogony in all of the syndinids leads to the formation of macro- and micro-dinospores (Cachon & Cachon, 1987). The different dinospores are not gametes and have a similar DNA content as other stages (Eaton *et al.*, 1991).

Species of *Hematodinium* have few morphological characters to identify them. Micropores, organelles for endocytosis, have been observed in haemolymph-dwelling stages of the parasite from *N. norvegicus* (Appleton & Vickerman, 1998). Micropores are an important morphological feature of the Apicomplexa, and are common to the superphylum Alveolata (Gajadhar *et al.*, 1991; Cavalier-Smith, 1993). For a review of the biology and effects of *Hematodium* infections, see Stentiford and Shields (2005). For a broader perspective on parasitic dinoflagellates in Crustacea, see Shields (1994).

Species of *Hematodinium* have damaged several fisheries including those for the Tanner crab, *Chionoecetes bairdi*, and snow crab, *C. opilio* (Meyers *et al.*, 1987, 1990, 1996; Taylor & Khan, 1995; Shields *et al.*, 2005), the edible crab, *Cancer pagurus* (Latrouite *et al.*, 1988; Stentiford *et al.*, 2002), the velvet crab, *Necora puber* (Wilhelm & Miahle, 1996), the harbour crab, *Liocarcinus depurator* (Wilhelm & Boulo, 1988), and the Norway lobster, *Nephrops norvegicus* (Field *et al.*, 1992, 1998; Stentiford *et al.*, 2001a). Infected Tanner and snow crabs develop a condition known as 'bitter crab disease' resulting in unpalatable, unmarketable crabs. Lobsters afflicted with the disease are also unmarketable.

Infections in the Norway lobster, *N. norvegicus*, have been reported from off Scotland (Field *et al.*, 1992, 1998; Stentiford *et al.*, 2001a), the Irish Sea (Field *et al.*, 1998; Briggs & McAliskey, 2002), and the Skagerrak (Tärnlund, 2000). An epizootic off Clyde, Scotland, in 1990, reached a prevalence of 70% with other nearby areas having prevalences of 30–50% (Field *et al.*, 1992). Prevalences have remained relatively high since then. The parasite is more common in females and postmoult lobsters, showing a distinct peak in spring months (Field *et al.*, 1998; Stentiford *et al.*, 2001a). The seasonal peak in prevalence is associated with the peak in the postmoult condition and suggests either an increase in patent infections in relation to the stress of moulting or an overlap in the presence of potentially infectious dinospores with the occurrence of 'soft' postmoult instars (Field *et al.*, 1992, 1998; Stentiford *et al.*, 2001a). Sexual differences in prevalence may be the result of differential moulting periods as the peak in moulting for females occurs primarily in the spring whereas it is later in the year for males (Field *et al.*, 1992; Stentiford *et al.*, 2001a). The prevalence of the disease is probably biased in trawled samples because infected animals show reduced capacity in their escape-swimming behaviour and spend less time within the burrows (Stentiford *et al.*, 2000a, 2001b).

Heavily-infected lobsters are lethargic, have a dull orange colour, milky white haemolymph, watery muscles and a shrunken green hepatopancreas (Field *et al.*, 1992). Initially in infection, the number of circulating haemocytes increases, the haematopoietic tissue is enlarged and haemal spaces in the heart, gills, midgut and haematopoietic tissue are distended with parasites. Narrow haemal spaces such as those in the gills and hepatopancreas can become occluded by dinoflagellates and haemocyte aggregations (Fig. 5.4). Later in infection, haemocytopenia (a reduction in haemocytes) occurs, probably as a result of the host defence process of encapsulation of the parasites (Field & Appleton, 1995). Atrophy of the skeletal muscle results in significant alterations to the biochemistry and ultrastructure of the muscle (Stentiford *et al.*, 2000b). The haemolymph of infected animals has a reduced copper content and the haemocyanin has a markedly reduced oxygen-carrying capacity, which may lead to ischaemic tissue damage and further morbidity (Taylor *et al.*, 1996). Dinospores exit the infected host through the gills (Appleton & Vickerman, 1998) and in the process kill their infected hosts presumably from extensive perforations to the gills (Stentiford *et al.*, 2001a).

Hematodinium parasites develop into extremely dense infections in their crustacean hosts. Thus, they seriously alter the metabolism of their hosts. Protein and carbohydrate constituents show significant decreases in relation to infection and are correlated with host morbidity (Stentiford *et al.*, 2000b, 2001c; Shields *et al.*, 2003). Tissue reserves of glycogen are significantly reduced in infected crabs and lobsters (Love *et al.*, 1996; Stentiford *et al.*, 2000b, 2001c; Shields *et al.*, 2003). Infected *N. norvegicus* show a marked decrease (up to 80%) in glycogen in the abdominal muscles (Stentiford *et al.*, 2000b). Elevations of crustacean hyperglycemic hormone (CHH) in the plasma probably result from a disruption of the feedback loop that controls its release from the sinus gland of infected lobsters (Stentiford *et al.*, 2001c). The increase in CHH also indicates an increased turnover of glucose in infected animals, which may be due to increased uptake of glucose by the parasite.

The free amino acid profile of infected *N. norvegicus* shows significant alteration with declines in serine and massive increases in taurine in relation to the progression of disease (Stentiford *et al.*, 1999). Taurine is present in the hepatopancreas, muscles and possibly the haemocytes of crustaceans; its mobilisation in the plasma indicates a disruption of the metabolism of these tissues that may be attributable to their atrophy (see Stentiford *et al.*, 1999).

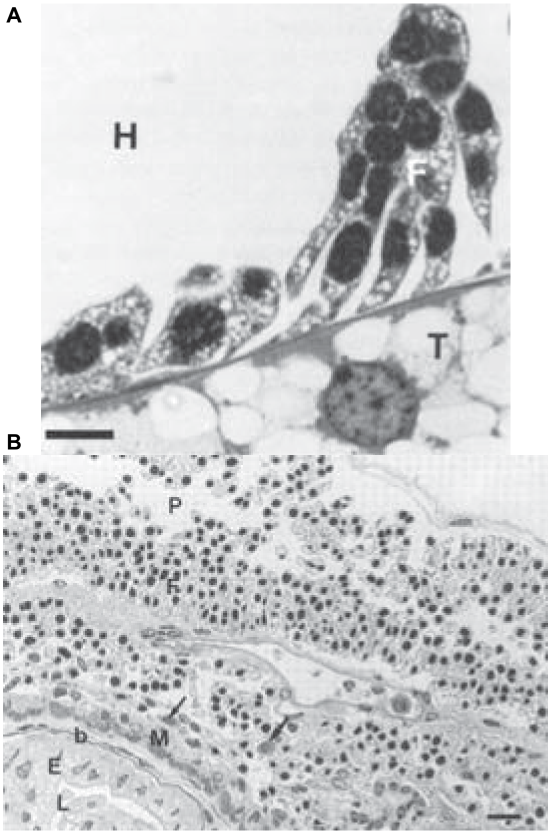

Fig. 5.4 Infection of *Hematodinium* sp. in the Norway lobster, *Nephrops norvegicus* from off western Scotland. (A) Gorgonlocks-like stage adhering to the outer wall of the hepatopancreatic tubule. H = haemal sinus, F = syncytium of parasite, T = epithelial cell in tubule. Bar = 15 m, H&E. (B) Wall of the midgut of a moderately infected lobster showing filamentous syncytium (F) and uninucleate parasites (P) in the haemolymph. M = circular muscle layer, b = basement membrane, E = epithelium of midgut, L = lumen. Toluidine blue, bar = 20 m. (From Field & Appleton, 1995.)

The *Hematodinium* parasite from the Norway lobster has been isolated and grown *in vitro*

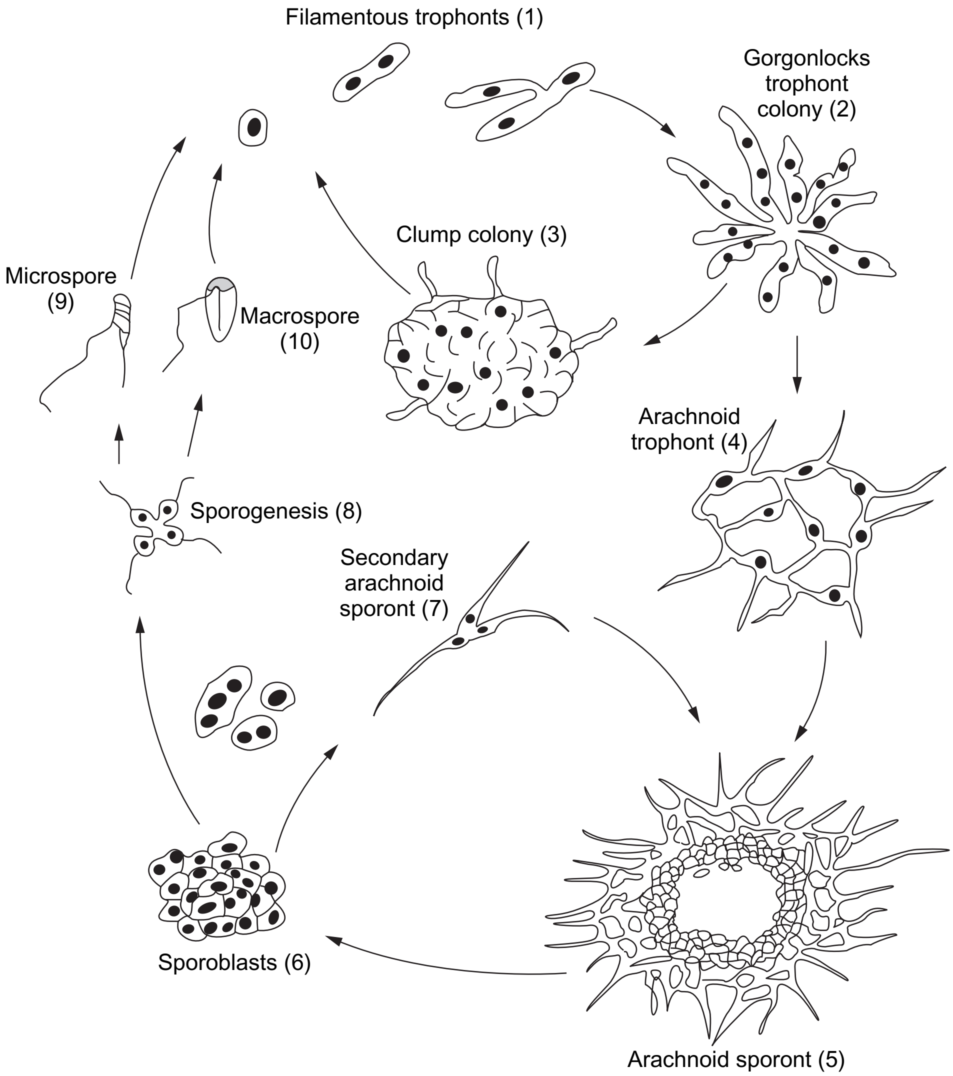

Fig. 5.5 Life cycle of *Hematodinium* sp. from *Nephrops norvegicus*. Life cycle based on *in vitro* culture. (1) Multinucleate filamentous trophonts, which can be found in the haemolymph, give rise to (2) the 'Gorgonlocks' stage that either becomes (3) a clump colony or develops into (4) a bizarre arachnoid trophont. The syncytial arachnoid trophont generates a mass known as (5) an arachnoid sporont that gives rise to (6) sporoblasts that either develop into (7) secondary arachnoid sporonts or undergo (8) sporogony to become (9) micro- or (10) macro-dinospores. The dinospores presumably leave the host and initiate a new infection. (From Appleton & Vickerman, 1998.)

(Appleton & Vickerman, 1998). In culture, the life cycle of the parasite is quite complex (Fig. 5.5). The macro- and micro-dinospores develop into a filamentous trophont that develops into a bizarre 'Gorgonlocks' in the hepatopancreas (Field & Appleton, 1995, 1996). The early life history stages have a predilection for this organ, developing or entwining within it (Field & Appleton, 1996). In culture, the Gorgonlocks can develop into two forms: a 'clump' colony that produces more filamentous trophonts, or an unusual plasmodial, arachnoid, trophont. The arachnoid trophont enlarges to form the arachnoid sporont, which undergoes sporogony to produce sporoblasts that then develop into the macro- or micro-form of the dinospore (Appleton & Vickerman, 1998). *In vitro* cultures of *Hematodinium* from the Norway lobster are not infectious (Appleton & Vickerman, 1998).

Transmission of *Hematodinium* parasites is thought to occur via the macro- or micro-dinospores, but this has not been determined. Ingestion of dinospores is thought to be a likely route of infection (Appleton & Vickerman, 1998), but the synchrony between the prevalence of infection and the postmoult condition suggests that transmission occurs around ecdysis (Field *et al.*, 1992, 1998; Stentiford *et al.*, 2001a). In the form from the Norway lobster, *in vitro* cultures of dinospores lead directly to the development of filamentous trophonts (Appleton & Vickerman, 1998).

Hematodinium infections have been transmitted via inoculation to a number of crab hosts (Meyers *et al.*, 1987; Hudson & Shields, 1994; Shields & Squyars, 2000), but surprisingly, not to the Norway lobster. As with many protozoan infections in crustaceans, cannibalism is a possible mode of transmission for *Hematodinium*. Sheppard *et al.* (2003) have reported successful transmission of disease to naive (not previously exposed to the disease) blue crabs via ingestion, but this mode of transmission has not been examined in other systems. Amphipods also serve as hosts for *Hematodinium*-like infections (Johnson, 1986) and there has been considerable speculation that they may serve as intermediate or reservoir hosts for infections in decapods (for review, see Stentiford & Shields, 2005). Indeed, amphipods from the fishing grounds for Norway lobster even have similar infections (Small, 2004; Small *et al.*, 2006), but the identification of the species of parasite remains to be determined.

A variety of methods are used to diagnose *Hematodinium* infections in the Norway lobster. Hosts with advanced infections often show a change in the colour or opacity of the carapace. However, examination of the haemolymph is more reliable for diagnosis. Pleopodal staging has been used effectively in evaluating infections in the Norway lobster (Field *et al.*, 1992; Field & Appleton, 1995). Basically, a pleopod is examined with a stereomicroscope and the opacity of the haemolymph indicates the severity of the infection (Field *et al.*, 1992, 1998; Stentiford *et al.*, 2001d). Fixed wet smears processed and stained with Giemsa or haematoxylin and eosin (H&E) provided consistent results in other studies of *Hematodinium* infections (e.g. Meyers *et al.*, 1987; Wilhelm & Mialhe, 1996; Messick & Shields, 2000; Pestal *et al.*, 2003). Several molecular diagnostic techniques also have been developed and tested. An indirect fluorescent antibody test using a polyclonal antibody revealed sub-patent infections in the Norway lobster (Field & Appleton, 1996). A Western-blot technique (Stentiford *et al.*, 2001d) and an ELISA-based diagnostic using these same polyclonal antibodies (Small *et al.*, 2002) showed that the prevalence was underestimated in the Scottish fishery for *N. norvegicus*. Curiously, while PCR-based techniques have been published for infections in the sand crab (*Portunus pelagicus*) and the American blue crab (*Callinectes sapidus*) (Hudson & Adlard, 1994, 1996; Gruebl *et al.*, 2002), no studies have evaluated PCR as a diagnostic tool for infections in the Norway lobster.

Hematodinium infections rank among the most economically significant diseases of Crustacea. Outbreaks have caused considerable damage to several fisheries, but more importantly, epizootics tend to occur in sublegal females and juveniles in several fisheries (Messick, 1994; Messick & Shields, 2000; Shields *et al.*, 2005); therefore, the impact of these diseases is often underestimated. There is clearly a need for more research on the biology, life cycle, transmission and ecology of *Hematodinium* infections in their crustacean hosts.

5.5.4 *Microsporidia*

The Microsporidia is a small phylum of parasites that are strictly intracellular and produce small (usually <6 μm), unicellular spores with a highly refractile and resilient spore wall. The phylum lacks mitochondria, but contains a characteristic extrusible, hollow polar tube that injects the germinal sporoplasm into the host cell. Microsporidian infections are rarely reported from lobsters. An infection was noted in *P. argus* from Florida (Bach & Beardsley, 1976), but details were lacking for an identification. From the description of the gross appearance of semi-opaque whitish muscle in the lobster, the disease resembles a condition known as 'cotton crab' or 'cotton shrimp' that is caused by similar infections in those hosts.

Microsporidia appear to be endemic in several species of lobster. In Australia, a species of *Ameson* appears to infect the musculature of several prawns and spiny lobsters including *P. cygnus* and *P. ornatus* (Plate 5.6) (Dennis & Munday, 1994; Owens & Glazebrook, 1988). Lobster fishermen report that severely affected animals often die soon after capture. More work should be done on microsporidian infections as their prevalence is likely to be under-reported and their potential to damage the industry should be investigated. No doubt several new species of parasite remain to be discovered.

5.5.5 Rhizopoda – **Paramoeba** *sp.*

In 1999, there was a large mortality of the American lobster, *Homarus americanus* in western Long Island Sound (WLIS) that heavily damaged the lobster fishery there. Lobster fishermen reported significant numbers of weak, flaccidly paralysed, moribund lobsters. Subsequently, a pathogenic amoeba, identified as *Paramoeba* sp. was diagnosed in moribund and dying lobsters in the area (Russell *et al*., 2000; Mullen *et al*., 2004). Mortalities in WLIS also occurred in several other species including the blue crab, *Callinectes sapidus*, spider crabs, *Libinia* spp., the rock crab, *Cancer irroratus,* and the horseshoe crab, *Limulus polyphemus*. However, other host species were not examined for pathology. Based on a study of the small sub-unit region of the rDNA, the causative agent has recently been characterised as a species of *Neoparamoeba* (Mullen *et al*., 2005).

In the lobster, the amoeba infects the ventral nerve cords, brain, neurosecretory organs of the eye, and other nerve tissues. Amoebae invade the nerve interstices, nerve cell cytoplasm and tegumental glands as well as the subcuticular connective tissues (Fig. 5.6). Pathologies include discolouration of the haemolymph and muscle, granulocytopenia, haemocytic infiltrates in nerve and connective tissues, inflammation and necrosis of nerve tissues, and coagulopathies (Mullen *et al*., 2004). In blue crabs, a related species, *Paramoeba perniciosa,* infects primarily the connective tissues and only rarely the nerves (Johnson, 1977). Lobsters in the end stages of the disease are limp or moribund and often present with altered, 'cloudy' eyes, but this state may not be associated with the amoebic disease (J. Shields, personal observation).

Transmission of the disease from infected to uninfected lobsters occurred in cohabitation experiments, but Koch's postulates were not fulfilled (Mullen *et al*., 2004). The possible roles of contaminants and environmental factors that may have initially stressed the lobsters, resulting in infection with the *Paramoeba,* remain unclear. However, sublethal doses of malathion, a pesticide sprayed in New York in 1999, have been shown to depress the phagocytosis in exposed lobsters (DeGuise *et al*., 2004) and increased production of manganese has been shown to limit phenoloxidase activity (Hernroth *et al*., 2004). Further, several alkylphenols, which can act as juvenile hormone analogues, have been shown to be present at relatively high levels in the tissues of lobsters from WLIS (Biggers & Laufer, 2004). These factors, coupled with the fact that the *Neoparamoeba* agent is always present in the sediments of WLIS (Gillevet & O'Kelly, 2003), suggest that several factors may have predisposed lobsters to infection with the amoeba.

Paramoeba pernicosa infections have been previously reported from the American lobster. Such infections are exceedingly rare in the lobster and are not considered a threat to the industry (Rosenfeld, 1976; Sawyer, 1976; Sawyer & MacLean, 1978); however, they should be considered separately from infections of the *Paramoeba* sp., which were clearly involved in the epizootic of 1999 (Mullen *et al*., 2004, 2005).

5.5.6 Apicomplexa – Gregarines

Gregarines are members of the phylum Apicomplexa. They infect invertebrates and can have direct life cycles or indirect life cycles. Those using lobsters as definitive hosts have a two-host life cycle (heteroxenous) and use gastropod molluscs as intermediate hosts. Two species have been reported

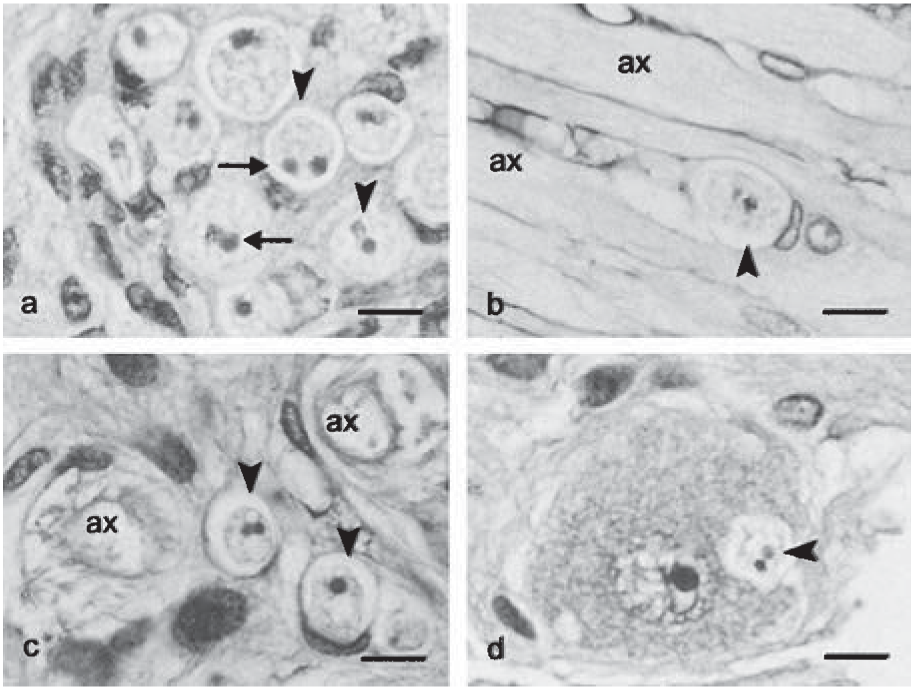

Fig. 5.6 *Paramoeba* sp. in the nerves of *Homarus americanus* from Long Island Sound, NY. (A) Nodular haemocytic aggregate surrounding several amoebae (arrows). H&E, bar = 50 m. (B) Amoeba located between two nerves (arrow); ax = nerve axon. H&E, bar = 50 m. (C) Nerve fibres with amoebae (arrows) located intracellularly within connective tissue cells or haemocytes. H&E, bar = 20 m. (D) Amoeba (arrow) located within the cytoplasm of a neuron. H&E, bar = 10 m. (From Mullen *et al.*, 2004.)

from the mid- and hindguts of lobsters. *Porospora gigantea* infects *H. americanus* (Montreuil, 1954; Théodoridès & Laird, 1970; Boghen, 1978; Brattey & Campbell, 1985a) and *H. gammarus* (Théodoridès, 1962), which at least in Europe uses *Trochocochlea mutabilis* as an intermediate host (Hatt, 1928), and *P. nephropis* infects *N. nephrops* (Leger & Duboscq, 1915; Tuzet & Ormières, 1961). Within the lobster, the characteristic trophonts can be found free in the lumen of the mid- and hindguts with their epimeres attached to the gut wall. Large (200–500 m), cyst-like reproductive stages known as gamontocysts attach to the cuticular lining of the hindgut and are thought to be shed at ecdysis (Brattey & Campbell, 1985a).

Porospora gigantea is reportedly the most common parasite of homarid lobsters. Off Nova Scotia, its prevalence has ranged from 43.6% to 84.2% (Brattey & Campbell, 1985a); in the Northumberland Straits, prevalence was >80% in juvenile and adult lobsters (>50 mm CL) (Boghen, 1978); and off the Magdalene Islands it reached a prevalence of 100% (Montreuil, 1954). However, it was absent from lobsters sampled in the Mid-Atlantic Bight (Van Engel *et al.*, 1986), which may indicate the absence of a suitable molluscan intermediate host.

Brattey & Campbell (1985a) noted a seasonal pattern in prevalence with fewer infections in spring and summer and more in fall and winter. Boghen (1978) found differences in prevalence in relation to size, with small juveniles (<50 mm CL) having a lower prevalence than larger juveniles and adults (>50 mm CL). This is likely to be due to a change in the diet of the larger juveniles, which are capable of handling larger molluscan prey. The molluscan intermediate host for *P. gigantea* in the western North Atlantic remains unknown, but studies on the diet of lobsters could point to the correct gastropod.

5.6 Helminths

5.6.1 Digenetic trematode infections

Digenetic trematodes are flatworms, or flukes, that are entirely parasitic, with most being hermaphrodites as well. They can have extremely complex life cycles often involving three or more hosts, but as a rule, the first intermediate host is a mollusc. In lobsters, all trematodes are encysted forms known as metacercariae. These cysts are often microscopic and thus difficult to detect unless one is searching for them or doing histological studies of tissues in which they encyst. Trematodes often use several species as second intermediate hosts, and this is the case for those using lobsters as hosts.

A microphallid trematode, *Thulakiotrema genitale,* occurs encysted in the gonad of *Panulirus cygnus* in Western Australia (Plate 5.7) (Deblock *et al*., 1991). The prevalence ranged from 47% to 87% depending on sample location. The vertebrate definitive host is unknown. A brachycoeliid trematode, *Cymatocarpus solearis* (= *C. undulatus*), occurs in the abdominal muscles of *P. argus* from the Caribbean Sea off Punta Allen, Mexico (Gomez del Prado-Rosas *et al*., 2003). Prevalence was 35.8% with the mean intensity of 26 cysts per host. The cysts were visible to the eye and were large, measuring up to 1.5 mm in size. The definitive host is the sea turtle *Caretta caretta* (Caballero, 1959). A turtle dissected by Linton (1910) had adult *C. undulatus* in the intestines and the remains of a spiny lobster in the stomach.

Stichocotyle nephropis is an aspidogastrid trematode found encysted in the wall of the midgut, hindgut and rectum of *N. nephrops* (Cunningham, 1887) and *H. americanus* (Montreuil, 1954; Brattey & Campbell, 1985a). Up to 8 larvae can be found in one cyst (MacKenzie, 1963). The first intermediate host is probably a mollusc, but some aspidogastreans also use fishes as first intermediate hosts. Lobsters probably obtain infections through ingestion of or contact with molluscan hosts. The parasite develops in the bile ducts and spiral valves of *Raja clavicula* (Odhner, 1898) and the barndoor ray, *Raja laevis*, off North America (Linton, 1940) as well as *Raja clavata* off Scotland (MacKenzie, 1963).

Prevalence in *N. nephrops* from the Firth of Forth was 25–33% (Cunningham, 1887) and prevalence ranged from 7–20% off western England, but lower levels occurred in lobsters from the the Irish Sea (Symonds, 1972). It has also been reported from *H. americanus* off Nova Scotia where its prevalence was extremely low (0.6%) (Montreuil, 1954; Brattey & Campbell, 1985a) and New England (1–2%) (Nickerson, 1894; Herrick, 1909), but not the Gulf of St Lawrence (Boghen, 1978) nor the Mid-Atlantic Bight (Van Engel, 1986). In *N. norvegicus,* prevalence is positively correlated with host size; lobsters <30 mm CL were not infected (Symonds, 1972).

5.6.2 Cestoda

Metacestodes of a tetraphyllidean cestode have been observed attached by their phyllidia to the foreguts of spiny lobsters, *Panulirus* spp., and *Scyllarides* sp., from the Great Barrier Reef (Fig. 5.7) (Shields, unpublished data). This order of cestodes uses only elasmobranchs as definitive hosts and typically uses arthropods as first intermediate hosts. The parasite can only be identified by feeding

Fig. 5.7 Metacestode (arrow) of a tetraphyllidean tapeworm attached to the foregut of *Panulirus versicolor* from the Great Barrier Reef, Australia.

the metacestodes to a suitable elasmobranch host as has been done for trypanorhynch metacestodes (e.g. Sakanari & Moser, 1989).

5.6.3 Nemertea – Carcinomertes *spp. and* Pseudocarcinonemertes

Nemertean worms are members of a small phylum that possess a characteristic rhynchocoelum, a body cavity housing a well-developed proboscis that is often armed with a stylet. Species in the genus *Carcinonemertes* are symbiotic or semi-parasitic egg-predators on crustaceans. In some cases, they have reached epidemic proportions on crab populations where their presence is thought to affect reproduction and production (Wickham, 1979, 1986; Hobbs & Botsford, 1989; Shields & Kuris, 1988; Kuris *et al.*, 1991). These worms can be difficult to observe and assess, but they may represent significant sources of mortality by decreasing fecundity; hence, studies of fecundity should be cognisant of their presence.

Carcinonemertes wickhami occurs on the eggs of *Panulirus interruptus* (Shields & Kuris, 1990) and *C. australiensis* occurs on the eggs of *P. cygnus* (Campbell *et al.*, 1989). Nemertean worms resembling *Carcinonemertes* also occur on *Jasus edwardsii,* but their identification remains to be determined (S. Frusher, personal communication). Both *C. wickhami* and *C. australiensis* are filiform, monostyliferous hoplonemerteans, each with a greatly reduced, slightly extrusible proboscis armed with a single stylet (Fig. 5.8). They have separate sexes, and females are typically longer than males. Eggs are fertilised internally and are extruded into a mucilaginous sheath, called an 'egg strand', that can often be seen in the egg clutch of the host. In *C. wickhami,* modified pilidium larvae hatch in synchrony with the hatching of the host (Shields & Kuris, 1990). Little else is known about the biology and ecology of either species.

Pseudocarcinonemertes homari is an egg-predatory tetrastemmatid nemertean that infests the clutches of *H. americanus* (Fleming & Gibson, 1981; Uhazy *et al.*, 1985). Females are 7–12 mm in length, males from 5–9 mm. The worms are found in low numbers on the exoskeleton of the abdomen, gills and limbs of lobsters but do not damage the host (Campbell *et al.*, 1986). During or shortly after oviposition of the lobster host, worms migrate into the egg clutch and begin feeding on eggs. Using an immunofluorescent antibody technique, Waddy and Aiken (1985) definitively demonstrated that the worms were egg predators. After eclosion, the worms migrate out of the clutch into protected sites on the exoskeleton, often in mucoid aggregations, or to the gills where they encyst between the gill filaments (Aiken *et al.*, 1985). Some leave the host and migrate to new hosts, others stay on the same host where they regress in size or die (Fleming & Gibson, 1981; Aiken *et al.*, 1985; Uhazy *et al.*, 1985). Apparently, up to three generations of worms can occur within one year (Brattey *et al.*, 1985a). Moulting by the host may shed the worms, particularly those in the gills, and carcinonemertids migrate to the new instar at ecdysis (Wickham *et al.*, 1984), but this has not been examined for *P. homari.*

Female worms lay 30–47 eggs in egg strands that adhere to the setae or egg funiculi of the host (Aiken *et al.*, 1985). Development is direct and juvenile worms hatch after approximately 60 days at 4–5°C to reinfest their host (Fleming & Gibson, 1981; Aiken *et al.*, 1985). Worms mature after feeding on lobster eggs, but they can survive for long periods without feeding, simply residing encysted within the gills or on the limb axillae of the host (Fleming & Gibson, 1981; Aiken *et al.*, 1983). Juveniles probably absorb amino acids that are leaked through the arthrodial membranes of their host, as this occurs in *Carcinonemertes errans* on *Cancer magister* (Roe *et al.*, 1981; Crowe *et al.*, 1982). There is some speculation that the worms can damage the gills of the host (Fleming & Gibson, 1981), and an ovigerous worm was found in a lesionous gill (Aiken *et al.*, 1985); but this is probably a rare occurrence that may have been stimulated by other factors, because these types of infestations rarely lead to gill damage (Aiken *et al.*, 1985).

High-intensity infections can develop on newly ovigerous lobsters if they have a pre-existing infestation (Aiken *et al.*, 1985). However, if they are infested later in embryogenesis, then the intensity of infection will remain low. The worms also prefer

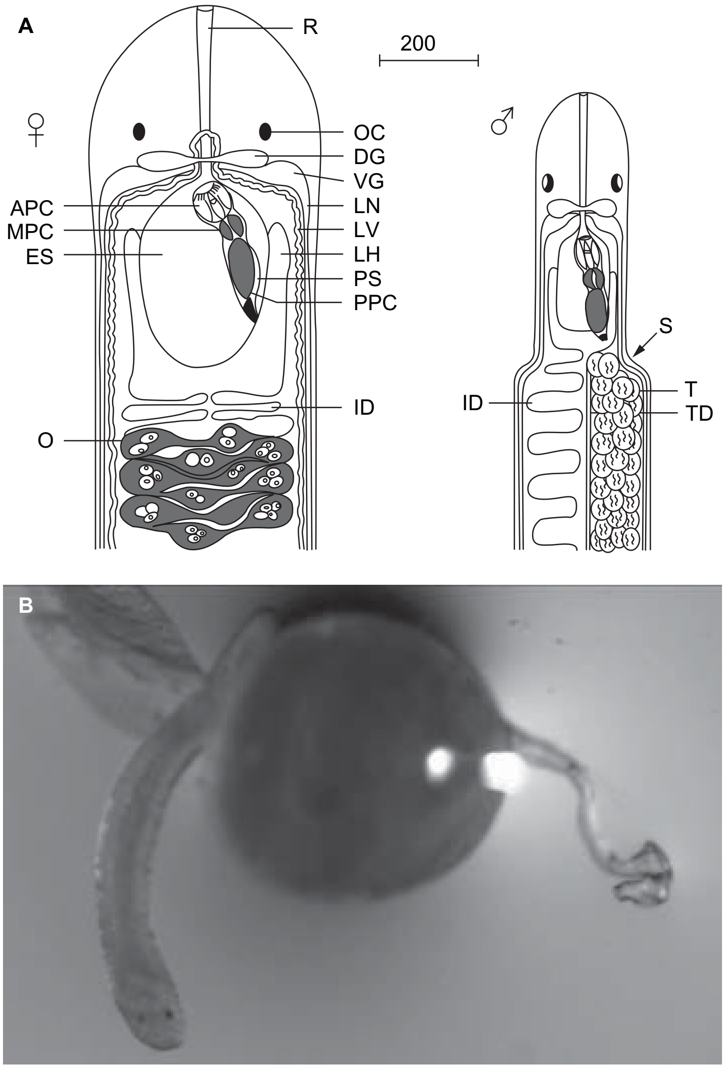

Fig. 5.8 (A) Composite drawing of *Carcinonemertes wickhami* from the clutch of *Panulirus interruptus* from the Santa Barbara Channel, California. Key to labels: APC = anterior proboscis chamber, DG = dorsal ganglia, ES = foregut, ID = intestinal diverticula, LH = lateral horn of intestine, LN = lateral nerve cord, LV = lateral blood vessel, MPC = middle proboscis chamber, OC = ocellus, O = ovary, PPC = posterior proboscis chamber, PS = proboscis sheath, R = rhynchodaeum, S = shoulder, T = testis, TD = Takakura's duct (seminal vesicle system), VG = ventral ganglion. (From Shields & Kuris, 1990.) (B) *Carcinonemertes australiensis* on the eggs of *Panulirus cygnus*.

the interior of the egg clutch, with more worms occurring on the second through fourth pleopods than on first and fifth pleopods (Campbell & Brattey, 1986). Grooming of the eggs by the female lobster and her removal of worms either reduces the effect of the worm or, in heavy infestations, can confound accurate assessment of egg mortality due to the worm (Aiken *et al.*, 1985). Interestingly, Aiken *et al.* (1985) showed that some female lobsters are fastidious 'cleaners' and have few to no worms, whereas others are 'non-cleaners' and have heavy infestations and many dead eggs. Eggs of infested females are often discoloured by the growth of ubiquitous fungi that live on dead and dying eggs (Miller & Fleming, 1983).

Egg mortality due to *P. homari* is correlated with the intensity of infection (Campbell & Brattey, 1986). In lobsters off Grand Manan Island, Nova Scotia, over 16% of the clutches assessed had >50% egg mortality and mortality was significantly correlated with worm density (worms/1000 eggs) (Campbell & Brattey, 1986). Egg mortality averaged between 38–43% of the clutch. An intensity of 14 000 worms was reported from a lobster, with a complete loss of eggs (Aiken *et al.*, 1985; Brattey *et al.*, 1985a). Although highly variable, egg mortality showed some seasonality that confounded the association with worm density. For *Carcinonemertes regicides* on the red king crab, *Paralithodes camtschaticus*, worm-related egg mortality increases over the summer and is significant only after extended periods of feeding (Kuris *et al.*, 1991).

Initial studies reported a low prevalence of infection of *P. homari* on lobsters. Only a few animals were examined by Fleming & Gibson (1981) and only 5% of ovigerous females from the Bay of Fundy were infested (Aiken *et al.*, 1983). In an extensive study of the geographic distribution and seasonality of the worm in the Canadian Maritimes, Brattey *et al.*, (1985a) showed that prevalence could be high. Ovigerous lobsters had the highest prevalence and intensity of infection. Off Grand Manan Island, ovigerous females had a prevalence of 78.7% and a mean intensity of 102.4 worms per infected host. Non-ovigerous females and males had much lower prevalences (<30% and <7.5%, respectively) and mean intensities of infection (14 and 6.5 worms per infected host, respectively) (Brattey *et al.*, 1985a). Prevalence did not vary with season, nor did mean intensity, which showed significant aseasonal fluctuations (Brattey *et al.*, 1985a; Campbell & Brattey, 1986). The prevalence of infection did, however, show a significant association with host size in lobsters less than 120 mm CL (Campbell & Brattey, 1986), but there was no association found in hosts over 120 mm CL (Brattey *et al.*, 1985a; Campbell & Brattey, 1986).

There is a relatively high degree of host specificity in *P. homari*. In experimental infections, ovigerous *H. gammarus* could become infected, but not *Cancer irroratus* (Aiken *et al.*, 1985). In an extensive survey off eastern Canada, Brattey *et al.* (1985b) found no nemerteans on five crustacean species, including *C. irroratus*. Therefore, it is likely that *P. homari* is specific only to *H. americanus* in the field. Species of *Carcinonemertes* range in their host specificity with some, such as *C. carcinophila,* being broad host 'generalists' and others being host 'specialists' (Humes, 1942).

Pseudocarcinonemertes homari can be treated by freshwater bathing (Charmantier *et al.*, 1991). Exposure to freshwater was lethal after four minutes, but ovigerous lobsters and their eggs were unaffected by short immersions. Low salinities are known to limit the distributions of several species of *Carcinonemertes* (Scrocco & Fabianek, 1970; McCabe *et al.*, 1987; Shields & Wood, 1993) and freshwater baths and low doses of malachite green have been used to control infestations of *C. errans* on *Cancer magister* (Wickham, 1988).

5.6.4 Acanthocephala – Polymorphus botulis

The Acanthocephala is a small phylum of strictly parasitic, pseudocoelomate, 'thorny-headed' worms. They have indirect life cycles and always use arthropods as first intermediate hosts. Montreuil (1954) and Uzmann (1970) reported *Corynosoma* sp. from *H. americanus*, but acanthocephalans can be difficult to identify and based on further examination, Brattey & Campbell (1985a) identified the worm as *Polymorphus botulis*, a common parasite of several species of sea ducks including eiders, *Fuligula mollissima* and scoters, *Melanitta* spp. The parasite apparently uses cancrid crabs as intermediate hosts; the lobster becomes an accidental or paratenic host when it preys on infected crabs and is unlikely to be preyed upon by sea ducks.

In the lobster, cystacanths of *P. botulis* can be found embedded in the intestinal wall, hepatopancreas, other organs, or free in the haemocoelom (Montreuil, 1954; Brattey & Campbell, 1985a). Interestingly, acanthocephalans can cause remarkable changes to their crustacean intermediate hosts including castration, changes to pigmentation, and alterations in behaviour, which make them more susceptible to predation (Crompton & Nickol, 1985; Moore & Gotelli, 1990). How lobsters may be affected by infections is unclear, but Brattey & Campbell (1985a) indicate that perforations in the midgut wall could potentially lead to mortalities.

Polymorphus botulis has been reported at relatively low prevalences from *H. americanus* from the Magdalene Islands in the Gulf of St Lawrence (Montreuil, 1954), the Canadian Maritimes (Brattey & Campbell, 1985a) and off New England (Uzmann, 1970). A single infected lobster was reported from the Mid-Atlantic Bight (Van Engel *et al.*, 1986).

5.6.5 *Annelida* – Histriobdella homari

Histriobdella homari is a eunicid polychaete worm found in the branchial chambers and egg masses of *Homarus gammarus* (Jennings & Gelder, 1976; Lerch & Uglem, 1996), *H. americanus* (Uzmann, 1967a; Brattey & Campbell, 1985b), and *Nephrops norvegicus* (Van Beneden, 1858; Lerch & Uglem, 1996; Briggs *et al.*, 1997). It was first described by Van Beneden in 1858 and so represents the second recorded symbiont for a lobster. The taxonomic position of *H. homari* and its freshwater relatives, *Stratiodrilus* spp., received significant debate in the early literature, but this seems largely resolved, placing it firmly in the Eunicidae (see Gelder & Jennings, 1975).

The worm is small, rarely more than 2 mm in length, and comprised of only nine post-cephalic segments (Jennings & Gelder, 1976). The posterior segment possesses two pairs of duo-adhesive glands that are used for attachment to the host (Gelder & Tyler, 1986). Reproduction is unusual as this is one of the few helminths that use hypodermic impregnation for copulation (Jamieson *et al.*, 1985). This type of copulation is more often found in tapeworms, the Cestoda. Females lay stalked egg capsules within the egg masses or on the internal margin of the carapace of the lobster host (Brattey & Campbell, 1985b). Development is direct (Haswell, 1913). Worms are transferred between hosts by direct contact and will crawl onto new instars at moulting (Simon, 1968; Gelder, 1980).

Histriobdella homari is a commensal because it grazes on bacteria and protozoa in the gills and on the embryos of its host (Jennings & Gelder, 1976). It was once thought to be an egg predator (Sund, 1914) or to inhibit egg hatching (Brattey & Campbell, 1985b), but high-intensity infections arising from laboratory-holding conditions showed no correlation with egg mortality (Lerch & Uglem, 1996). The highest intensity reported from the field was 699 worms from an ovigerous female (Brattey & Campbell, 1985b).

When present, the worm can often be quite abundant. Uzmann (1967a) reported prevalences up to 100% and mean intensities from 12 to 61 worms per infected host in lobsters collected off New England. Simon (1968) reported 100% prevalence on 27 lobsters examined off Woods Hole, Massachusetts. Boghen (1978) reported a low 11% prevalence from Northumberland Strait. Van Engel *et al.* (1986) found only one specimen of *H. homari* from their survey of 218 lobsters from the Mid-Atlantic Bight. Brattey and Campbell (1985b) reported a range of prevalences for *H. homari* on male (51.8–96.0%) and non-ovigerous females (39.6–87.5%), with ovigerous females often having the highest prevalences (76.7–100%). Generally, ovigerous females also had higher intensities of worms than males and non-ovigerous females (Brattey & Campbell, 1985b). Increased fouling due to the ovigerous state was thought to contribute to the higher worm intensities on these females.

5.6.6 *Nematoda*

Only two nematodes are known to infect lobsters and both infect *H. americanus*. *Ascarophis* sp. uses the lobster as an intermediate host and is found encysted in the wall of the hindgut. *Hysterothylacium* sp. is an accidental parasite found in the wall of the foregut and apparently survives only a short time because the lobster is an accidental host. *Ascarophis* sp. is an intestinal parasite of fishes (Jackson *et al.*, 1997). Lobsters probably become infected by ingesting eggs or larvae of the parasite or by ingesting other infected crustaceans. Relatively high prevalences have been reported, from 17.9% off the Mid-Atlantic Bight (Van Engel *et al.*, 1986) to 24.5% from Georges Bank (Uzmann, 1967b). The prevalence of *Ascarophis* sp. is apparently inversely related to lobster size. Only small lobsters (<80 mm CL) were infected with the parasite (prevalence of 46%) from the Mid-Atlantic Bight (Van Engel, 1986). Further, Boghen (1978) probably misidentified *Ascarophis* sp. from the gills of lobsters (35.2% prevalence) from the Northumberland Strait. Based on its location in the host, this parasite could not have been *Ascarophis* as this is strictly an internal parasite in its intermediate host (Brattey & Campbell, 1985a; J. Shields personal observation). It is doubtful that the parasite had entered the host via the gills as none was found in the hindgut or haemocoel. Perhaps it was *Pseudocarcinonemertes homari,* a nemertean worm that can reside in the gills of male and non-ovigerous female hosts (see Section 5.6.3).

Ascarophis sp. infects lobsters from offshore canyons and deeper waters and thus, may be an indicator of offshore to inshore migrations (Uzmann, 1970). Lobsters migrate from Georges Bank to offshore areas of Nova Scotia (Campbell & Stasko, 1985), thus this parasite should be present in these locations. However, the parasite was not reported from the Canadian Maritimes even though the sample size was large and lobsters were collected over a broad range of depths (Brattey & Campbell, 1985a). Given that only small lobsters are infected with the parasite (Van Engel, 1986), and that the Canadian survey did not sample animals <80 mm CL (except for those from Northumberland Strait, Brattey & Campbell, 1985a), the survey did not sample the appropriately-sized host for the presence of the worm. To further complicate the issue, smaller lobsters may not migrate long distances (Estrella & Morrissey, 1997; Rowe, 2001), thus accounting for the presumed lack of *Ascarophis* in Canadian waters.

Hysterothylacium sp. is an intestinal parasite of fishes that uses invertebrates and fishes as intermediate hosts. Lobsters obtained infections by eating infected fish that were used as bait (Brattey & Campbell, 1985a). Most of the worms were encapsulated and necrotic indicating that the lobster was a poor paratenic host, but viable specimens were present in the foregut along with partially digested fish. The prevalence of the worm varied from 1.1% to 5.6% and intensities were quite low; nonetheless, these values provide evidence that the use of fish bait by the fishery provides a parasite to the lobster. However, the threat to the lobster is extremely low as the parasite is successfully destroyed by the host (Brattey & Campbell, 1985). Perhaps this type of information could be used to model the contribution that bait supply makes to lobster production.

5.6.7 Miscellaneous helminths

Commensal turbellaria have been observed on the mouthparts and gills of spiny lobsters, *Panulirus* spp., from the Great Barrier Reef (J. Shields, unpublished data). These resemble *Monocelis* or *Ectocotyla* spp. that have been observed on the egg masses and gill chambers of snow crabs (Fleming *et al.*, 1981; Kuris *et al.*, 1991).

5.7 Miscellaneous metazoan symbionts

5.7.1 Nicothoidae – parasitic copepods

Nicothoe astaci is a nicothoid (= choniostomatid) copepod parasitic on the gills of *H. gammarus* in the Orkney and Bernera Islands, Scotland. This represents the earliest recognised parasite of a lobster, as it was orginally described by Audoin & Milne-Edwards in 1826. Mason (1959) reviewed the life cycle and biology of the parasite. The copepod attaches to a gill filament with a highly-modified suctorial mouth and pierces the gill with styliform, piercing mandibles. It then sucks the haemolymph from the host. This distinguishes this copepod from other copepods, which are not parasitic, found in the gill chambers of lobsters. Females are up to 1.7 mm in length, but they have elongate ovarian wings up to 4 mm in size. Egg sacs can carry several hundred eggs. The last-stage copepodid larva is infectious to the lobster, and several were found on lobsters in various stages of the moult cycle, but particularly on soft-shelled hosts, suggesting that perhaps lobsters acquire infections during the postmoult state. Mason (1959) examined several juvenile stages and found no trace of male parasites, and females were inseminated prior to settling on lobsters. The copepods are shed when the host moults. Larvae are released throughout the year, but peak production occurs in November (Mason, 1959).

Three other species of *Nicothoe* occur on the gills of lobsters. *Nicothoe analata* infects *Nephrops sinensis* (Kabata, 1966), *Nicothoe brucei* infects *Nephrops sagamiensis* from Japan and *Nephrops andamanicus* from South Africa, and *Nicothoe simplex* infects *Nephrops japonicus* from Japan (Kabata, 1967). The egg-predatory copepod *Choniomyzon panuliri* is another nicothoid, and it infects the clutches of *Panulirus* spp. from India (Pillai, 1962). The same copepod or a similar species can be found on the eggs of *Panulirus* spp.

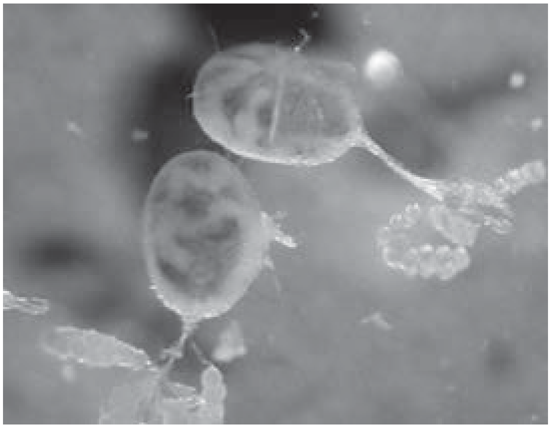

Fig. 5.9 *Choniomyzon* cf. *panuliri* from *Panulirus versicolor* from the Great Barrier Reef, Australia.

from the Great Barrier Reef (Fig. 5.9) (J. Shields, personal observation). Larval stages of *Choniomyzon* can also be found in the gills of non-ovigerous hosts. Nicothoids in the egg masses of crustaceans are typically egg predators and can cause significant damage to the fecundity of individual hosts (Shields & Wood, 1993). Gordon (1966) mentions that *Nicothoe homari* occurs on *Palinurus elephas* and that an *Anchorella*-like copepod occurs in the vas deferens of *Nephrops norvegicus*; however, these sightings require confirmation.

At least three other copepods are known to occur on lobsters. *Paramphiascopsis* sp. lives on the gills of both male and female *Jasus edwardsii* and *Sagmariasus verreauxi* (J. Booth, personal communication), *Unicaleuthes* sp. has been reported on the carapace of *H. americanus* (Sindermann, 1990), and a *Sunaristes*-like copepod occurs on the gills of *Panulirus* spp. from the Great Barrier Reef (J. Shields, personal observation). No doubt more symbiotic copepods will be discovered living either commensally or even parasitically on lobsters.

5.7.2 Amphipods

Amphipods can be surprisingly common on the egg masses or branchial chambers of spiny lobsters, yet there have been few studies of these symbionts on lobsters. *Parapleustes commensalis* can be found on the pleopods and egg masses of *Panulirus interruptus* and *Cancer anthonyi* (Shoemaker, 1952; J. Shields personal observation) and *Paralithodes californiensis* (Wicksten, 1982). It has been observed as an egg predator in experimental systems using crab eggs (J. Shields, unpublished data) but its relationship with the lobster is probably commensal. *Ischyroceros* sp. has been reported in large numbers from the egg masses of ovigerous red king crabs, *Paralithodes camtschaticus*, where it was correlated with significant egg mortality (Kuris *et al.*, 1991). Another species, *Gitanopsis iseebi* occurs in the branchial chambers of *Panulirus japonicus* (Yamato, 1993), where it probably has a symbiotic relationshp with the host, as do other members of the amphiolochid amphipods. *Isaea elmhirsti* is symbiotic on the mouthparts of *H. gammarus* (McGrath, 1981, in Costello *et al.*, 1990). Symbiotic or egg-predatory amphipods may be much more common on lobsters, but they may leave the host upon capture or may only occur on them when they are ovigerous, making them a more cryptic member of the symbiotic fauna. Given their potential as egg predators (Kuris *et al.*, 1991), these symbionts may warrant further attention, particularly in studies of fecundity or reproductive behaviours.

5.7.3 Fouling organisms

No doubt lobsters can host a remarkably diverse fouling community, but we have chosen to highlight only a few examples. Dexter (1955) reported that fully 79% of the ovigerous lobsters examined from Connecticut had at least one fouling organism, with the majority having an encrusting bryozoan, *Alcyonidium polyoum,* or a barnacle, *Balanus crenatus*. Even recently-moulted lobsters were colonised by fouling organisms. Some fouling agents are true symbionts. For example, several species of the pedunculate barnacle *Octolasmis* use the scyllarid lobster *Thenus orientalis*, as well as other decapods as hosts (Jeffries *et al.*, 1984). These barnacles are highly adapted to life in the gills of their crustacean hosts as well as the moult cycle of the host. In crabs, the fouling community has been used to examine biological and ecological questions (for reviews see Key *et al.*, 1996, 1997, 1999). Large decapods represent a biologically-active substrate on a mobile platform. Thus, the carapace is an ideal habitat for several sessile, short-lived organisms. Finally, in small numbers, fouling agents have little, if any, effect on their host. However, heavily-fouled blue crabs show an increased energy demand (e.g. Gannon & Wheatly, 1992, 1995). In addition, the egg clutches of females can have an entirely different community of fouling agents and saprophytic organisms that feed on dead and dying eggs.

5.8 Diseases of non-infectious or unknown causes

5.8.1 Ammonia/nitrite toxicity

Many lobster-holding recirculating facilities now have sophisticated recirculating filtration systems to maintain water quality at close to the optimum for the species (Crear *et al.*, 2003). The concentration of ammonia that has toxic effects has been investigated in several lobster species including *Homarus americanus*, *Panulirus cygnus* and *Jasus edwardsii*. The trend mirrors that of other Crustacea such as *Penaeus japonicus* (Chen & Chen, 1996) which are relatively unaffected by short-term exposure to ammonia, in comparison with marine finfish which are extremely susceptible to ammonia. Total ammonia–nitrogen in lobster-holding facilities should remain below $2\,\mathrm{mgL^{-1}}$ for *P. cygnus* and *J. edwardsii* and nitrite should remain below $5\,\mathrm{mgL^{-1}}$.

5.8.2 Air exposure

Air exposure is detrimental to *Panulirus cygnus* and results in hypoxia, increased lactic acid and magnesium ions in the haemolymph (Crear & Allen, 2002). These changes can result in death of the lobsters up to several days after the exposure. Weak lobsters are more likely to suffer from severe lactic acidosis and are more likely to die. Spraying lobsters with water during transport had no impact on the severity of hypoxia and lactic acidosis, and immersion was necessary to prevent this condition. In addition to ensuring that lobsters are not held out of water for significant periods of time, the dissolved oxygen in their water should be maintained at above 80% saturation (Crear & Allen, 2002).

5.8.3 Turgid lobster syndrome

'Turgid lobster syndrome' is a poorly understood condition that occurs in *Jasus edwardsii* (Diggles, 1999; A. Brown, personal communcation) from New Zealand and *Panulirus ornatus* (L.H. Evans, personal communication) from Australia. In this condition, the less sclerotised portions of the tergites of the abdomen become inflated with the clear, watery haemolymph. Affected animals stop feeding, become lethargic and up to 50% of the affected animals eventually die. Salinity alterations or suboptimal water quality, such as high levels of ammonia during transport, have been suggested as possible contributing factors by some investigators. However, Diggles (1999) noted that the condition may be associated with starvation or from physiological abnormalities in early premoult.

Wada *et al.*, (1994) described a similar condition in which affected lobsters showed weakness and had grossly visible swellings of the cuticular folds of the abdomen. The condition was characterised by mild to severe myocarditis with haemocytic infiltration of the degenerating and necrotic cardiac muscles. These were grossly apparent as white nodules in the heart. The condition occurred in freshly-caught lobsters as well as those held in the laboratory. No microbial agents were identified and the pathogenesis of this condition remains unexplained.

5.8.4 Shell blisters

'Shell blister syndrome' is distinct from shell disease (see Section 5.3.2). Shell blisters apparently form when the thin, undamaged cuticle of the telson and uropods lifts off the epidermal layer in a fluid-filled blister. In *Cancer* crabs, large blisters can be associated with problems in fluid uptake during moulting (J. Shields, personal observation). The aetiology for lobsters is unclear but shell blisters have been reported to precede the appearance of shell lesions in some instances (Geddes *et al.*, 2003).

5.8.5 Nutritional diseases – moult death syndrome and deformities

Deaths of Crustacea just before, during, or soon after ecdysis are a commonly-reported phenomenon. There are several reasons for this mortality, including increased stress resulting from the physiological events that occur before and during ecdysis, and failure to complete the moult because of adhesions between the old and the new exoskeleton. The latter is a common event when there have been infections and lesions resulting in a host defence response in the subcuticular area, or injury, or deposition of minerals or other material beneath the cuticle. Examples of this process are the failure to moult and resultant mortality reported in other Crustacea, including Chinese mitten crabs, *Eriochier chinensis,* that were experimentally infected with *Aphanomyces astaci* (Benisch, 1940), and the stunting of shrimp such as *Litopenaeus vannamei* that survive outbreaks of infectious hypodermal and haematopoietic necrosis virus (Lightner, 1996). Similarly, adhesions and deposits between the new and old exoskeleton have been reported to increase mortality around the time of moult in American lobsters with shell disease (Floreto *et al.*, 2000).

American lobsters with abnormal deposits of calcium in or beneath the exoskeleton also failed to moult with resultant mortality (Bowser & Rosemark, 1981). The dietary and/or environmental factors that resulted in these calcium deposits remain poorly understood, but deficiencies in phospholipids, fatty acids (particularly n-3 polyunsaturated fatty acids) and cholesterol as well as amino acid imbalances have been implicated in moult death syndrome of juvenile American lobsters with shell disease (Floreto *et al.*, 2000). Moult death syndrome may be related to calcinosis (see Section 5.8.7) as they both indicate a metabolic dysfunction in calcium buffering or storage.

5.8.6 Pink lobster syndrome

A poorly understood condition has been reported in western rock lobster, *P. cygnus,* that have pink to orange flesh and haemolymph. Affected lobsters are weak, have a bitter taste and are unlikely to survive transport to markets. The condition is most often reported in holding facilities but is sometimes reported by lobster fishermen at the site of harvest. The chemicals and pathophysiological processes responsible for the colour change have not been identified, but pink to orange haemolymph has been attributed to several causes including: increases in astaxanthin in the premoult stage of the moult cycle (Musgrove, 2001), the presence of vitellin or vitellogenin in pre-vitellogenic or early vitellogenic females, an increase in reserve inclusion cells at certain stage of the moult cycle, calcinosis (Dove *et al.*, 2004) and signs of *Hematodinium* infections in *Nephrops norvegicus* (Field *et al.*, 1992), or possibly melanin precursors of the prophenoloxidase cascade. Further investigation into the causes of discolouration of lobster flesh and haemolymph in both normal and diseased lobsters is needed so that normal biochemical and physiological processes can be distinguished from those resulting from disease processes.

5.8.7 Calcinosis

Calcinosis is a recently described metabolic disease of *H. americanus.* The condition was first described after a mortality that occurred in central and eastern Long Island Sound in 2002 (Dove *et al.*, 2004). Moribund lobsters had a distinctly orange colouration of the abdomen. Extensive multi-focal granulomas were observed microscopically in the gills leading to occlusion and ischaemia-induced necrosis (Plate 5.8). Reserve inclusion cells in the gills were depleted. Heavily calcified lesions (caliculi) were also observed in the antennal gland and caused disruption to the surrounding tissues. Naked crystals of calcium carbonate were observed in the antennal glands and gills in two of the sixteen afflicted lobsters that were examined. Dove *et al.* (2004) hypothesised that the lesions were the result of disruption of normal acid–base regulation leading to the formation of calcium carbonate following long-term exposure to high water temperature. By manipulating temperature in an experimental setting, Dove *et al.* (2005) demonstrated significant disruption to the acid–base regulation in lobsters held at 23°C compared with animals held at 16°C. Affected animals were also hyperchloremic and hyperproteinemic (Dove *et al.*, 2004). Curiously, total haemocyte density increased in animals held at the higher temperature, but phagocytosis activity decreased markedly. Ultrastructurally, the calculi were typical of excretory calcinosis described in other species (Dove *et al.*, 2004).

5.8.8 Light damage to the retina of Nephrops norvegicus

Loew (1976) was the first to report light damage to the eye of the Norway lobster. Under normal conditions, it does not occur in *Homarus* spp. (Shelton *et al.*, 1985; Maniscalco & Shields, in press; J. Shields, personal observation). The retinas of *Nephrops norvegicus* that are held in the dark for long periods, and then exposed to fluorescent light, exhibit significant and permanent damage. In controlled studies, Shelton *et al.* (1985) showed that short exposures (9 minutes) to light can cause pathological changes to the retina that were noticeable after one month, and longer exposures (2–6 hours) caused increasingly more damage to the eyes that culminated in loss of the retinula cells in ommatidia and infiltration of haemocytes into the necrotic ommatodia. Furthermore, dark-adapted animals experienced significantly more damage to the eyes than light-adapated animals (Shelton *et al.*, 1985, 1986). Initially, the proximal screening pigments move, concentrating around the retinula. With more extensive damage, the retinula cells become necrotic and haemocyte infiltration is widespread with apparent phagocytosis of the pigments. Both retinula and tapetal cells are affected by exposure (Gaten, 1988). Gaten (1988) found a good agreement between a stereoscopic method and a histological method for assessing the damage to eyes of affected lobsters. In a field assessment of the condition, using a tagging study and both the stereoscopic and histological methods, Chapman *et al.* (2000) showed that light-induced damage had little effect on the mortality of affected animals compared with unaffected animals. However, the sustained damage was irreversible, occurring in animals tagged and recaptured after several years. Interestingly, female lobsters had a significantly better recapture rate than males, but light-induced damage was not a factor.

5.9 Lobster defence mechanisms

The study of the immune defence systems of crustaceans has undergone a marvellous transformation with the advent of new biochemical and molecular techniques. It seems that new or homologous cellular and humoral processes are being discovered every day. Thus, a critical review of crustacean defensive responses is beyond the scope of this chapter. However, we briefly address key features of both the cellular and humoral responses, such as phagocytosis, opsonisation, and the role of the prophenyloxidase (proPO) system, lectins, and new antimicrobial peptides. For reviews of haemocyte morphology and function, see Johnson (1980), Bauchau (1981), Hose *et al.* (1990) and Battison *et al.* (2003). For pertinent observations on the earlier literature, see Sindermann (1971, 1990), and for newer syntheses, see Smith and Chisholm (1992), Söderhäll and Cerenius (1992), Bachère *et al.*, (1995), Holmblad and Söderhäll (1999).

Lobsters have similar defence mechanisms to other decapods, including shrimp and freshwater crayfish. Understanding of the internal defence mechanisms of crustaceans began with research on phagocytosis and the inflammatory response in the 1880s and on the humoral defense response between 1910 and the 1930s. Work then languished until the 1960s (Sindermann, 1971) when crustacean diseases broke out in economically important fisheries, particularly gaffkaemia in lobsters and fungal infections of freshwater crayfish.

Cellular defence mechanisms can be divided into three broad groupings: maintenance of exoskeleton integrity; recognition, inactivation and elimination of foreign agents; and repair of damage by toxins. These systems share five basic processes: coagulation (clotting), phagocytosis, degranulation, encapsulation, and haemocytosis, and are particularly dependent on circulating haemocytes, fixed phagocytes which surround the blood vessels, and fibrocytes. Circulating haemocytes arise from haematopoietic tissues that are located on the dorsal aspect of the foregut in lobsters (Martin *et al.*, 1993; J. Shields personal observation). Haemocytes are generally considered to have three forms, hyalinocytes, semi-granulocytes (small granule haemocytes) and granulocytes (large granule haemocytes) (Hearing & Vernick, 1967; Hose *et al.*, 1990: Johansson *et al.*, 2000); however, Battison *et al.* (2003) reported 11 types of haemocytes in *H. americanus,* several of which were considered precursors to the above cell types, including a 'stem cell' precursor. So-called 'reserve cells', involved in lipid transport, may appear in the haemolymph at moult but are generally ignored in haemocyte classification systems.

The defence mechanisms, being enzyme-based, are temperature-dependent, yet few studies have explored the relationship between optimal temperature and immunocompetency with moulting, reproduction or even susceptibility to infection. This is surprising because glycogen, lipids, fatty acids and other products of oxidative and glycolic metabolism are mobilised for moult (Travis, 1955), and it is becoming apparent that many of these constituents have multiple roles, including involvement in humoral defensive responses (e.g. lipoproteins and clotting, Hall *et al.*, 1995; histones and antibacterial activity, Patat *et al.*, 2004).

5.9.1 Maintenance of exoskeleton integrity

The exoskeleton of lobsters provides an effective barrier against the entry of infectious agents as well as providing muscle anchorage and protecting the underlying soft tissue. The first barrier of the exoskeleton is the very thin proteolipid, polyphenolic epicuticular membrane or 'surface waxy layer' (Unestam, 1973; Malloy, 1978; Fisher, 1988). Relatively little work has been published on the chemical properties of this layer, which is assumed to have bactericidal and anti-fouling function. Beneath this layer is the calcified and tanned, lipoproteinaceous epicuticle above a thin, quinone-hardened layer (Travis, 1955) that is very difficult to penetrate, even for disease agents secreting extracellular chitinases. By contrast, the soft non-calcified endocuticle is easily penetrated by such agents (Unestam, 1973). Maintenance of the waxy layer and epicuticle is via pore canals and is dependent on the nutritional status of the animal (Fisher *et al.*, 1976a).

Any break in the exoskeleton must be sealed to prevent loss of haemolymph, maintain osmotic integrity and minimise opportunistic invasion. Wound repair in lobsters is initiated by haemocyte aggregation at the wound site and rapid clotting followed by melanisation and tanning.

Aggregation of semi-granulocytes and granulocytes is accomplished by a combination of binding by pseudopodia and humoral factors. Cellular aggregating proteins are liberated from haemocytes after activation of the prophenoloxidase system (Sritunyalucksana & Söderhäll, 2000). Aggregation occurs in response to cell damage, as well as foreign agents such as *Vibrio* spp. (Johnson, 1976; Newman & Feng, 1982) and is the precursor to encapsulation of cellular debris and foreign agents too large to phagocytose. Aggregation against vibrios is often accompanied by extensive pre-mortem clotting of plasma and, in severe cases, the aggregation and plasma clotting can obstruct haemolymph leading to massive focal necrosis, particularly in the gills (Johnson, 1976).

The rapid production of haemocytes in response to 'insults' is critical for maintaining the defence against infection. The fall in haemocyte numbers following an insult and the use of 'total haemocyte counts' to detect the immune status of lobsters has, therefore, been extensively studied (Cornick & Stewart, 1968; Manjula *et al.*, 1999; Jussila *et al.*, 2001). Haematopoetic tissue has been identified in *Homarus americanus* (Martin *et al.*, 1993), and at least in blue crabs it is stimulated to produce more haemocytes with changes in temperature or infection (Johnson, 1980). However, hematopoiesis also changes with the moult cycle (Johnson, 1980), and that may obscure a response directed to infectious agents. Though haemocyte numbers and proportions of cell types vary between animals, environmental stimuli, endocrine activity and infection (see review by Moullac & Haffner, 2000), the role of haematopoetic tissue in compensatory generation of haemocyte types remains unclear. Nonetheless, activation of the haematopoietic tissue and factors controlling sequestration of haemocytes are fruitful areas for investigating the nature of inducible cellular responses in crustaceans.

5.9.2 *Coagulation*

Clotting not only stops leakage of haemolymph through wounds but also traps and isolates foreign particles. Clotting is initiated by the rupture of hyalinocytes following contact with seawater or oxygen (Durliat & Vranckx, 1989; Hose & Martin, 1989). The granules in the hyalinocytes and semi-granulocytes dehisce, or lyse, by means of exocytosis and release their products into the extracellular matrix (Hose *et al.*, 1990). The rupture releases a transglutaminase that in the presence of Ca++ coagulates a soluble clotting protein (coagulogen) in the haemolymph (Doolittle & Fuller, 1972; Doolittle & Riley, 1990; Aono & Mori, 1996; Montaño-Pérez *et al.*, 1999; Sritunyalucksana & Söderhäll, 2000). The release of transglutaminase into the haemolymph can also be initiated by pattern-binding proteins complexing with their target and binding to receptors on the haemocytes. Clotting activity may be modulated by ∞2-macroglobulin-like protease inhibitors in the haemolymph (Hergenhahn & Söderhäll, 1985).

Semi-granulocytes adjacent to the wound then cue the migration and activation of granulocytes that release prophenoloxidase, which initiates melanisation of the wound area to form a dense black membrane beneath which the new epidermis forms. Melanin is produced by the action of the enzyme prophenoloxidase on phenolic melanin precursors (Unestam & Nylund, 1972; Bauchau, 1981) and has antimicrobial properties (Nyhlen & Unestam, 1980; Söderhäll & Ajaxon, 1982). The epidermis involutes into the wound utilising the haemocyte network as a basal support. New cuticle is formed by this epidermal layer and lies beneath the melanin membrane (Fontaine, 1975). A dense network of collagen-like fibres forms in association with the haemocyte response. This fibrous tissue is not resorbed but remains as a scar (Fontaine & Lightner, 1975). Damaged tissues and non-self particles are removed by phagocytosis or encapsulation.

5.9.3 *Foreign agent recognition*

Inflammation has been studied in penaeid shrimps and the process appears to be identical in spiny lobsters (Martin *et al.*, 2000). Injection of shrimp with carmine (a neutral contaminant) is followed by accumulation of carmine in the dorsal abdominal artery, ventral abdominal vein, heart and gills. By 30 hours post-injection, carmine is only visible in the gills, heart and injection site (Fontaine & Lightner, 1974). Histologically, the carmine forms tightly packed extracellular masses at the injection site, which are infiltrated and phagocytosed by haemocytes. Circulating carmine particles are then trapped by fixed phagocytes lining the blood vessels and in sinusoids of the gill filaments. These particles finally accumulate in the distal gill filaments and heart. Brown melanised nodules, consisting of necrotic haemocytes containing phagocytosed carmine, develop in the pereiopods, and as cysts in the connective tissues of the gill, by a process of filtration rather than through the action of fixed phagocytes and are subsequently shed at moulting (Martin *et al.*, 2000). Dye-containing haemocytes also migrate through the midgut epithelium and into the lumen of the antennal gland.

Foreign proteins such as lipopolysaccharides (LPS), ′ -1,3-glucans (BG) or peptidoglycans (PG) are detected and bound on the haemocytes by pattern-recognition proteins which are serine-protease homologues (Lee & Söderhäll, 2001). These proteins, when complexed with the target molecule in turn bind to a haemocyte receptor (reviewed by Söderhäll *et al.*, 1996; Sritunalucksana & Söderhäll, 2000). This triggers release of prophenloxidase, by degranulation, from semi-granulocytes and granulocytes. Prophenoloxidase is activated by a serine protease, found in the cuticle and in haemocytes (Hernández-López *et al.*, 2003), moderated by inhibitors (Hergenhahn & Söderhäll, 1985) and results in the production of melanin (the proPO system, see below).

Lectins are also a part of the self/non-self recognition system in crustaceans and they have been studied in both spiny lobsters (Tyler & Scheer, 1945; Imai *et al.*, 1994; Manjula *et al.*, 1999) and clawed lobsters (Hall & Rowland, 1974a, b). Lectins are polyvalent proteins or glycoproteins with binding affinities for specific carbohydrates, primarily polysaccharides and lipopolysaccharides. The role of lectins is somewhat speculative, but they are considered to facilitate agglutination of bacteria, activate haemocytes for phagocytosis of agglutinated particles, and serve as opsonins for recognition of non-self particles by haemocytes (Hardy *et al*., 1977; Vasta & Marchalonis, 1983; Ey, 1991). Those identified in *H. americanus* include one specific for sialic acid residues and one for N-acetyl-galactosamine (Durliat & Vranckx, 1989). The resulting complexes are susceptible to phagocytosis or encapsulation. For a comparative review of lectins in invertebrates and vertebrates, see Arason (1996).

5.9.4 Cellular responses

Phagocytosis is a primary defence mechanism in invertebrates. It occurs in fixed phagocytes and the circulating semi-granulocytes of lobsters (Cornick & Stewart, 1968; Hose *et al*., 1990). Phagocytosis assays have been developed for *H. americanus* (Paterson & Stewart, 1974), but not for other species of lobsters. Such assays can give an insight into the immune status of the host. For example, temperature has been shown to have a major effect on phagocytosis in *H. americanus* (Steenbergen *et al*., 1978). Above 22°C, phagocytosis of non-pathogenic *Aerococcus viridans* was nearly 75% lower than in lobsters held at 16°C. Similarly, lobsters exposed to malathion exhibited significant declines in their phagocytosis (DeGuise *et al*., 2004). In addition, increased levels of manganese brought about by eutrophication, has been shown to induce suppression of proPO, presumably through induced haemocytopenia (Hernroth *et al*., 2004). In all of these cases, the authors speculated that animals exposed to these stressors may be more susceptible to disease due to inhibited immune response; and all of these, temperature stress, pesticides and hypoxic production of manganese, may have been associated with outbreaks of *Paramoeba* in Long Island Sound (see Section 5.5.5).

In other decapods, phagocytosis is stimulated by opsonins, which are proteins such as peroxinectin and ′ -1,3-glucan binding proteins (BGBP). Peroxinectin is a peroxidase synthesised and stored in granulocytes and semi-granulocytes of crayfish, shrimps and crabs, and is activated after its release from these cells (Sritunyalucksana & Söderhäll, 2000; Liu *et al*., 2005). It functions in degranulation (Johansson & Söderhäll, 1989), encapsulation (Kobayashi *et al*., 1990), opsonisation (Thörnqvist *et al*., 1994), and as a peroxidase (Johansson *et al*., 1995). Peroxinectin stimulates adhesion and spreading of haemocytes, promoting encapsulation by the semi-granular and granular haemocytes. Extracellular superoxide dismutase may function as a receptor for peroxinectin and, together with binding proteins, may bind to integrins present in the haemocyte membrane (Johansson *et al*., 1999; Sritunyalucksana & Söderhäll, 2000). BGBP is also an opsonin and stimulates phagocytosis of fungal invaders (Thörnqvist *et al*., 1994), facilitates release of prophenoloxidase from granulocytes (Lee *et al*., 2000) as well as enhancing cell spreading (Barracco *et al*., 1991).

Spheroids are aggregates of haemocytes that often form in shrimps during viral infections (Hasson *et al*., 1999). The lymphoid organ is commonly affected by spheroid formations because the organ is thought to function as a haemolymph filter (Bell & Lightner, 1988). Anggraeni & Owens (reported in Hasson *et al*., 1999) showed that spheroids were of haemocyte origin and Hasson *et al*. (1999) experimentally induced spheroid formation associated with Taura syndrome virus. They suggested that spheroids (both in the lymphoid organ and elsewhere) are part of the chronic inflammatory response and represent a form of aggregation associated with the phagocytic process and are involved in trapping and neutralising unwanted particles. Spheroids are yet to be reported from lobsters, perhaps because of the paucity of viruses infecting them.

Haemocyte degranulation is a process by which granulocytes lyse, releasing toxic substances and lytic factors capable of killing microbes and nearby cells. In shrimps (Destoumieux *et al*., 2000; Munoz *et al*., 2002) and crabs (Relf *et al*., 1999), granulocytes manufacture, store and release, by cell lysis, anti-microbial peptides of the penaedin family, as well as prophenoloxidase. Penaedin-positive bacteria are then phagocytosed by hyaline haemocytes (Munoz *et al*., 2002). The mechanism in lobsters is probably similar. The damage caused by degranulating granulocytes is localised through protease inhibitors to prevent digestion of non-target tissues; and a broad spectrum inhibitor, ∞2-macroglobulin, has been identified from lobsters as well as several other crustaceans (e.g. Spycher *et al.*, 1987; Gollas-Galvan *et al.*, 2003). Semi-granulocytes and granulocytes also contain N-acetyl-glucosamine, which may function in wound repair and encapsulation (Martin *et al.*, 2003).

Melanisation and the related prophenoloxidase (proPO) cascade are complex processes initiated by the cellular defences of crustaceans as well as other invertebrates. Söderhäll (1982), Johansson & Söderhäll (1989), and Söderhäll & Cerenius (1992) provide reviews of the proPO cascade. Melanisation is part of the encapsulation and nodulation process that is part of the response to isolate foreign invaders or repair wounds. Phenoloxidase triggers melanisation. Granulocytes sequester the inactive proenzyme, proPO (Johansson & Söderhäll, 1989; Hose *et al.*, 1990). The proenzyme is activated in a complex cascade involving a series of peptides and other enzymes (for review, see Söderhäll & Cerenius, 1992, 1998). This process involves cellular communication between the semi-granulocytes and the granulocytes. The semi-granulocytes are triggered to degranulate upon contact with the lipopolysaccharides (LPS) of Gram-negative bacterial cell walls, peptidoglycans in fungal cell walls, and presumably some metazoan invaders. Peroxinecten, released by the semi-granulocytes, stimulates the degranulation of granulocytes, which then release proPO. LPS, peptidoglycans, and ′ -1,3-glucans, also stimulate degranulation of the granulocytes directly by binding with beta-glucan binding protein (BGBP) in the haemolymph. Phenoloxidase is catalysed from proPO by a serine protease called prophenoloxidase-activating enzyme. The phenoloxidase then acts on phenols in the haemolymph to produce quinones that polymerise to form melanin. Several enzymes and other proteins are involved in regulating the level of encapsulation, melanisation, cell adhesion, and degranulation (Johansson & Söderhäll, 1989; Söderhäll & Cerenius, 1998).

In spiny lobsters, prophenoloxidase is apparently located in the plasma and not the haemocytes (Hernández-López *et al.*, 2003), but it also occurs in the granulocytes (Fig. 5.10) (J. Shields, personal observation), and activation to phenoloxidase is still orchestrated through the granulocytes. Interestingly, haemocyanin fragments have phenoloxidase activity (Lee *et al.*, 2004), thus the decreases in haemocyanin that occur with *Hematodinium* infections in the Norway lobster may further weaken the melanisation response in infected hosts and perhaps account for alterations in the tanning of the cuticle.

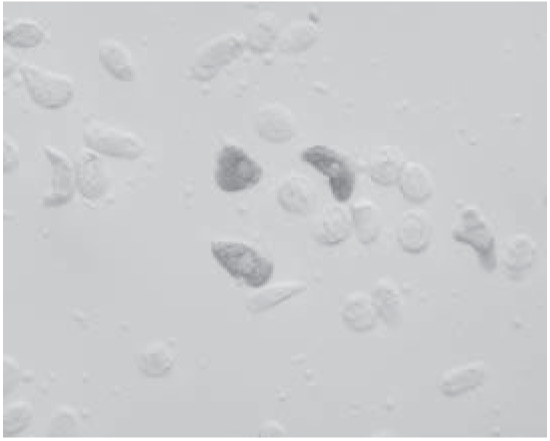

Fig. 5.10 Haemocytes of *Panulirus argus* in Grace's medium. Granulocytes incubated with L-dopa stain dark brown (arrows), indicating the presence of prophenoloxidase within the cells, and not within the serum which is absent from the medium. Hoffman modulation contrast, 400x. (Photograph courtesy of Caiwen Li, VIMS.)

Phenoloxidase activity varies with season and moult stage in spiny lobsters (Ferrer *et al.*, 1989). However, the increased variance in activity in May to September was confounded by moulting, which had a much more significant association with the activity of the enzyme (Ferrer *et al.*, 1989). Moderate to rapid cooling and low temperatures caused decreases in haemocyte density and phenoloxidase activity in spiny lobsters (Gomez-Jimenez *et al.*, 2000), but the changes were not apparent after long-term immersion at 7°C. In *Carcinus maenas*, phenoloxidase activity showed a significant association with seasonality and bacterial abundance (Hauton *et al.*, 1997). Surprisingly, changes in activity were not associated with changes in granulocyte densities, but were thought to be due to increased production of enzyme (Hauton *et al.*, 1997). Furthermore, phenoloxidase activity was negatively associated with tidal height (Hauton *et al.*, 1995). Given that bacterial infections are common in crabs during summer months (Tubiash *et al.*, 1975; Davis & Sizemore, 1982; Welsh & Sizemore, 1985), an enhanced phenoloxidase production could explain why infected crabs survive relatively heavy infections.

The DNA sequence of proPO and BGBP has been determined for *H. gammarus* (Hauton *et al.*, 2005). The proPO gene shared a 61–63% homology and the BGBP gene shared a 69–72% homology with various prawn sequences. Furthermore, a runt-domain protein, which facilitates differentiation of haemocytes, has recently been identified in the Norway lobster (Hernroth *et al.*, 2004). Thus, clawed lobsters have phenoloxidase, cell recognition and developmental signalling molecules homologous with other decapods.

Bactericidins are circulating peptides with antibacterial activity. They have been identified from the haemolymph of *Panulirus argus* and *P. interuptus* (Evans *et al.*, 1968, 1969a, b; Weinheimer *et al.*, 1969a, b) as well as *H. americanus* (Stewart & Zwicker, 1972; Mori & Stewart, 1978). They probably serve as opsonins as well as having distinct antimicrobial activity.

Penaeidins and callinectin are small peptides that exhibit specific activity against Gram-negative bacteria and fungal pathogens. These peptides are localised on the cell surface of haemocytes (Noga *et al.*, 1996) or within the granules of the granulocytes, which release them during exocytosis (Destoumieux *et al.*, 2000). Interestingly, callinectin levels decreased in association with shell disease in blue crabs from polluted waters (Noga *et al.*, 1994). Correlations between antimicrobial peptides and environmental stressors should be investigated in lobsters.

5.9.5 Repair of damage by toxins

Toxins come from three main sources: environmental contaminants; toxins associated with foreign invaders (Bowser *et al.*, 1981); and toxins resulting from tissue damage and haemocyte degranulation. While there are numerous papers that describe the toxicity of chemical compounds to lobsters (see Mercaldo-Allen & Kuropat, 1994), the majority of these document the concentrations at which biological effects are seen without attempting to describe any tissue damage associated with the toxin. This is probably because acute toxicity often kills an animal before it can develop overt histopathological changes. Furthermore, the physiology of crustaceans is linked to the moult cycle, and the susceptibility to toxins often depends on the moult stage (Wright, 1977; Daly *et al.*, 1992). However, few studies report toxic effects over a moult cycle or on a particular moult stage. The chronic effects of chemicals have likewise been little investigated.

Reactions to toxins in shrimps have been studied using injected irritant substances such as turpentine (Fontaine *et al.*, 1975). The heart is the organ most affected by circulating turpentine in the haemolymph (Fontaine *et al.*, 1975). An acute inflammatory reaction produces melanised haemocytic nodules in the heart followed by an influx of haemocytes and fibrocytes. Scar tissue is also formed as collagen-like fibres proliferate and replace myocardial fibres in which numerous melanised nodules are interspersed. The myocarditis reported by Wada *et al.* (1994) in *Panulirus japonicus* may represent the result of such event.

Decapods have active mechanisms to detoxify and remove metals including enzyme-based detoxifaction using metallothionein (Valls *et al.*, 2001; Chavez-Crooker *et al.*, 2003). It is beyond the scope of this chapter to review enzyme pathways for toxicants; however, the cellular mechanisms which do this are in most cases the same as those used to cope with foreign body inactivation and removal. Thus histopathology, with few exceptions, provides few clues about the cause of the original insult.

5.9.6 Organ-derived components

Several organ systems in crustaceans are actively or passively involved in the cellular defences. The gills passively filter bacteria-containing nodules formed by haemocytes. The flow of haemolymph to the gills is under positive pressure (Maynard, 1960) with the return flow being under negative pressure. Therefore, the gills serve as passive ‘sinks’ for foreign particles and reacting haemocytes and localised nodules (Cornick & Stewart, 1968; Solangi & Lightner, 1976; Smith & Ratcliffe, 1978, 1980; White & Ratcliffe, 1982; White *et al.*, 1985; Martin *et al.*, 1998). Lectins facilitate the deposition of nodules in the narrow spaces of gill lamellae (Smith & Ratcliffe, 1980; Martin *et al.*, 1998, 2000). The thin, membranous, gill lamellae are permeable and may allow removal of waste products directly or by sloughing of melanised capsules with ecdysis. Both the gills and the antennal glands clear foreign proteins and small particles such as virions (McCumber & Clem, 1977; Johnson, 1980; Clem *et al.*, 1984) and the hepatopancreas can clear small particles (McCumber & Clem, 1977; McCumber *et al.*, 1979).

5.10 Conclusions

Diseases are an integral part of lobster populations. They have obvious negative impacts on individuals, but extrapolation to host populations and their dynamics can be difficult. Nonetheless, pathogens such as PaV1, *Hematodinium* sp., *Aerococcus viridans* and *Anophryoides haemophila* may seriously affect their hosts and may play a role in the population dynamics of host stocks. These pathogens cause both direct and indirect losses of their hosts to the fisheries.

Direct losses can be obvious, such as those caused by epizootics that impact the socio-economic fabric of the fishing community (Connecticut Department of Environmental Protection, 2000). Direct losses may also occur as marketability issues, such as unsightly lesions of shell disease, or moribund animals unfit for market, and market losses can directly influence public opinion about the quality of the product. Direct losses may also occur in unfished segments of the lobster population, that is, juveniles are often at greater risk of disease than adults for several commercially exploited decapods (e.g. Messick & Shields, 2000; Shields & Behringer, 2004; Shields *et al.*, 2005).

Indirect effects are harder to gauge, but diseased lobsters may be more susceptible to predation or cannibalism, and thereby effect transmission of their parasites, or they may suffer increased egg predation that can limit larval populations through increased mortality of broods (e.g., Brattey *et al.* 1985a).

With the advent of live shipping of lobsters over long distances there is now the increased threat of the accidental introduction of pathogenic agents to new regions (cf. *Aerococcus viridans*, Steenbergen & Schapiro, 1974) with the potential for consequences in other lobster species. Understanding transmission and pathogenicity of the different pathogens is, therefore, critical to minimising their spread in this fashion. This should not be taken lightly as introduced viruses have wreaked havoc on the shrimp industry worldwide (Flegel, 1997; Lightner & Redman, 1998). For animals held for live shipping to international markets, health examinations may provide a modicum of protection against the further spread of disease agents (e.g. International Office of Epizootics, World Health Organization).

There are a few practical control measures that can mitigate the impacts of disease agents on any crustacean fishery (Shields & Overstreet, 2005). Simple measures such as ‘culling’ infected individuals on station or within an impoundment, removing dead animals for disposal in onshore fertiliser processing plants, limiting transportation of live animals and changing ‘baiting practices’ may limit the spread of pathogens to new locations. Furthermore, several state and regional fishery management agencies have stock-assessment programmes for lobster fisheries. These assessments should include information on the number of dead or moribund animals or animals that are discoloured or fouled in some way (e.g. Pestal *et al.*, 2003; Shields *et al.*, 2005). Such information can provide a wealth of data on disease prevalence and association with host factors and environmental variables.

Stressors appear to play an important role in lobster diseases and mortalities. Seasonal hypoxia and temperature extremes are often associated with disease or death, but neither stressor has received much attention in this respect. For example, the eventful mortalities in Long Island Sound highlighted by infections of *Paramoeba* could be related to temperature stress, hypoxia, increased manganese concentrations, pesticides, other pollutants, or combinations of these. Such stressors should be examined in laboratory and mesocosm studies as they no doubt contribute to the health status of lobsters.

Finally, parasites and diseases can serve as biological indicators or ‘tags’ for their lobster hosts. Two examples will suffice. First, the outbreak of the ‘epizootic’ form of shell disease on *H. americanus* in eastern Long Island Sound (Castro & Angell, 2000), but not elsewhere, perhaps indicates that these lobsters represent a separate stock from those off the Gulf of Maine, or even those within central and western Long Island Sound. Alternatively, an as yet unidentified stressor acts only within these waters. Second, the nematode *Ascarophis* sp., is primarily a parasite of juvenile *H. americanus* from deep water canyons and the continental shelf (Uzmann, 1970). It may be a useful marker indicating the proportion of juveniles that migrate from shelf locations to shallower waters. Surprisingly, no studies have really evaluated the nematode for its biological information. These types of ‘indicator’ species are not difficult to assess, they should be developed for assessments of migrations and water quality on their lobster hosts.

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Chapter 6

Nutrition of Wild and Cultured Lobsters

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6.1 From the wild

Lobsters are a large and diverse group classified into 45 clawless species called rock (spiny) lobsters and 30 clawed species. Interest in rock lobsters usually extends to those belonging to the *Palinurus*, *Panulirus* and *Jasus* genera, whilst clawed lobster research has concentrated on the American, *Homarus americanus*, and European, *Homarus gammarus*, lobsters and to a lesser extent the Norwegian lobster, *Nephrops norvegicus*.

As with other species under development for aquaculture, the starting point when considering their nutrient requirements and the ultimate fabrication of a suitable artificial diet is what the animals consume in the wild. However, the natural diet of larvae are as yet unknown, although larvae of *Jasus edwardsii* and the packhorse lobster, *Sagmariasus verreauxi*, have the ability to feed on a range of food types (Nelson *et al.*, 2002; Cox & Johnston, 2003a; Johnston *et al.*, 2004) and based on signature lipid profiling have been associated with a number of zooplankton species (Jeffs *et al.*, 2004). Postlarval *H. americanus* were found to exist on a mixture of detritus and small invertebrates such as sea urchins, mussels, rock crabs, polynoid and nereid polychaetes, and brittlestars (Carter & Steele, 1982b), copepods, decapod larvae, fish eggs and insect parts (Juinio & Cobb, 1992), while the juvenile western rock lobster, *Panulirus cygnus*, primarily consumed molluscs but were found to occasionally feed on foliose coralline algae (Joll & Phillips, 1984). The diet of the European rock lobster, *Palinurus elephas*, consists largely of molluscs, crustaceans and sea urchins (Goñi *et al.*, 2001) and the South African rock lobster, *Jasus lalandii*, feeds on sea urchins and black mussels (Barkai *et al.*, 1996; Mayfield *et al.*, 2001), abalone (Mayfield & Branch, 2000; Mayfield *et al.*, 2001) and winkles (Van Zyl *et al.*, 1998).

All these investigations show that lobsters are generalist feeders taking a wide variety of food items, but mostly slow moving benthic invertebrates including bivalves, polychaetes, echinoderms, gastropods, as well as algae and other material scavenged from the seafloor. There are marked dietary differences between species but these tend to relate more to food availability in different habitats, as the same species feeding in different locations will consume different food. Likewise, there are marked differences in the food of individuals of the same species, but of different sizes, which tend to reflect the increased mobility of the larger animals and an ability to tackle larger prey items.

To date, the bulk of nutrition research on decapods has concentrated on penaeid prawns, driven entirely by the commercial importance of the two main species, the giant tiger prawn, *Penaeus monodon*, and the kuruma prawn, *Penaeus japonicus*. Like lobsters, prawns feed on a wide variety of benthic organisms and detritus and consequently both lobsters and prawns could be considered to be omnivorous scavengers. Hence, making use of the extensive data gathered for prawn nutrition provides an excellent place from which to start when considering the nutritional requirements of lobsters.

To understand the basics of lobster nutrition and set the scene for the endeavours so far made to formulate an artificial diet for aquaculture, it is important to mention some of the physical and physiological characteristics which set them apart from other higher animals and directly impacts on their ability to gather, consume and digest food to meet their nutritional needs. These characteristics were well defined by Guillaume and Ceccaldi (2001) and with additions are presented below:

- The growth of crustaceans is accomplished by moults, which means that crustaceans are committed to cycles of laying down reserves and subsequent reutilisation of nutrients leading to a 'discontinuity in nutrient flux'.
- During the moult cycle as the animal prepares to accomplish a moulting, moulting itself and recovery from the process, there exists periods when the animal is forced to fast.
- As well as shedding and replacement of the external carapace for crustaceans there is also renewal of the walls of the uppermost portion of the digestive tract or oesophagus.
- Crustaceans possess a 'unique anatomy for mastication and absorption' whereby a significant portion of the processing of the food is carried out externally, compared to finfish where food items are swallowed whole.
- Crustaceans have specific mechanisms for digestion and absorption such as the presence of a calcareous arrangement located anterior to the restriction between the cardiac and pyloric chambers of the stomach known as the gastric mill. The purpose of this apparatus is to crush and grind the ingested food, the size of which is purported to be inversely related to the size and efficiency of the mandibles. In addition, crustaceans possess an organ known as the digestive gland or hepatopancreas, which accomplishes functions such as production of digestive enzymes, nutrient absorption and nutrient storage.
- Crustaceans also have certain unique enzymes, in addition to enzymes equivalent to those found in vertebrates such as astacin, which is a very broad-spectrum protease.

This means that diets designed for crustaceans, in addition to providing adequate nutrition, need to possess more appropriate physical characteristics, such as a firm texture and higher water resistance to nutrient leaching, than those designed for finfish. These issues appear to have been largely ignored in the fabrication of diets for prawns.

One constant in the research and development of diets for lobster aquaculture has been the consistent use of fresh, live mussels (e.g. *Mytilus edulis* and *Perna canaliculus*). Examples include *Homarus americanus* (Floreto *et al.*, 2001), small juvenile *Panulirus cygnus* (Glencross *et al.*, 2001), post-puerulus *Jasus lalandii* (Dubber *et al.*, 2004), and post-puerulus (James & Tong, 1997) and juvenile *Jasus edwardsii* (James & Tong, 1998; Jeffs & James, 2001; Crear *et al.*, 2002; Johnston *et al.*, 2003; Ward *et al.*, 2003). Even phyllosoma larvae are fed mussels, as with *Palinurus elephas* (Kittaka *et al.*, 2001), the Japanese rock lobster, *Panulirus japonicus* (Yamakawa *et al.*, 1989), *Jasus edwardsii* (Ritar, 2001; Ritar *et al.*, 2002, 2003) and a number of other palinurid species (Kittaka, 1997a). Fresh, live mussels have become a default reference diet, as they appear to perform consistently well as food for lobsters.

The future of any commercial lobster aquaculture venture will depend on the ability to take the next step beyond live or wet feeds. Indeed, studies have shown that using live feeds such as mussels is not cost-effective and impractical on a large commercial culture scale (Jeffs & Hooker, 2000). Therefore, development of formulated feeds that are specifically designed to meet the requirements of species and life history stages is vital for the success of future commercial lobster aquaculture.

6.2 Proteins

Protein is an essential component of any diet. Protein provides the main building block for tissues and can also be utilised effectively to produce energy to drive metabolic processes.

6.2.1 Amino acids

Crustaceans, like fishes, have 10 amino acids (AA) that are essential for growth. These are arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine (Table 6.1). Much of this information has been gained through research on penaeid prawns (Hew & Cuzon, 1982; Kanazawa, 1982; Guillaume, 1989; Chen, 1993; Teshima *et al.*, 1997). Researchers have confirmed the shared essentiality of these 10 AA in other crustacean species (Claybrook, 1976; Lasser & Allen, 1976), including the clawed lobster, *Homarus americanus* (Gallagher, 1976). However, determining essentiality and the exact requirements of AA are quite different. Determining the AA budget for any species is difficult, and further exacerbated in crustaceans by the high amount of proteins bound and continually lost in the exoskeleton at each moult, and the difference of arginine-based rather than creatine-based phosphagen for anaerobic energy production (escape response). Deshimaru (1981) found that juvenile and adult prawns could not assimilate crystalline or free AA (assimilation rate <0.6%), while protein-bound AA was assimilated readily (assimilation rate >90%). Chen (1993) found that *Penaeus monodon* was able to assimilate free AA that had been microencapsulated, most likely because microencapsulation slows the release at the protein synthesis site, therefore increasing the assimilation rate of AA. In addition, due to the feeding habit and therefore protracted consumption of the test diets, microencapsulation would reduce the degree of leaching. Perhaps the best method to determine AA requirements for crustaceans is to manufacture a test diet with purified casein supplemented with microencapsulated AA, or enrichment by covalently bonding the AA of interest to the casein (Guillaume, 1997). Further work is needed to confirm the essential AA in lobsters and ascertain their dietary requirements, which may vary for different species (Table 6.1).

Table 6.1 Suggested amino acid profiles for postlarval and juvenile *Penaeus japonicus* and *P. monodon.*

	Percentage of Diet		
Amino Acid	*P. japonicus*	*P. monodon*	Reference
Arginine*	4.15	2.5	Guillaume (1989), Chen (1993)
	2.2–3.2	1.85	Hew & Cuzon (1982), Millamena *et al.* (1998)
Histidine*	1.17	—	Guillaume (1989)
Isoleucine*	3.70	—	Guillaume (1989)
Lysine*	3.9	2	Guillaume (1989), Millamena *et al.* (1998)
	6.3	—	Hew & Cuzon (1982)
Lysine : Arginine ratio	1.5–2	—	Hew & Cuzon (1982)
Methionine*	1.57	0.89	Guillaume (1989), Millamena *et al.* (1996a)
Methionine + Cystine	1.7	1.4	Guillaume (1989)
	—	1.3	Millamena *et al.* (1996a)
Phenylalanine*	1.96	—	Guillaume (1989)
Phenylalanine + Tyrosine	4.32	—	Guillaume (1989)
Threonine*	3.03	1.4	Guillaume (1989), Shiau *et al.* (1991); Millamena *et al.* (1997)
Tryptophan*	0.47	—	Guillaume (1989)
Valine*	2.01	3.75	Guillaume (1989), Millamena *et al.* (1996b)

*Essential amino acids.

6.2.2 Protein to energy ratio

Proteins can be used effectively for energy production. To maximise the efficiency of protein utilisation for somatic growth, it is imperative to balance the supply of protein and non-protein energy in the diet. For instance, if insufficient carbohydrate and/or lipid are present in the diet, crustaceans will use protein for energy instead of growth. Excess dietary protein may also lead to energy loss and reduction in growth due to the diversion of energy toward the deamination of excess AA. Diet formulators have the option to use higher amounts of lipid in diet formulations to spare protein from energy production to somatic growth (Table 6.2). Crustaceans, although very capable of utilising lipid to yield energy, appear unable to tolerate high lipid (>10%) diet levels that are commonly used in artificial finfish diets.

In a study on *Jasus edwardsii*, lobsters were fed diets containing crude protein concentrations varying from 24 to 50%, and one of two lipid levels, 5% and 9% (Ward *et al.*, 2003). The optimal digestible dietary crude protein (DCP) was 29% at 5% lipid, and 31% DCP with 9% lipid, with both diets having an optimal digestible protein/digestible energy ratio of 29 g DCP MJ (DE)$^{-1}$. The slightly higher protein requirement at the 9% lipid level suggests that *J. edwardsii* may be unable to utilise the extra lipid as an energy source. However, the extra lipid had no adverse effects. Differences in weight gain were not significant. There was also no significant difference in the feed intake or digestibility between the different diets. The feed conversion ratios (FCR) for the optimal diets were 3.1 : 1 and 5.69 : 1, respectively. Lobsters were best able to utilise lipid included at below 5%. The optimal protein requirement of *J. edwardsii* is similar to that of *Homarus americanus* (Conklin *et al.*, 1975), but at the lower end of the protein requirements of other crustaceans (25–55%) (Guillaume, 1997).

In contrast to *J. edwardsii*, *Panulirus cygnus* (post-puerulus, 0.3–0.5 g) had a higher protein requirement and poorer lipid utilisation. A diet of 55% protein and 6% lipid supported best growth and produced the lowest FCR (2.5 : 1), while lobsters fed a 10% lipid diet with the same protein level grew more slowly. However, the artificial diets performed poorly compared to a diet of live mussel, *Mytilus edulis*, producing a specific growth rate (SGR) of 6.11, compared to the 55% protein, 6% lipid diet, with an SGR of 2.78.

In a similar experiment with tropical rock lobsters, *Panulirus ornatus* (Smith *et al.*, 1998), animals of 1.2–2.5 g were fed diets containing varying amounts of protein (30–55%) and lipid (6 or 10%). The results showed that maximum growth occurred at 47% protein; 6% lipid and 53% protein; or 10% lipid; with the diets having similar protein to energy (P : E) ratios of 29 and 28 g DCP MJ DE^{-1}, respectively. However, the growth rate on all artificial diets was slow compared to mussel. Smith *et al.*, (2003) suggested an optimal dietary protein (530 g kg^{-1}) and lipid (100 g kg^{-1}) content of diet for juvenile *P. ornatus*. More recently, Smith *et al.* (2005) found that juvenile *Panulirus ornatus* had highest survival (79%) and growth (1.38% day^{-1}) over eight weeks on pelleted diets containing 10 g kg^{-1} crude protein on a dry matter (DM) basis and a digestible protein to digestible energy (P : E) ratio of 29.8 mg kJ^{-1}. All pelleted diets contained 130 g kg^{-1} DM of lipid. Animals fed a reference diet of frozen green-lip mussels, *Perna canaliculus*, had faired comparatively worse (41% survival and 0.80% day^{-1} growth) (Smith *et al.*, 2005). Lobsters appear to have a very high dietary protein requirement compared to other aquaculture species, such as finfish, although results so far suggest the requirement to be more similar to that of prawns.

Larger lobsters may have a higher protein requirement. Wild *J. edwardsii* show an ontogenetic shift in diet at around 20 g body mass, possibly due to changes in their nutritional requirements (Edmunds, 1995). Crear *et al.* (1998) found that *J. edwardsii* with a mean initial mass of 70 g generally showed best growth at 40–44% digestible crude protein, although results were not significant.

Bautista (1986) investigated the optimal protein and protein to energy (P : E) ratios for *Penaeus monodon*. Diets containing 40–50% protein (casein and gelatine), 20% carbohydrate (sucrose) and 5–10% lipid (cod liver and soybean oil) produced maximum growth and best survival. The optimal P : E ratio was found to be between 32–36 g DCP

Table 6.2 Optimal protein levels and protein : lipid ratios for crustaceans.

Crustacean	Protein (%)	Protein : Lipid (g DCP MJ DE^{-1})	Protein type	Reference
Homarus americanus	—	19.1	—	Capuzzo & Lancaster (1979)
	60	—	Casein	Castell & Budson (1974)
Penaeus japonicus	52–60	—	—	Guillaume (1989)
Penaeus monodon	35–40	—	Fish & squid meal	Lin *et al*. (1982), Alava & Lim (1983)
	40–50	32.2–36.3	Casein	Bautista (1986)

MJ DE^{-1}. The protein content in the diet could be dropped from 50% to 40% without significantly affecting the growth, if the energy level of the diet was kept constant at 14 MJ kg^{-1}. Growth of the prawns decreased significantly with 30–40% carbohydrates and 15% lipid in the diet (Table 6.2).

A number of studies have investigated the effects of using different protein types in artificial diets. The cost-effective replacement of marine protein with plant-based proteins is of particular interest as a means of reducing feed ingredient costs for aquaculture. Boghen and Castell (1982) investigated the different growth and survival rates of *Homarus americanus* fed diets containing 50% protein from *Artemia* (brine shrimp), casein, sea urchin, mussel, crab or penaeid prawn. Lobsters fed *Artemia* and casein had the lowest growth and survival (*Artemia* SGR = 1.3, survival = 87.1%; casein SGR = 1.73, survival = 7.5%), while lobsters fed crab, *Cancer irroratus*, had the best growth (SGR = 2.2) and survival (95%). Casein is known to be deficient in a number of AA, however, the difference in the growth and survival rates cannot be simply attributed to the lack of AA. It should be noted that some researchers have produced excellent growth rates from exclusively feeding *Artemia* to *Homarus americanus* (Conklin *et al.*, 1977; Fiore & Tlusty, 2005; Tlusty *et al.*, 2005). The high macromolecular variability of different *Artemia* strains (Abatzopoulos *et al.*, 1989; Ahmadi *et al.*, 1990) may account for this variability in performance.

Low-fat soybean meal (SBM) has been found to be a good protein substitute in the feed of crustaceans. Floreto *et al.* (2000) investigated the effects of replacing 0–100% of fishmeal with SBM on growth and survival of *Homarus americanus*. The diets contained a total of 40% protein, and half of the diets were supplemented with arginine, leucine, methionine and tryptophan. Supplementation of AA and inclusion of SBM up to 50% of dietary protein (42% of diet) produced significantly faster growth than diets without supplementation, or those that contained higher proportions of SBM. The growth rate declined with increasing proportions of SBM. There was no significant difference in the SGR between the 0–50% SBM diets. Growth of lobsters on 50% SBM plus supplement (SGR = 2.64) was similar to the growth of lobsters fed *M. edulis* (SGR = 2.54). The survival of lobsters that were fed some fishmeal was not significantly different (approximately 60%). However, lobsters fed 100% SBM suffered from early mortality (37% survival). Supplementation with AA or some fishmeal in the diet was found to be necessary for moulting success. SBM can make up to 35% of the diet for *Penaeus japonicus* (Kanazawa, 1992) and 50% of the diet for *P. monodon* (Akiyama, 1990).

In a study on *Litopenaeus vannamei*, up to 80% of the fishmeal used in the prawn diet was replaced with co-extruded soybean poultry by-product meal (SBP) or flash dried poultry by-product meal (FDP) (Davis & Arnold, 2000). The authors prepared a range of diets all containing 32% total protein and 8% lipid and found that there was no significant difference in the survival between any of the dietary treatments. Replacement of up to 80% fish meal with SBP resulted in no significant difference in growth or feed efficiency, while replacement of 40–80% fish meal with FDP resulted in significantly higher weight gain and feed efficiency. These results showed that up to 24 g of fish meal per 100 g diet can be replaced by poultry by-product meals, and demonstrated that any effects on the growth, feed efficiency or survival of *L. vannamei* are likely to be beneficial. Fishmeal could also be totally replaced in diet of other crustaceans such as the giant freshwater prawn, *Macrobrachium rosenbergii*, with no detrimental effect (Davis & Arnold, 2000).

Squid is often added to crustacean diets to increase the growth and attractiveness of artificial diets. In a series of experiments with *Penaeus japonicus*, Cruz-Ricque *et al.* (1989) identified squid protein as a potent growth factor. The authors found that the replacement of squid lipids (polar lipids (PL), cholesterol, or highly unsaturated fatty acids (HUFA, $\propto C_{20}$) with cod liver oil, or the removal of the attractant hydroalcohol soluble extract (Hae) from squid had no significant effect on growth, although the removal of Hae reduced the feed intake of the prawns. However, the replacement of squid protein with fish protein significantly depressed the growth rate without affecting the feed intake. These results show that the enhanced growth is not due to increase in feed intake using the diet of squid, but is likely to be due to an unidentified substance(s) in the squid protein. As the AA profiles of squid and fishmeal are similar, it is unlikely that different AA concentrations alone are responsible for the enhanced growth. In a second experiment, varying levels of squid (*Loligo* sp.) protein (0–16%) was added to the diet of *Penaeus japonicus*; the Pacific blue prawn, *P. stylirostris*; the whiteleg prawn, *P. vannamei*; *P. monodon*; and the banana prawn, *P. indicus.* The first four species showed a similar trend in response to the squid protein supplement. Growth increased significantly with increasing levels of squid protein up to 6%, thereafter growth reached a plateau. The level of response differed between the species. *Penaeus stylirostris* and *P. japonicus* showed the greatest response with a supplement of 6% squid protein causing the growth rate to double. *Penaeus vannamei* and *P. monodon* showed a moderate growth response to the squid protein, while *P. indicus* did not show any significant response.

Protein hydrolysates (the product of solubilising protein enzymatically in the raw material by a limited protein hydrolysis; Córdova-Murueta & García-Carreño, 2002) are thought to benefit the growth of crustaceans. In an experiment carried out by Córdova-Murueta & García-Carreño (2002) on *Penaeus vannamei*, the effect of a hydrolysed protein supplement from fish or krill (*Euphausia* sp.) on the growth and survival of the prawns was studied. Hydrolysates were added to a commercial diet containing 35% protein at 3, 9 or 15% of the total protein. Addition of 3 or 9% fish hydrolysate (FH) produced significantly better growth than the control or the 15% FH diet. All the diets supplemented with krill hydrolysate (KH) preformed better than the control, but there was no significant different in the growth or survival between the krill treatments. The authors hypothesise that large amounts of FH may interfere with AA assimilation because FH was found to contain a large number of small peptides. Thus, small amount*s* of protein hydrolysates (3–9%) were recommended as a growth supplement for *P. vannamei* (Córdova-Murueta & García-Carreño, 2002).

6.3 Carbohydrates

Carbohydrates are fundamental components of living organisms and can be divided into three broad categories: nutritive, non-nutritive and structural. Nutritive includes sugars and starches; non-nutritive is fibre, which includes a variety of polysaccharides such as cellulose and hemicellulose; and structural is chitin, a polysaccharide made from the monosaccharide glucosamine.

6.3.1 Nutritive carbohydrates

Crustaceans will utilise valuable protein for growth if sufficient non-protein energy sources are unavailable. Hence, the most efficient artificial diets provide a sufficient quantity of non-protein energy to allow the more costly protein dietary ingredients to be spared for somatic growth. Although lobsters and crustaceans in general can utilise lipid, their capacity is limited when compared to finfishes, such as salmon. Lobsters and fishes are different in this respect as fishes cannot make use of high carbohydrate in their diet, while lobsters can to varying degrees depending on the type of carbohydrate supplied. For example, Kanazawa (1982) demonstrated that simple sugars, such as glucose and galactose, are poorly utilised by some crustaceans and that including more than 10% of these monosaccharides in a formulated diet inhibited the growth of marine prawn, *Penaeus japonicus*. In contrast, disaccharides (sucrose and maltose) and polysaccharides (starch and dextrin) have a high nutritional value, are readily digestible and used for energy production, thus sparing protein in *P. japonicus* (Kanazawa, 1982). Bautista (1986) and Guillaume (1989) suggested that a dietary carbohydrate level of 15–20% is optimal for *Penaeus japonicus* and *P. monodon*. Nevertheless, a *carte blanche* acceptance that all complex carbohydrates are a suitable non-protein source of energy would be inaccurate. Radford (personal communication) noted that exceptions include algal polysaccharides such as carrageenans and alginates, which, despite being complex, were not digestible by the rock lobster *Jasus edwardsii*. Agar was still found to be highly digestible even though it is derived from marine algae (Radford, personal communication). From examination of carbohydrate activities in midgut-gland extracts of *Homarus gammarus*, Glass and Stark (1995) suggested that pretreatment of dietary starches may increase the nutritional value of formulated diets.

6.3.2 Non-nutritive carbohydrates

There is little information on the effects, beneficial or otherwise, of fibre in lobster diets or even crustaceans in general. Effects of dietary fibre differ depending on the solubility. Soluble fibre, such as pectin or carboxymethylcellulose, reduces gut transit time by contribution of viscous qualities to the diet structure. In fishes this leads to an improved growth response brought about by the delayed absorption of the nutritive carbohydrates in the diet permitted by the longer residence time in the gut (Shiau, 1997), thus allowing more time for the complete digestion and absorption of the nutritive carbohydrate. The insoluble fibre, cellulose, has the opposite effect and increases gut transit time, which generally leads to the decrease of nutrient absorption. This was found to be the case in diets for penaeid prawn (Fair *et al.*, 1980).

6.3.3 Structural carbohydrates

The chitin exoskeleton of crustaceans is derived from glucose in the form of glucosamine. Results from studies on the dietary requirements for chitin and glucosamine are inconclusive. Kitabayashi *et al.* (1971) found that addition of 0.53% glucosamine enhanced the growth of *Penaeus japonicu*s, whilst the addition of chitin inhibited growth. Similarly, 0.8% glucosamine was found to increase the growth of *P. indicus* (Vattheeswaran & Ali, 1986). In contrast, Akiyama *et al.* (1992) found that chitin had a growth-promoting effect and recommended a minimal level of 0.5% in prawn diets. Deshimaru and Kuroki (1974) found no dietary requirement for glucosamine and report that glucosamine inhibits the growth-promoting effect of cholesterol.

6.3.4 Carbohydrate to lipid ratio

The important relationship between the non-protein sources of energy and their combined effects on growth and performance has been demonstrated in several studies. For example, in two freshwater prawn species, *Macrobrachium rosenbergii*, and the Monsson River prawn, *M. malcolmsonii*, carbohydrate to lipid ratios of between 4 : 1 and 3 : 1 gave the best performance (Das *et al.*, 1995; D'Abramo, 1998). More recently, Johnston *et al.* (2003) investigated the effect of varying carbohydrate and lipid levels on juvenile *Jasus edwardsii* and demonstrated the benefits of optimised carbohydrate and lipid ration on growth and performance. They tested four experimental diets containing a constant 32% protein, and varied carbohydrate between 15–50% and lipid from 3–19%. The best growth rates were achieved in the juvenile rock lobsters fed the diet formulated with a 2 : 1 ratio of carbohydrate to lipid, which corresponds to an optimal diet inclusion level of 27 and 13.5% for carbohydrate and lipid, respectively. This finding was corroborated by subsequent analysis of the whole body, digestive gland and histological sections of the digestive gland, which showed that the levels of lipid and dry matter in these tissues was greatest in the 2 : 1 diet (Johnston *et al.*, 2003).

6.4 Lipids

Although information regarding the roles of proteins, carbohydrates, lipids, vitamins and inorganic elements is equally important, much less is known about lipid nutrition (Sargent *et al.*, 2002). Knowledge of lipid composition of marine organisms provides a basis for understanding energy storage, buoyancy strategies, trophodynamic interactions and nutritional requirements. The most common marine lipids, and thus most often studied, are fatty acids (FA), sterols (ST), triacylglycerols (TAG), polar lipids (PL) and wax esters (WE) (Nevenzel, 1970; Lee *et al.*, 1972; Benson & Lee, 1975; Sargent *et al.*, 1976; Sargent, 1978; Lee & Patton, 1989). Diacylglyceryl ethers (DAGE) are generally less common in marine organisms, although they have been reported to occur in pteropod molluscs at up to 41% of total lipid (Phleger *et al.*, 1997; Kattner *et al.*, 1998). There is little information on the specific classes and quantities of lipid necessary for inclusion in lobster diets (specific PL, FA and ST requirements). However, there is considerably more information for crustaceans in general as is reviewed below.

6.4.1 Polar lipids

Crustaceans have a limited ability to biosynthesise PL (phospholipids) and consequently cannot synthesise enough to meet their requirements (Shieh, 1969). Hence it is necessary for some PL to be supplied in their diet. A dietary level of 1.25–6.5% PL from soybean has been recommended for prawn (Coutteau *et al.*, 1997). Addition of 3.1% PL to diets containing 5% lipid from coconut, soybean, linseed, peanut or menhaden was found to significantly improve the growth rate of *Litopenaeus vannamei* (González-Félix *et al.*, 2002). The inclusion of up to 2.7% PL (L-′ -phosphatidylcholine) in the diet of *P. monodon* was also found to significantly increase the digestion of neutral lipids (Glencross *et al.*, 1998). Olive oil was used as the neutral lipid source in this experiment. The increase in the digestibility caused by PL may not be so great if marine oil is used instead (Glencross *et al.*, 1998).

In the clawed lobster, *Homarus americanus*, ‘moult death syndrome’ (inability to complete ecdysis resulting in death) is a problem that has been regularly encountered when the animals are fed artificial diets. Conklin *et al.* (1980) found that the addition of 6–8% soy lecithin in casein-based diets decreased the incidence of moult death. Additionally, a lack of dietary lecithin (any of a group of polar lipids containing choline, phosphoric acid, fatty acids and glycerol) was associated with lower haemolymph levels of PL and cholesterol (D’Abramo *et al.*, 1982). The authors suggested that moult death was caused by the impairment of cholesterol transport due to the lack of PL. However, the lack of lecithin in crab protein diets did not result in moult deaths (Kean *et al.*, 1985a). Furthermore, Baum *et al.* (1990) found that the levels of cholesterol were similar in tissues of *H. americanus* fed crab protein or casein both with and without lecithin. The authors concluded that the serum and lipoprotein cholesterol levels in lobsters were influenced by the presence of dietary lecithin, but not by the protein source. Lobsters fed crab diets containing no lecithin had similarly low cholesterol levels as lobsters fed unsupplemented casein. However, these animals did not suffer from moult death syndrome. The authors concluded that the lack of lecithin does not impair cholesterol transport in crustaceans.

In a study on *Litopenaeus vannamei*, Gong *et al.* (2000a) found a highly significant interaction between cholesterol and PL on prawn growth. A dietary cholesterol level of 0.2% or 0.5% produced a similar growth rate at any PL level (0–5%). Increasing amounts of PL decreased the amount of cholesterol required to produce maximum growth (Table 6.3). Increasing PL levels caused a significant increase in the growth rate at 0% cholesterol, but the growth enhancement diminished with increasing cholesterol levels. Similarly, Kean *et al.*, (1985a) found that if cholesterol was present in the diet there was no significant effect of lecithin (0–6%) on the growth of *Homarus americanus.*

The type of PL has also been shown to be important. Gong *et al*. (2000b) investigated the effect on *Litopenaeus vannamei* of the main PL in soybean lecithin: phosphatidylcholine (PC), phosphatidylethanolamine (PE) and phosphatidylinositol (PI). Based on growth and survival results, there appears to be no dietary requirement for PC (0–4.2%). However, when PC was supplied at 0.35% or 0.52% in combination with increasing levels of PE and PI combined, growth was significantly enhanced. No interaction was found between PC and cholesterol. Other studies have found that only PC is required for crustacean growth. For example, Coutteau *et al*. (1996) found that addition of 1.5% PC increased the growth of *Penaeus vannamei* postlarvae. It is likely that the type and amount of PL required is dependent on the particular species and its developmental stage.

Polar lipids are the primary energy storage component of the puerulus of the rock lobster, *Jasus edwardsii*, and diacylglycerols appear to play a much less important role (Pearce, 1997; Jeffs *et al*., 1999, 2001a, b; Phleger *et al*., 2001). These non-feeding postlarvae swim over considerable distances, up to hundreds of km, from the open ocean into shallow coastal waters where they settle (Jeffs *et al*., 1999, 2001a, b). This development phase may last up to four weeks after settlement (Booth & Kittaka, 2000; Kittaka, 2000). Histological studies of *J. edwardsii* indicate that large quantities of stored PL are mobilised by the hepatopancreas to fuel the substantial morphological changes during this period (Nishida *et al*., 1995; Jeffs *et al*., 2001a). This was confirmed by lipid analysis of developing pueruli of *J. edwardsii* (Pearce, 1997). It is very likely that following moulting, the first instar juvenile has a severe energy deficit that can only be solved by immediate benthic feeding. In the aquaculture of rock lobsters this is a critical phase when most mortality of cultured pueruli occurs, probably as a direct result of this energy deficit (Kittaka, 2000; Jeffs, 2001). The phyllosoma larvae may similarly have a requirement for PL. Studies on both wild (Phleger *et al*., 2001) and cultured (Nelson *et al*., 2003, 2004) phyllosomal larvae of *Jasus edwardsii*, as well as their potential prey items (Jeffs *et al*., 2004), indicate that wild phyllosomal larvae largely obtain, and therefore may require, lipid in a PL form. This may also hold true in other rock lobster species, as Liddy *et al*. (2004) demonstrated with *Panulirus cygnus*. Therefore, the inclusion of PL in the diet of both larval and adult stages of lobsters should be considered as likely to be essential, however, the exact dietary requirements and composition of the PL remains to be elucidated.

Table 6.3 Polar lipid and cholesterol levels required for optimal growth of *Litopenaeus vannamei* (Gong *et al*., 2000a).

Polar lipid (%)	Cholesterol (%)
0	0.35
1.5	0.14
3	0.13
5	0.05

6.4.2 Sterols

Over 120 sterols have been isolated in marine invertebrates (Goad, 1978), although the major sterol (ST) for most marine species is cholesterol (Tucker, 1989). Crustaceans cannot synthesise cholesterol, therefore they require it to be supplied in the diet. Kean *et al*. (1985a) found that total mortality of *Homarus americanus* occurred within 14 weeks if the lobsters were not fed cholesterol. Table 6.4 shows the optimal cholesterol requirements for

Table 6.4 Optimal cholesterol requirements for selected crustaceans.

Species	Cholesterol (% diet)	Reference
Penaeus japonicus	0.5 0.26–0.6	Kanazawa (1982) Teshima *et al.* (1997)
Penaeus monodon	0.17	Smith *et al.* (2001)
Homarus americanus	0.25	Kean *et al.* (1985a)
Litopenaeus vannamei	0.2	Gong *et al.* (2000a)

various crustaceans, with most requiring a dietary cholesterol level of 0.2–0.5%, as percentage of diet. It was found that if the main protein source in the diet was derived from animal origin, there might be sufficient cholesterol present in the protein already to meet requirements and so negate the need for supplementation of the diet. The cholesterol requirement of *Penaeus monodon* was found to be $75\,\mathrm{mg\,kg^{-1}}$ body mass and a diet containing 35% DCP from fish and squid meal was found to be sufficient (Smith *et al.*, 2001). Cholesterol is one of the most expensive ingredients in artificial diets, with an addition of 0.2% cholesterol representing around 10% of the total cost (Smith *et al.*, 2001). Therefore, it is important to optimise the requirements to allow least cost formulation of crustacean diets.

6.4.3 Essential fatty acids

Essential fatty acids (EFA) are those that must be supplied in the diet for normal growth and development. In crustaceans, five FA have been identified as essential for growth and survival: ′ -linolenic acid (ALA, 18:3(n-3)), eicosapentaenoic acid (EPA, 20:5(n-3)), linoleic acid (LA, 18:2(n-6)), docosahexaenoic acid (DHA, 22:6(n-3)) and arachidonic acid (ARA, 20:4(n-6)). The omega-3 long-chain ($\propto C_{20}$) polyunsaturated fatty acids (LC-PUFA), particularly DHA, are important for the functioning of the nervous system, and provide immunity to infections and parasitic diseases of fishes (Kolakowska *et al.*, 2003). Evidence suggests this essentiality for LC-PUFA exists for both adult clawed (Castell & Covey, 1976; Dall, 1981; Boghen & Castell, 1982; Kean *et al.*, 1985a; Saski *et al.*, 1996) and rock (Kanazawa & Koshio, 1994; Glencross *et al.*, 2001) lobsters and prawns (Chandumpai *et al.*, 1991; Hopkins *et al.*, 1993; Glencross *et al.*, 1998).

In the rock lobster *Jasus edwardsii*, for the larval transformation to occur, broodstock should be given a high quality diet (Smith, 1999) and phyllosomal larvae must be provided with adequate lipid. To this end, the diet must supply larvae with energy-rich lipid, including the PUFA considered essential to crustaceans (Kanazawa *et al.*, 1979). Unless enriched with EFA, brine shrimp, *Artemia*, fail to provide a nutritionally balanced dietary food source for phyllosomal larvae. DHA and EPA have been the focus of enrichments for *Artemia* used for finfish larvae (Léger *et al.*, 1987; Rees *et al.*, 1994; Rasowo *et al.*, 1995; Evjemo *et al.*, 1997; Narciso *et al.*, 1999), although ARA also has recently been highlighted as a key element for *J. edwardsii* (Smith *et al.*, 2002).

Nelson *et al.* (2005) compared adult *Jasus edwardsii* held in culture while fed diets of fresh mussels and squid or a pelleted formulated prawn diet. While the tail and leg muscle lipid was predominantly PL, the lipid of digestive gland was largely TAG. Lipid class and PUFA content of cultured and wild lobsters were generally similar.

For *Penaeus monodon*, both ALA and DHA were found to be essential for this species of crustacean. Merican and Shim (1996) conducted an experiment on *P. monodon* comprised of five dietary treatments containing a blend of the aforementioned EFA, with each treatment differentiated from the rest by exclusion of one of the EFA. A control group was fed a diet containing no EFA supplements, and a reference group was fed a diet containing all five EFA. The reference group had the greatest growth (464%), while the control group showed the poorest (151%). Survival was similar for all the groups (~80%) except for the control group, which had significantly lower survival (40%). Of the five treatment groups, weight gain was significantly reduced when ALA or DHA was omitted, to the point that there was no significant difference in growth of these two groups when compared to the control with no EFA supplementation. Omission of EPA, LA or ARA produced a moderate, although significant, reduction in growth. In a second experiment, three treatment groups were fed a 4% mixture of palmitic (16:0) and oleic (18:1(n-9)) acids and either 1% of EPA or DHA, or an equal mixture of both EPA and DHA. The apparent growth of the prawn was in descending order: reference diet > DHA diet > DHA + EPA > EPA diet > control (Merican & Shim, 1996).

In a subsequent study, Merican & Shim (1997) investigated the quantitative requirements of ALA and DHA for *P. monodon*. Animals were fed diets containing 0–3% ALA and 0.12–2% DHA. The optimal requirement for ALA and DHA was 2.5%

and 1.4%, respectively. Studies on other penaeid prawns have found that 2% ALA was optimal for *P. indicus* (Read, 1981) and 1–2% was optimal for *P. aztecus* (Shewbart & Mies, 1973). In comparison, Kanazawa (1982) found that 0.5–1% was the optimal total EFA requirement of *P. japonicus*.

Glencross and Smith (1999) investigated the requirement of *Penaeus monodon* for LA and ALA in the absence of other PUFA. They found that this penaeid prawn can elongate and desaturate LA and ALA into other PUFA, namely ARA, EPA and DHA, though probably at a rate insufficient to meet their dietary requirements (Kanazawa & Teshima, 1977). Provision of 14% LA (of total FA composition, 1.5% of diet) and 21% ALA (1% diet) produced the best growth, comparable to the reference diet of cod liver oil. The study also showed that an excessive amount of either EFA would significantly depress the growth rate. It was also found that omega-6 – (n-6) – FA produced a greater growth response than omega-3 – (n-3) – series. This was also the case in studies conducted with *P. indicus* (Read, 1981), while the opposite was found to be true for *P. japonicus* (Kanazawa, 1982) and *Homarus americanus* (Harrison *et al*., 1988). Castell and Covey (1976) found that adult *H. americanus* had best growth when fed a diet with 5% cod liver oil, an oil containing (n-3) FA. Juvenile *H. americanus* were found to have significantly higher growth when fed on 10% lipid than on 5% (Boghen & Castell, 1982). Juvenile *H. americanus* fed diets containing SBM (which is high in ALA), were found to have best growth when SBM was included at <50% (Floreto *et al*., 2000). The authors found that decreasing dietary SBM resulted in higher (n-3) PUFA and better growth (Floreto *et al*., 2000, 2001).

6.5 Vitamins and minerals

Little is known about the vitamin and mineral requirements of crustaceans. Vitamin and mineral premixes based on terrestrial or fish requirements are routinely added to crustacean feeds, and due to lack of knowledge, vitamins may often be supplied in excess of requirements (Conklin *et al*., 1991). Excessive levels of certain vitamins may be detrimental to growth. For example, Kanazawa (1982) found that the addition of some vitamin C enhanced prawn growth while the addition of too much inhibited growth.

Table 6.5 shows the recommended vitamin requirements for *Penaeus japonicus* and *P. monodon*. In general, *P. japonicus* has a much higher vitamin requirement than *P. monodon*

Table 6.5 Recommended vitamin levels for selected crustaceans.

Nutrient (mg kg^{-1})	*Penaeus monodon*	*Penaeus japonicus*	*Eriocheir sinensis*	Reference
Thiamine (B_1)	14	60–120	—	Chen (1993)
Riboflavin (B_2)	22.5	80	—	Chen (1993)
Pyridoxine (B_6)	120 (general crustacean recommendation)			Conklin *et al.* (1991)
Cobalamin (B_{12})	0.05–0.4	—	—	Chen (1993)
Folic acid (B-complex)	2–8	—	—	Chen (1993)
Niacin (B-complex)	6.4	400	—	Chen (1993)
Ascorbic acid (C)	2000–2500	10 000	—	Chen (1993)
	—	2 200	—	Kanazawa (1982)
	∞200	∞2 000	—	Lavens *et al.* (1998)
Vitamin D_3	0.02	—	—	Chen (1993)
Vitamin E	—	—	200–400	Ai *et al.* (2002)

Table 6.6 Recommended mineral levels for selected crustaceans.

Mineral (%)	*Penaeus japonicus*	*Penaeus vannamei*	*Homarus americanus*
Phosphorus	1	0.5–1	—
Potassium	0.9	—	—
Calcium	1	1	—
Magnesium	0.3	—	—
Calcium : Phosphorus	1 : 1, 2 : 1	—	1 : 2
Copper	0.006	0.0032	—
Reference	Cuzon (1982), Kanazawa *et al.* (1984)	Davis *et al.* (1993a, b)	Gallagher (1976)

(Chen, 1993). *Homarus* spp. probably do not require vitamin C or K supplements (Kean *et al.*, 1985b; Conklin *et al.*, 1991), and their vitamin A and D requirements would be minimal as they can synthesise vitamin A from carotenoids and vitamin D from sterols (Conklin *et al.*, 1991).

Crustaceans can absorb most minerals (except phosphorus) from seawater and consequently their dietary mineral requirements have not been well studied. However, it is not known whether crustaceans can absorb minerals at a sufficient rate to meet their requirements. Davis and Gatlin (1996) have recommended that seven minerals be included in crustacean feeds: calcium, copper, phosphorus, potassium, magnesium, selenium and zinc. Other minerals have been found to have negative effects. For example, the addition of 0.006% iron or 0.003% manganese was found to inhibit growth (Kanazawa, 1982). Also, 0.16% copper was found to be excessive and depressed prawn growth (Kean *et al.*, 1985c). Table 6.6 shows the recommended mineral requirements.

6.6 Attractants

6.6.1 Low molecular weight compounds

The majority of studies on chemoattraction in crustaceans have shown that low molecular weight (LMW; <1000 daltons) compounds such as AA, amines, nucleotides and organic acids are the most attractive individual compounds (Carter & Steele, 1982a; Derby *et al.*, 1984; Daniel & Bayer, 1987). The results from a behavioural study on juvenile and adult *Homarus americanus* support this hypothesis (Daniel & Bayer, 1987). Test lobsters were placed in a tank of flowing seawater and a herring leachate was injected into the middle of the tank. The raw leachate was prepared by soaking chopped herring, *Clupea harengus*, in seawater for 1.5 hours and then filtering the mixture. The proteins and peptides in the raw leachate were separated from the dissolved AA and amines by adding methanol to the leachate, evaporating the mixture and separating the fractions with chromatography. The authors found that the removal of proteins and peptides from the raw leachate (leaving dissolved AA and amines) did not significantly affect the attractiveness of the leachate. Furthermore, the attractiveness of the leachate increased with increasing concentrations of dissolved AA, suggesting that AA are a major class of attractants for *Homarus americanus*. However, AA are not solely responsible for the attractiveness of prey since synthetic mixtures of AA, that replicate the concentrations found in natural foods, are not as attractive as the natural extracts (Zimmer-Faust *et al.*, 1984b; Carr & Derby, 1986). This may be because the synthetic D-forms of AA are not as attractive as the natural L-forms, as was suggested for *Homarus gammarus* (Mackie, 1973). The most attractive feeds for crustaceans generally appear to be complex mixtures that are typical of natural prey extracts.

The results of a behavioural study by Carter and Steele (1982a) on immature *H. americanus* showed that lobsters were highly attracted to prey extracts of rock crab (92% food-searching response), mussel (80%) and sea urchin (66.7%). Prey were dried, crushed and strained through a 1 mm sieve. The powder was then diluted to 10% with seawater (Carter & Steele, 1982a). The lobsters were also significantly attracted to $1 \cdot 10^{-1}$ M to $2 \cdot 10^{-4}$ M solutions of proline, ammonia, arginine, lysine, alanine, glycine and valine (in order of decreasing attractiveness). Chemical analysis of the prey extracts showed that rock crabs contained the highest levels of proline and relatively high levels of ammonia, which may account for their high attractiveness. The most attractive compound tested was the AA proline, which also happens to be the most soluble compound. The authors suggest that solubility is more important at the chemoreceptor surface, with more soluble compounds being easier to detect.

The attractiveness of compounds appears to be species-specific. For example, the rock lobster, *Panulirus argus*, is most responsive to citric acid, ascorbic acid, succinic acid, taurine and glycine (Johnson & Ache, 1978), whereas *P. interruptus* showed the greatest response to glycine, alanine, serine, succinic acid, oxalic acid and adenosine 5 -triphosphate (ATP) (Zimmer-Faust *et al.*, 1984b; Zimmer-Faust, 1987). In another study, Zimmer-Faust *et al.* (1984b) found that adenosine 5 -monophosphoric acid (AMP) is highly inhibitory to *P. interruptus*, whereas AMP is a potent attractant for the daggerblade grass prawn *Palaemonetes pugio* (Carr & Thompson, 1983) and for *Homarus gammarus* larvae (Kurmaly *et al.*, 1990).

It is generally assumed that LMW compounds are the most effective attractants/stimulants because of their rapid diffusion rate (Carter & Steele, 1982a; Derby *et al.*, 1984; Daniel & Bayer, 1987). However, this conclusion may be premature, as only a few studies have tested both LMW and high molecular weight (HMW) fractions (e.g. Carr & Gurin, 1975; Derby *et al.*, 1984; Trott & Robertson, 1984; Zimmer-Faust *et al.*, 1984a; Daniel & Bayer, 1987; Holland & Borski, 1993). Zimmer-Faust *et al.* (1984a) showed that *Panulirus interruptus* was stimulated by the HMW fraction (>1000 daltons) of abalone extract, but not the LMW fraction (<1000 daltons). Peptides and proteins were major stimulants for the lobster (see Section 6.6.2 for details) (Zimmer-Faust & Case, 1982; Zimmer-Faust *et al.*, 1984b). Carr and Gurin (1975) also found that *Palaemonetes pugio* responded to the HMW fraction. However, for some species it appears that LMW compounds are indeed the major attractants. In a laboratory feeding trial, *Litopenaeus vannamei* ate significantly more agar blocks infused with the <1000-dalton fraction of squid or prawn head than the >1000-dalton blocks (Holland & Borski, 1993). The prawns showed no preference for the whole extract over the <1000-dalton fraction, indicating that the LMW compounds are responsible for the attractiveness of the extract (Holland & Borski, 1993). The ghost crab, *Ocypode quadrata*, and *Homarus americanus* are two other examples of crustaceans that only respond to the LMW fraction of prey extracts (Derby *et al.*, 1984; Trott & Robertson, 1984; Daniel & Bayer, 1987).

6.6.2 Suppression and synergism

The initial chemosensory studies that tested individual chemicals were important in identifying which chemicals within prey are most likely to stimulate a physical attraction and/or stimulate feeding. However, often the effect of a particular chemical is different when it is presented in a mixture of chemicals. Suppression and synergism describe the effect of a mixture interaction where the effect cannot be predicted by adding the individual effects together. Suppression occurs when the mixture is less effective than the individual compounds, and synergism occurs when the mixture is more effective than the individual compounds (Carr & Derby, 1986).

The results from several studies have shown that attraction to LMW compounds is not universal for crustaceans. Johnson and Atema (1983) found that certain LMW compounds that are abundant in animal flesh actually suppress the neural responses of lobsters and crab chemoreceptors. Field studies on *Panulirus interruptus* showed that lobsters were most attracted to abalone, *Haliotis rufescens* baits after 24–48 hours although most of the small molecules are released from the baits within the first three hours (Zimmer-Faust & Case, 1982). Laboratory trials showed that *P. interruptus* were significantly attracted to the HMW fraction of the abalone muscle (>1000 daltons), but not the LMW fraction (Zimmer-Faust *et al.*, 1984b).

In a behavioural study on *P. interruptus*, Zimmer-Faust *et al.* (1984a) clearly showed that tests using single compounds couldn't reliably predict the attractiveness of mixtures. The authors tested the effects of 32 individual compounds found within abalone muscle on adult lobsters. They found that 10 single compounds at a solution concentration of 10^{-2} M induced feeding behaviour. They were the AA glycine, alanine, serine, methionine, isoleucine, leucine, glutamic acid, and lysine, as well as succinic acid and betaine. Feeding behaviour comprised of antennule flicking, pereiopod probing and antennule wiping. Several other compounds induced one or two of these behaviours only. They then tested the effect of mixing glycine with urea, ammonium or taurine, and the effect of mixing succinic acid with ammonium or urea. The results show that the glycine/urea and glycine/ammonium mixtures induced significantly less pereiopod probing, antennule wiping and locomotion, and the effect of the glycine/taurine mixture was not significantly different from the effect of glycine alone. Ammonium and urea also suppressed the stimulatory effect of succinic acid. In contrast, a mixture of the organic acids succinic and oxalic acid, with the AA glycine, alanine and serin, was more attractive in combination (inducing an increase in antennule wiping and locomotion) than in single class mixtures. The authors concluded that results may not be valid unless each component within a natural extract is tested by itself and in all possible combinations, as the effects of mixtures are rarely additive (Zimmer-Faust *et al.*, 1984a).

Another example of suppression by a feeding attractant is that of adenosine 5 -triphosphate (ATP) by adenosine 5 -monophosphate (AMP) (Zimmer-Faust, 1993). ATP is a nearly universal carrier of chemical energy in metabolic pathways. Zimmer-Faust (1993) found that ATP stimulated feeding in *Panulirus interruptus*. ATP decays rapidly to AMP when cells die and AMP was found to inhibit feeding. However, a mixture of ATP and AMP caused the number of lobsters attracted to the source to decrease more than three-fold, clearly showing that AMP inhibits the attractiveness of ATP. Lobsters may use the relative levels of ATP and AMP as an indication of the freshness of prey (Zimmer-Faust, 1993).

6.6.3 Food conditioning

Conditioning refers to conditioned response, the action taken by an animal in response to a stimulus; a behaviour that is the result of experience and affects the acceptability of food to organisms. Most research on food conditioning has focused on the effect of starvation on lowering physiological and behavioural thresholds (Derby & Atema, 1981; Costa-Pierce & Laws, 1985; Daniel & Bayer, 1987; Kurmaly *et al.*, 1990). However, crustaceans also show a conditioned response to food to which they are accustomed. For example, Derby and Atema (1981) showed that *Homarus americanus* fed exclusively on one type of mussel (either *Modiolus modiolus* or *Mytilus edulis*) for two months showed lower behavioural response thresholds to those mussels, than to mussels they never tasted (they ate them more readily). Similarly, Fine-Levy and Derby (1991) demonstrated that *Panulirus argus* had a greater response to a prawn feed to which they had been conditioned than to an unconditioned oyster feed.

In a study on the effect of a commercial chemoattractant on *Litopenaeus vannamei*, Costero and Meyers (1993) coated feed pellets with the attractant 'Langobuds'. Langobuds is a commercial attractant made by Quali Tech, Inc. It primarily contains betaine, other amino acids and natural marine products. The prawns were conditioned with uncoated pellets for five days prior to the experiment. On the first day more prawns arrived at the uncoated pellets than the coated pellets, but more coated pellets were eaten. During the next five days significantly more prawns arrived and ingested the coated pellets. Therefore, although the prawns were originally conditioned to favour the uncoated diet, they quickly developed a preference for the diet coated with attractant. The authors also showed that after a period of starvation the prawns detected and arrived at the coated diet faster than the uncoated diet, and the responses became faster as the period of starvation increased.

Conditioning can also reduce future intake as shown by Kurmaly *et al.* (1990). The authors showed that while *Homarus gammarus* larvae initially ate microencapsulated diets they soon became conditioned to reject them. The authors hypothesise that this was because of the poor nutritional quality of the microencapsulated diets compared to the natural larval diet of mysids. Further research is necessary to clarify the effects of food conditioning.

6.7 Diet format

Guillaume and Ceccaldi (2001) aptly described decapod crustaceans as 'nibblers' which means that unlike most fishes where the food items are consumed whole, crustaceans pull, tear, crush and manipulate food items with the aim of reducing the size of food particles to fit into the mouth. The result of this external manipulation, reduction and mastication can be that significant amounts of food are not ingested because it is reduced to such a small size that it cannot be consumed by that animal. There is some evidence to suggest that tailoring the size of the diet to the size of the animal can lead to a reduction of feed wastage and therefore improve the efficiency of feed consumption (Sheppard, 2001; Sheppard *et al.*, 2002), although if this approach to improving the efficiency of feed consumption were adopted, then a wide range of different sized diets would be required. Possibly a better approach would be to modify the texture of artificial diets to resist crumbling and remain stable in water for an extended period of days rather than hours.

The growth of juvenile *Jasus edwardsii* (initial mass 7.75 g) fed six commercial prawn diets (three *Penaeus monodon* diets and three *P. japonicus* diets) was compared to the growth of lobsters fed mussels, *Mytilus edulis* (Crear *et al.*, 2002). The feed intake (0.83–1.26% WBW day^{-1}) and FCR ratio (1.34 : 1–2.48 : 1) of all the commercial diets were similar to the mussel diet (feed intake = 1.03% WBW day^{-1}, FCR = 1.55). Growth of lobsters fed the commercial diets was similar, with the only significant difference occurring between the worst commercial diet (SGR = 0.52) and the best commercial diet (SGR = 0.61). None of the commercial diets could match the growth of lobsters reared on mussels (SGR = 0.71), however the commercial diets performed reasonably well with the best commercial diet producing 80% of the growth of mussel-fed lobster. The best commercial diet also had the lowest feed intake and FCR, making it a very efficient feed. The similar feed intake and FCR of the mussels and the commercial diets indicate that growth is not limited by ingestion rate or attractiveness of the artificial diets. It appears that artificial diets are still lacking in some essential nutrient (or that the combination of nutrients is unsuitable) for *Jasus edwardsii*. In a second experiment, mussels were replaced with a formulated diet for three or six days per week. Growth and survival were not significantly different than for lobsters fed mussels exclusively. The partial replacement of mussels with a cost-effective formulated feed was estimated to reduce the cost of feed by up to 75%. In this experiment the mussels and the formulated diets had similar feed intakes, however, Williams (1998) found that the addition of 5% fresh mussel (equivalent to 1% DM) into formulated feeds increased the feed intake five-fold, showing that the artificial diets still lack attractiveness.

Glencross *et al.* (1999) formulated a reference diet (a diet formulated from chemically well-defined ingredients) for *Penaeus monodon* that contained 350 g kg^{-1} casein and 50 g kg^{-1} egg albumin as the primary protein sources. Growth of prawns fed the reference diet was compared to a practical diet (a wet diet manufactured in-house) and a commercial prawn diet. The practical diet produced the best growth over six weeks (142%), followed by the reference diet (121%) and then the commercial diet (91%). There was no significant difference between the practical diet and the reference diet. Although there were no obvious nutritional differences between the practical and reference diets, animals fed the practical diet had a much higher feed intake, indicating a higher attractiveness (the practical diet contained mainly marine protein). There was also no significant difference in growth between prawns fed the reference diet *ad libitum* and those fed to sub-satiation (75%), however, prawns that were fed to sub-satiation showed a significantly better FCR (sub-

Table 6.7 Diet composition of the experimental diets used in Lim *et al.* (1997).

Diet A	43% squid meal, 29% fish meal, 14% salmon roe meal and 14% prawn meal
Diet B	35% squid meal, 29% fish meal and 36% prawn meal
Rotation diet	Frozen prawn, *Anisomysis ijimai*, live lug worm, *Perinereis vancaurica* spp. *tetradentata*, and kuruma prawn feed (Nippai Co.) in a daily rotation.

satiation 2.08 compared to *ad libitum* 1.58), making it much more economical to feed prawns to sub-satiation.

Lim *et al.* (1997) compared the performance of two artificial diets for *Homarus americanus*, that were rotated daily in one treatment and in the other treatments only one of the feeds was used (Table 6.7). Survival between lobsters fed the diets was not significantly different, but the two artificial diets produced markedly inferior growth (A = 150 ± 59%, B = 116 ± 44%) compared to the rotational diet (376 ± 67%).

Ward *et al.* (2003) manufactured a custom-made diet for *Jasus edwardsii* primarily based on fishmeal. The authors found that a diet of 29% DCP and 5% lipid was optimal, however, the percentage body mass increase (99%) was approximately half that of mussel-fed lobsters (186%). Sheppard *et al.* (2002) investigated the optimal pellet size for *J. edwardsii* feed. Three sizes of lobsters (25–30 mm CL, 35–45 mm CL, 60–70 mm CL) were fed three different sized pellets (3 · 3 mm, 5 · 5 mm and 7 · 7 mm). The size of pellets was found to influence the amount of food wastage, with up to 50% of the feed being wasted. The largest lobsters consumed the 7 · 7 mm pellets (94% consumed) more efficiently than the smaller sizes, while the medium sized lobsters consumed the 5 · 5 mm pellets most efficiently (69%). There were no differences in the consumption efficiency of the smallest lobsters when they were fed different sized pellets (approximately 50%). Consumption efficiency was also found to increase with size regardless of the pellet size. This study demonstrates that by feeding lobsters the optimal sized pellet for their size, the amount of food wasted could be reduced by up to 19%.

One of the most successful live feeds to date for early stage *J. edwardsii* phyllosoma larvae has been *Artemia*, especially when grown to a size of approximately 1.5 mm over 5–9 days (Tong *et al.*, 1997; Ritar, 2001). Using *Artemia* has also been successful with *Homarus americanus* (Fiore & Tlusty, 2005; Tlusty *et al.*, 2005). However, without an enrichment period prior to use, *Artemia* fail to provide a nutritional balance, especially for EFA, which are necessary for survival and growth (McEvoy & Sargent, 1998; Narciso *et al.*, 1999). Methods and the effects of using various commercial enrichment media have been described (McEvoy & Sargent, 1998; Sorgeloos *et al.*, 1998), although most techniques and products are designed for newly hatched *Artemia*, with 24 hours of enrichment, and are formulated to meet the requirements of larval fish and prawns (Rees *et al.*, 1994; McEvoy & Sargent, 1998).

Artemia 'figure prominently, perhaps too prominently, in marine larvae production' and are unsuitable for supplying polar lipid and the omega-3 LC-PUFA DHA (Sargent *et al.*, 2002), especially since *Artemia* are highly active in retroconverting DHA to EPA (Barclay & Zeller, 1996; Navarro *et al.*, 1999). With this in mind, and since phyllosomal larvae do consume static food items (mussel pieces) (Kittaka, 1997b; Matsuda & Yamakawa, 2000), Nelson *et al.* (2002) observed the feeding capabilities of larval rock lobsters, *Jasus edwardsii* and *Sagmariasus verreauxi*. Their observations supported use of feed stations (formulated diet attached to aquaria), a format currently receiving attention (Cox & Johnston, 2003b). Early trials comparing *J. edwardsii* feed-station-fed larvae to animals fed *Artemia* showed some promise (Nelson *et al.*, 2003), and this avenue may prove successful for larval culture of rock lobster. Use of *Artemia* for some stages of larval culture is not discounted, and continued research into the suitability of *Artemia* shows promise (Ritar *et al.*, 2004).

6.8 Feeding regimes

One of the theories as to why artificial diets perform poorly in comparison to a natural diet of mussels is that nutrients are readily leached from artificial feeds. However, Tolomei *et al.* (2003) found that pre-soaking a commercial prawn diet for up to 8 hours before feeding had no effect on the growth, survival, food conversion or carapace colour of *Jasus edwardsii*. The three diets differed in attractability and when offered a choice of two diets, lobsters chose the non-soaked diet over mussels (*Mytilus edulis*) and chose mussels over the pre-soaked diet. However, when only one diet was offered, lobsters would eventually eat similar amounts of the pre-soaked diet as the non-soaked diet, indicating that there is no growth benefit by feeding lobsters several small meals per day instead of one large meal. It should be noted that the prawn diet used in this study was over-supplied with many nutrients compared to the known optimal levels for *J. edwardsii*. Immersion of the diets did not reduce the nutrient levels to sub-optimal, for example, the protein to energy (P : E) ratio was reduced from 36 g crude protein (CP) MJ gross energy (GE)$^{-1}$ to 28 g CP MG GE^{-1} (the optimal P : E for *J. edwardsii* being 29 g CP MJ GE^{-1}). However, if diets are formulated on the known optimal levels for *J. edwardsii*, leaching may cause a significant decrease in the growth rate.

The amount of feed and frequency of feeding was found to significantly affect the survival of captive *J. edwardsii* (Thomas *et al.*, 2003). Juvenile lobsters (5–22 g) were fed high rations (4% body weight (BW) day^{-1}) or low rations (0.5% BW day^{-1}), divided into one, two or four meals. Lobsters fed any of the high ration diets did not differ in growth or survival indicating that there is no advantage in feeding lobsters smaller portions multiple times per day. Furthermore, it appears that any leaching of vitamins and/or nutrients from the feed does not significantly affect growth. Lobsters that were fed the low ration four times per day had significantly lower survival due to cannibalism, with small lobsters more readily cannibalised. The number of small lobsters cannibalised in the low ration group was more than double the number cannibalised in the high ration group. Growth was found to be a poor measure of food competition as lobsters fed the low rations actually grew more than the lobsters fed the high rations. The faster growth rate of the low ration lobsters was attributed to the extra nutrients provided by cannibalism of other lobsters. The results of this study show that if ample food is provided at least once per day, then aggressive behaviour and competition for food among lobsters is much reduced. Multiple feeding in the high ration group was found to decrease the amount of agnostic behaviour, however growth and survival was not affected. Therefore it is recommended that captive *J. edwardsii* be fed to excess once per day at dusk.

6.9 To the table

Understanding the nutritional requirements of lobsters and the ability to grow healthy animals is a task and an achievement. In aquaculture, however, it is no more than academic if the final result is not marketable. The aquaculture of lobsters will rely on achieving important consumer preferences for colour, taste and texture of the lobster flesh, as well as the colour of the carapace.

It seems to be generally accepted that high quality lobster flesh should be white (Bremner & Veith, 1980; Fatima & Qadri, 1985; Yearsley *et al.*, 2001). Tasmanian lobster tasters now prefer bright white meat and the two colour photographs in the 'Mure's book' (Bennett *et al.*, 2002) clearly show no sign of pinkness in the flesh. Crear *et al.* (2002) found that a carotenoid level of 115 mg kg^{-1} was required in formulated diets to produce similar colour in the exoskeleton to wild-caught *Jasus edwardsii* juveniles. Compared to wild-caught animals, any decrease in the darkening of the exoskeleton may have implications for immunocompetence and marketing (Van Barneveld, 1999).

In a taste panel triangle test, adult *J. edwardsii* held on culture while fed diets of fresh mussels (*Mytilus edulis*) and squid (*Nototodarus sloanii*), or a pelleted formulated prawn diet, were compared to wild-caught animals (Nelson *et al.*, 2005). In this preliminary study, 14 inexperienced tasters indicated that the cultured animals could not be statistically distinguished by taste from wild samples. Although this is promising for taste, excessive colour in the flesh of some lobsters fed the formulated prawn diet, and the texture of the small lobsters fed both fresh diet and formulated diet needs further investigation.

6.10 Conclusions and recommendations

Several vital nutritional aspects of culture of lobsters can be identified. Although not unique to lobsters, they must be resolved in a manner appropriate to the species and developmental stage. These aspects include determination of the appropriate ratios of macromolecules, requirements for additional nutritional elements, further exploration of feeding capabilities, and optimal exposure of animals to a food source.

Overall, there is generally more available energy in a diet if the level of carbohydrates is at least double that of lipid. Crustaceans require 10 essential AA (arginine, methionine, valine, threonine, isoleucine, lysine, histidine, phenylalanine and tryptophan) and five essential PUFA (′ -linolenic acid eicosapentaenoic acid, linoleic acid, docosahexaenoic acid and arachidonic acid). Seven minerals should be included in crustacean feeds (calcium, copper, phosphorus, potassium, magnesium, selenium and zinc). The outcome of research on the three main species under investigation for culture showed that the optimal dietary protein levels for the southern, western and tropical rock lobsters were estimated to be 29%, 55% and 47% respectively, with an optimal crude protein/digestible energy ratio for the three species of approximately 30 g DCP MJ DE^{-1}. Generally, lipid should comprise 5–10% of the diet in adult lobsters, with attention paid to the inclusion of PL, cholesterol, and ratios of (n-3) to (n-6) PUFA, specific to the species and stage of development. While *Artemia* may be appropriate for early stages of rock lobster phyllosomal larvae, later stage phyllosoma will benefit by co-feeding of live feed and use of formulated feeds and feed stations, an approach that avoids the often unpredictable metabolic complications of using live feeds, and ultimately can provide high DHA in polar lipid form. A similar approach is useful to supplement a diet of mussel, and can provide supplementation of vitamins, minerals, pigments and attractants. Also, depending upon the animal and diet, multiple feedings per day may not be necessary.

As with larval lobsters (Nelson *et al*., 2002), appropriate format of feeds is a critical aspect of adult lobster culture (Sheppard *et al*., 2002). There is considerable scope for further optimisation of diets. Perhaps increased knowledge of lobster feeding capabilities, and of the confounding effects of aquarium design and microbial loading, may aid in clarifying the nutritional requirements of lobsters. However, perseverance and empirical methods remain the most effective method.

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Chapter 7

Larval and Postlarval Ecology

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7.1 Introduction

A review of the early life history of spiny lobsters was made by Booth and Phillips (1994) and this review focuses on information which has become available since that time. It also overlaps a review by Butler and Herrnkind (2000) which dealt only with the postlarva and early juveniles of palinurid lobsters, as well as a recent review by Booth *et al.* (2005) on the larvae and postlarva of scyllarids.

There is still a paucity of recent ecological and behavioural information on the scyllarids. Few scyllarid lobsters (even the larger sized such as those of *Scyllarides*, *Paribacus*, *Evibacus*, *Ibacus* and *Thenus*) form significant fisheries; and most scyllarid species are taken as a by-catch in other fisheries (see Holthuis, 1991), so there has been little research expended on their early development. Although development of the larva and postlarva is known for representatives of all genera in the four subfamilies comprising the Scyllaridae – Arctidinae, Ibacinae, Scyllariae and Theninae (see Holthuis, 1985, 1991) arranged in order of the more primitive to the more recent (specialised) group (see also Baisre, 1994) – far less is known of their ecology and behaviour than for those of the commercially important, shallow-water, palinurid species of *Jasus*, *Sagmariasus* and *Panulirus*.

Lobsters (spiny and clawed) provide an interesting lesson in life-history evolution, particularly in reference to the larval stage. Larval stages are very common among marine invertebrates and are assumed to confer some selective advantage, usually taken to be dispersal (Pechenik, 1999). Despite this advantage, there must also be disadvantages, as not all marine invertebrates have a larval stage. Spiny and clawed lobsters may shed some light on this, as they share common but distant phylogenetic roots (the Palinuridae and the Astacidae separated in the Permotriassic, about 250 milllion years ago). They also share many ecological characteristics, yet play very different games when it comes to the larval stage. In brief, much of clawed lobster development takes place in large, yolky eggs, females provide parental care by carrying the eggs for nearly a year, clutch size is small relative to many other decapods, and the larvae are large and spend a short time (weeks) in the plankton before metamorphosis. Spiny lobsters, in contrast, have relatively large clutches, small eggs hatch within weeks of fertilisation, and the larvae spend months in the plankton before metamorphosis. Such divergent evolution in ecologically similar groups that have been separate for 250 million years (Schram, 1982) may be instructive.

7.2 Spiny lobsters and slipper lobsters

Nothing characterises more the early life history of palinurids and scyllarids than the distinctive phyllosoma larva (from the Greek *phyllon* – leaf, and *soma* – body). Reaching 80 mm or so in total length

Fig. 7.1 Final-stage phyllosoma larvae of the palinurid *Jasus edwardsii* (upper pair) and the scyllarid *Ibacus alticrenatus*.

in some species, this flat, virtually transparent, long-lived larva – which is often widely dispersed in the open ocean – seldom fails to capture the awe of the observer (Fig. 7.1). Furthermore, the phyllosomas of some species are among the longest-lived larvae of any invertebrate.

There are many similarities in larval development and behaviour between the very closely allied Palinuridae and Scyllaridae. There are also similarities with the foregoing families, in larval development of the two species of *Palinurellus* which comprise the Synaxidae (coral lobsters). The phyllosomas of *Palibythus magnificus* are unknown, and whether this genus should be placed in the Synaxidae or the Palinuridae is still unresolved (Chapter 4). Finding some mid-and/or late stage larvae of this species could help resolve this taxonomic dilemma, but the chance of such findings is rare.

Palinurid and scyllarid lobsters produce large numbers (thousands to tens of thousands) of small eggs (about 1 mm diameter) that are carried for a short period (weeks to several months for some species) before hatching into the larval phase that can last weeks to many months. Early development in both families comprises a 'prelarva' (naupliosoma) in some species, a larval phase (phyllosoma), and a postlarval phase (puerulus in palinurids, nisto in scyllarids) which precedes the first juvenile stage.

The naupliosoma is a short-lived (hours) and small prezoea (1–2 mm) that hatches from the egg. So far it is known to occur naturally in early development of the more 'primitive' palinurid and scyllarid genera, i.e. *Sagmariasus verreauxi*, and certain species of *Jasus*, *Scyllarides* and *Ibacus*, and is regarded as a plesiomorphic (primitive) character (Baisre, 1994). The naupliosoma phase is embryonised in the more recently evolved genera in both families (e.g. *Panulirus*, members of the Scyllaridae, and the highly specialised *Thenus*). Earlier accounts of a free-living naupliosoma occurring naturally in *Panulirus* species (*in vivo* or *in vitro*) are controversial and more likely to be due to physical or chemical factors – such as mechanical damage to the egg membrane or adverse salinities. The naupliosoma moults into the phyllosoma, a leaf-like, planktonic zoea that passes through a number of instars to reach 10–80 mm total length (TL), depending on the species.

Phyllosomal instars are usually grouped into stages, based on their level of development. After weeks or months developing in coastal (some scyllarids) or more distant waters (other scyllarids and all palinurids), phyllosomas metamorphose to the postlarva. This short-lived transparent form can reach up to 20 mm carapace length (CL) or more in some species. Metamorphosis signals the end of the planktonic phase when the postlarva, after assuming the role of returning the lobster to the benthic habitat of the adult, moults to the first-instar juvenile.

7.2.1 Phyllosoma larvae

The lengthy larval life and the often highly dispersed larval distributions have been major obstacles to research and management, this fascinating aspect of the early life history of spiny and slipper lobsters being only recently understood in any detail. The open ocean is a particularly testing environment to sample, usually requiring large vessels, often fishing with large nets at night. Whereas earlier understandings were based almost entirely on field collections, our knowledge of larval recruitment processes has more recently benefited from simulations of larval trajectories incorporating detailed information on oceanography. The oceanography has been described from satellite-tracked drifters, satellite-derived sea level altimetry, sea colour and surface temperature imagery, shipboard hydrography, and moored current and temperature measurement probes.

At the same time, larval culture has led to new insights into biology, many species now having been grown towards or to metamorphosis. Whereas earlier work was aimed at elucidating development, the main motivation for most larval culture work in recent times has been the pursuit of aquaculture opportunities. Nevertheless, in only about 20% of the 48 known palinurid species, and similar proportions of the 80 or so recognised scyllarids, is there anything known about the larvae beyond the first few instars, and for only a few does there exist what might be described as a reasonable knowledge of their biology.

This section reviews our knowledge of the larval phases of palinurids and scyllarids – including their development, ecology, and behaviour – focusing on studies published since 1990. (Useful previous reviews include those of Phillips & Sastry (1980), Booth & Phillips (1994), Butler & Herrnkind (2000) and Booth (2002) for palinurids; and Phillips & Sastry (1980), Booth *et al.* (2005) and Sekiguchi *et al.* (2006) for scyllarids.) The number of phyllosoma stages and length of larval life for palinurids and scyllarids, based on field and laboratory studies, are given in Tables 7.1 and 7.2 respectively. As far as possible, these tables have been arranged in phylogenetic sequence from the earlier to the more recent genera in each family (Baisre, 1994; McWilliam, 1995). Much more is known of the larval development and ecology of shallow-water species (those confined mainly to depths less than 200 m) than the deep ones, more and more species of which – particularly among the scyllarids – are being discovered as offshore waters are sampled for the first time.

Larval identification and development

Distinguishing palinurid phyllosomas from scyllarids is not necessarily straightforward. Scyllarid phyllosomas have a uniramous third maxilliped – there is no exopod – whereas in palinurids it is generally biramous (Baisre, 1994); this is a feature that can be used for all stages of development because the third maxilliped is usually well developed at hatching. But there are exceptions: (1) *Jasus* phyllosomas do not have this setose exopod, (2) it seems likely that *Projasus*, being so closely related to *Jasus*, also lacks one; and (3) *Sagmariasus* (previously *Jasus*) *verreauxi* does not have this exopod at hatching, but develops (or partly develops) one by the final stage (Kittaka *et al.*, 1997). On the other hand, it also seems likely that a fully developed fifth pereiopod (with setose exopod) occurs in larval development of *Projasus*, regarded as intermediate between *Palinurellus* and *Jasus* (George & Grindley, 1964), as it does in the earlier genera, *Palinurellus* and *Sagmariasus* (Baisre, 1994). Another important difference is that mid- to late-stage phyllosomas of scyllarids have dorsoventrally compressed second antennae bearing a lateral process whereas in palinurids the second antennae are cylindrical. The shape and proportions of the cephalic shields are useful in identifying the genera in the two families, and also in separating mid- and late stages of the different larval series in some of the smaller (albeit, unidentified) scyllarine species. Developmental sequences and the size ratios of various appendages are often also crucial to identification.

Morphological characters therefore allow most larvae of both families – particularly those fairly advanced in their development – to be distinguished to genus (Baisre, 1994) but there continue to be difficulties in distinguishing larvae within genera. In *Panulirus*, the most diverse palinurid genus (40% of the recognised species), late-stage larvae form distinct morphological groups (McWilliam & Phillips, 1992; McWilliam, 1995) that were distinguishable in field samples (Baisre & Alfonso, 1994) and yet cultured *P. longipes femoristriga* now *Panulirus femoristriga* (Chan & Ng, 2001; Sekiguchi & George, 2005) were indistinguishable from same-group *P. japonicus* larvae (Matsuda &

Table 7.1 Palinurid and synaxid larval parameters. For larvae, [a]denotes data based on wild lobsters; [b]denotes data based on cultured lobsters; mo, months. Number of instars given only if an estimate is available (otherwise it is at least the number of stages). Mid- and late-phyllosoma stages of all listed species are found in oceanic waters, usually well beyond the shelf break.

Species	No. instars	No. stages	Length of larval life
Palinurellus gundlachi		12[a29]	10 mo[a29]
Sagmariasus verreauxi	17[b9]	11[b9]	9–12 mo[a11] 6–12 mo[b9,33]
Jasus lalandii	15[b1]	13[a2], 11[a3,b1]	9–18 mo[a2,10] 10 mo[b1]
Jasus edwardsii	17[b5]	11[a6]	12–24 mo[a6,7,8] 7–11 mo[b4,5] 12 mo[b35]
Palinurus elephas	6–9[b12]	6–10[ab12]	>3–4 mo[a13] 2–4.5 mo[b12]
Panulirus femoristriga	21–23[b32]	10[b32]	9.5 mo[b32]
Panulirus marginatus		11[a24]	6–11 mo[a28]
Panulirus argus		11[a14]	6–10[a14,31]
Panulirus japonicus	27–29[b15–17]	11[a18,34,b15]	8–14 mo[a34,b15–17]
Panulirus cygnus	15[a19]	9[a20]	9–11 mo[a20,21]
Panulirus interruptus		11[a22]	7.75 mo[a23]
Panulirus penicillatus		11[a24]	>7–8 mo[a25]
Panulirus homarus homarus		10[a26]	
Panulirus homarus rubellus		9[a27]	4–6 mo[a27]
Panulirus ornatus			4–7 mo[a30]

[1]Kittaka (1988), [2]Lazarus (1967), [3]Silberbauer (1971), [4]Kittaka *et al.* (1988), [5]Kittaka *et al.* (2005), [6]Lesser (1978), [7]Booth (1994), [8]Bruce *et al.* (2000), [9]Kittaka *et al.* (1997), [10]Pollock (1986), [11]Montgomery & Kittaka (1994), [12]Kittaka *et al.* (2001), [13]Bouvier (1914), [14]Lewis (1951), [15]Kittaka & Kimura (1989), [16]Yamakawa *et al.* (1989), [17]Sekine *et al.* (2000), [18]Inoue (1978), [19]Braine *et al.* (1979), [20]Chittleborough & Thomas (1969), [21]Phillips (1981), [22]Johnson (1956), [23]Johnson (1960), [24]Johnson (1968a), [25]Johnson (1971a), [26]Prasad & Tampi (1959, misidentified as *P. penicillatus*), [27]Berry (1974), [28]MacDonald (1986), [29]Sims (1966), [30]Dennis *et al.* (2001), [31]Cruz *et al.* (2001), [32]Matsuda & Yamakawa (2000), [33]Moss *et al.* (2000), [34]Inoue (1981), [35]A.Ritar pers. comm.

Yamakawa, 2000). Indeed, among North Atlantic *Panulirus* spp., and also within the diverse genus *Jasus*, larvae could be categorically identified to species only by using genetics (Silberman & Walsh, 1992; Booth & Ovenden, 2000).

Scyllarine species are usually the numerically dominant scyllarid phyllosomas collected from coastal and near-shelf waters (Rothlisberg *et al.*, 1964; McWilliam *et al.*, 1995) and are frequently the most abundant of all phyllosomas found in these regions. The high species diversity in this group of scyllarids, more apparent in warm than in temperate waters (see McWilliam *et al.*, 1995), means that there are more gaps in larval development morphologies and identifications in this family, than in the palinurids. For example, although there are descriptions of at least 57 scyllarine (formerly *Scyllarus* – see Holthuis, 2002) species of phyllosoma, most are confined to one or just a few stages and no more than 20 have been given names of known species. Indeed, much of the scyllarid material remains frustratingly obscure

Table 7.2 Scyllarid larval parameters (based on Booth *et al.*, 2005). For larvae, [a]denotes data based on wild lobsters; [b]denotes data based on cultured lobsters; d, days; wk, weeks; mo, months. Number of instars given only if an estimate is available (otherwise it is at least the number of stages). For extent of offshore distribution: coastal, mainly over continental shelf; intermediate, within but also beyond shelf break; oceanic, mainly well beyond shelf break, including within ocean basins.

Subfamily/species	No. instars	No. stages	Length of larval life	Extent of offshore distribution of late-stage larvae
Arctidinae				
Arctides guineensis		13[a13]	~8–9 mo[a13]	Oceanic[13]
Scyllarides aequinoctialis		11[ab14]	~8–9 mo[ab14]	Oceanic[14,15]
Scyllarides nodifer		~11[a14]	~8–9 mo[a14]	Oceanic[14]
Scyllarides herklotsii		11[a16]		Oceanic[16]
Scyllarides astori				Oceanic[2]
Scyllarides squammosus				Oceanic[10–12,17]
Ibacinae				
Parribacus antarcticus		>11[a11]	~9 mo[a11]	Oceanic[11,12]
Ibacus peronii	6[b7]	7[a8]	71–97 d[b7]	Intermediate and oceanic[8–10]
Ibacus alticrenatus		7[a3]	4–6 mo[a3]	Intermediate[3]
Ibacus ciliatus	7–8[b4,5]		54–76 d[b4,5]	Coastal and intermediate[6]
Ibacus novemdentatus	7[b5]	7[a6]	65 d[b5]	Coastal and intermediate[6]
Evibacus princeps		11[a1]		Coastal and intermediate[1,2]
Scyllarinae				
Antipodarctus aoteanus		10[a21]	Several mo[a21]	Intermediate and oceanic[21]
Galearctus timidus		9[a11]		?Intermediate and oceanic[11]
Galearctus kitanoviriosus		8[a34]		Coastal and intermediate[22,23,34]
Eduarctus martensii		8–10[a20,24,25]	2–3 mo[b25]	Coastal and intermediate[17,20,22,25]
Eduarctus modestus		8[a11]		?Intermediate and oceanic[11]
Petrarctus demani	8[b18]	6[ab19]	42–53 d[b18]	Coastal and intermediate[19]
Petrarctus rugosus		12[a12,20]		Coastal and intermediate[20]
Scammarctus batei		10[a20]		Coastal and intermediate[20]
Chelarctus cultrifer		11–12[a12,20]		Coastal and intermediate[12,20,22,23,33]
Biarctus sordidus		8[a19]		Coastal and intermediate[19]
Scyllarus americanus	6–7[ab26]	6–7[ab26,27]	32–40 d[b26]	Coastal and intermediate[15,26,27]
Scyllarus depressus		9–10[ab28]	2.5 mo[ab28]	Coastal, intermediate and oceanic[28]
Scyllarus chacei				Coastal and intermediate[15]
Scyllarus planorbis	8[b29]	8[b29]	54 d[b29]	
Theninae				
Thenus orientalis	4[b30,31]	4[ab30–32]	27–45 d[b30,31]	Coastal[32]
Thenus sp.	4[b31]	4[b31]	~27–45 d[b31]	

[1]Johnson (1968b), [2]Johnson (1971a), [3]Atkinson & Boustead (1982), [4]Mikami & Takashima (1993), [5]Takahashi & Saisho (1978), [6]Shojima (1973), [7]Marinovich *et al.* (1994), [8]Ritz & Thomas (1973), [9]Phillips *et al.* (1981), [10]McWilliam & Phillips (1983), [11]Johnson (1971b), [12]Berry (1974), [13]Robertson (1969a), [14]Robertson (1969b), [15]Yeung & McGowan (1991), [16]Crosnier (1972), [17]Coutures (2000), [18]Ito & Lucas (1990), [19]Ritz (1977), [20]Prasad *et al.* (1975), [21]Webber & Booth (2001), [22]Inoue *et al.* (2001), [23]Sekiguchi & Inoue (2002), [24]Phillips & McWilliam (1986), [25]Rothlisberg *et al.* (1994), [26]Robertson (1968), [27]Olvera Limas & Ordonez Alcala (1988), [28]Robertson (1971), [29]Robertson (1979), [30]Mikami & Greenwood (1997b), [31]Mikami & Greenwood (1997a), [32]Barnett *et al.* (1984), [33]Higa & Shokita (2004) [34]Wada *et al.*, (1985).

because of continuing difficulties with larval identity, incorrect or unresolved identifications being a particular problem with field-caught larvae in the early scyllarid literature (e.g. Holthuis, 1985; McWilliam *et al*., 1995; Higa & Shokita, 2004). The rearing of late phyllosomas, collected from the plankton, through metamorphosis to puerulus, juvenile and adult of *Chelarctus* (formerly *Scyllarus*) *cultrifer* (Higa & Shokita, 2004), should help to resolve some phyllosoma misidentifications evident in the more recent descriptive literature.

Larval culture allows confirmation of larval identities and developmental morphologies. Palinurids cultured from egg to settlement are *Jasus lalandii*, *J. edwardsii*, *Sagmariasus* (as *Jasus*) *verreauxi*, *Palinurus elephas*, *Panulirus japonicus*, and *P. longipes femoristriga* (Kittaka, 1988; Kittaka & Ikegami, 1988; Kittaka *et al*., 1988, 1997, 2001, 2005; Yamakawa *et al*., 1989; Matsuda & Yamakawa, 2000; Moss *et al*., 2000). Scyllarid species cultured through most or all their larval stages include *Ibacus ciliatus*, *I. novemdentatus*, *I. peronii*, *Scyllarus americanus*, *S. depressus*, *Petrarctus* (as *Scyllarus*) *demani*, *Thenus orientalis*, and *Thenus* sp. (Robertson, 1968, 1971; Takahashi & Saisho, 1978; Ito & Lucas, 1990; Mikami & Takashima, 1993; Marinovich *et al*., 1994; Mikami & Greenwood, 1997a, b). Although larval duration and number of instars may be different in the laboratory to those estimated for larvae in nature, the general sequence of development has been the same.

Food, feeding and predators

Different swimming – and presumably food capture behaviours – appear to exist between genera within both families. Some, such as the scyllarid *Thenus orientalis*, appear to be particularly weak swimmers, even in their late stages (Barnett *et al*., 1984), whereas even early instars of *Palinurus elephas* and *Jasus edwardsii* can be described as active and rapacious predators (Kittaka & Abrunhosa, 1997; Cox & Bruce, 2003). *Thenus* is a much more specialised (i.e. recently evolved) scyllarid genus (Holthuis, 1985; Baisre, 1994). Species-specific – and probably stage-specific – optimal food characteristics are therefore suggested. Foods such as *Artemia*, fish larvae, bivalve gonad, and jellyfish have been useful in phyllosoma culture, particularly for the early stages. In nature, such food items are more abundant in areas of high primary production near land, at upwellings, and along water mass boundaries than in offshore oligotrophic waters. Nevertheless, appropriate foods necessarily occur offshore, where many phyllosomas are found.

Laboratory studies indicate that both palinurid and scyllarid phyllosomas are primarily predators that use their pereiopods to fix and hold food items; their mouth and foregut structure, and digestive system, suggest consumption of soft fleshy foods (e.g. Marinovich *et al*., 1994; Mikami *et al*., 1994; Mikami & Greenwood, 1997a; Kittaka, 2000; Mikami & Takashima, 2000; Cox & Johnston, 2003a, b, 2004; Johnston & Ritar, 2001; Nelson *et al*., 2002; Johnston *et al*., 2004a, b; Johnston, 2006). Near-field water movement receptors may assist food detection in some species (Nishida & Kittaka, 1992; Cox & Bruce, 2003). However, other, less direct food sources may also be used: dissolved organic matter absorbed via the digestive tract and the integument (Souza *et al*., 1999), and in *Palinurus elephas*, filter feeding of small particles, using the scaphognathite of the second maxillae to create water currents (Kittaka, 1997).

Cultured larvae have generally reached/survived metamorphosis at very low rates, consistent with poor nutrition. Varying the diet of the broodstock had no discernable effect on larval competency (Smith *et al*., 2004). Larvae taken in the wild might be expected to suggest diets useful in larval culture, but typically the food canals of field-caught larvae have been virtually empty or else composed of food items so macerated as to be unidentifiable. Furthermore, analyses of protein, carbohydrate, and lipid signatures in larval tissues have not been particularly helpful in establishing natural diets (e.g., Phleger *et al*., 2001; Wells *et al*., 2001; Jeffs *et al*., 2004). However, it remains likely that DNA analyses of alimentary canal contents will be a good way forward in identifying specific foods.

Although a number of species may be quite strong swimmers, they cannot escape larger predators such as tuna, and for the most part phyllosomas must rely on their virtual transparency to avoid predation. Early-stage phyllosomas are eaten by

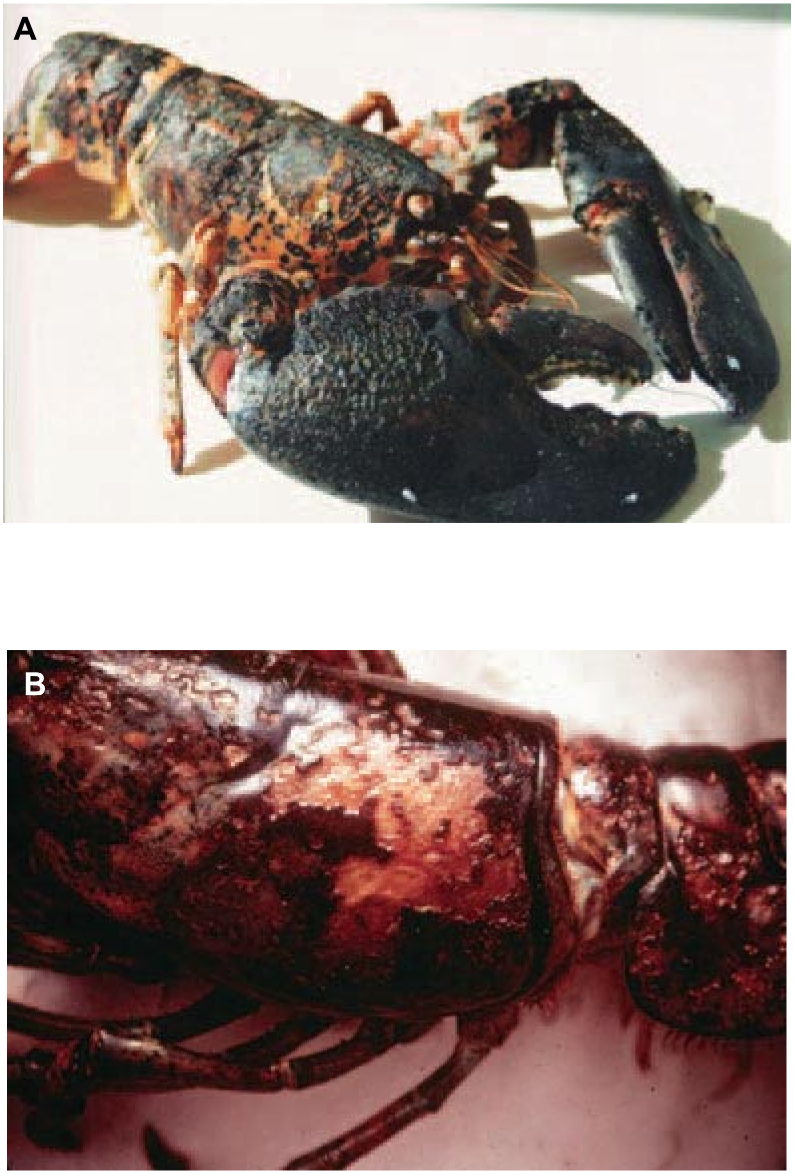


Plate 5.1 (A) An example of epizootic shell disease on *Homarus americanus* from eastern Long Island Sound. (B) Carapace of a lobster with epizootic shell disease. (Photographs courtesy of B. Estrella, Massachusetts Division of Marine Fisheries.)

Plate 5.2 Tail fan necrosis or shell disease in a western rock lobster, *Panulirus cygnus*. This lobster had been held in a fibreglass aquaculture tank for several months. This type of lesion is often associated with localised infections with chitonoclastic bacteria such as *Vibrio* spp.

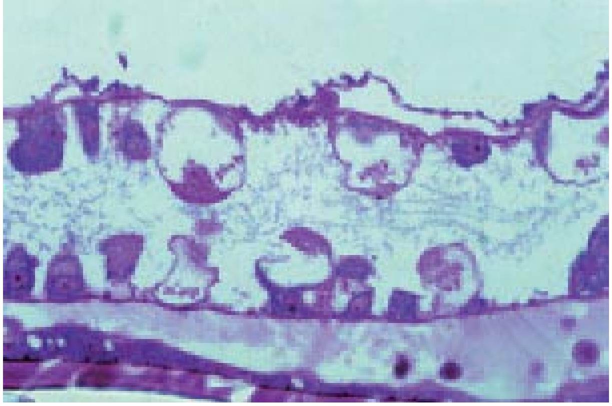


Plate 5.3 Signs of *Vibrio* infection in a phyllosoma of *Jasus edwardsii*. Vacuolation, necrosis and sloughing of epithelial cells within a hepatopancreatic tubule of a stage VII phyllosoma larva. The epithelial cells have become discontinuous and the basement membrane has been exposed. This pathology is frequently associated with ill thrift and infection with various species of *Vibrio*. The phyllosoma was embedded in a glycol methachrylate resin and 2 µm sections were cut because morphology was difficult to examine using standard histological paraffin embedding techniques. H&E, 400x. (Photograph courtesy of D. Johnston.)

Plate 5.4 A western rock lobster, *Panulirus cygnus*, infected with the fungus *Fusarium solani*. This infection was prevalent in wild lobsters during one fishing season in the 1970s in Western Australia. (Photograph courtesy of Murdoch University, Division of Veterinary and Biomedical Sciences.)

Plate 5.5 *Anophyroides haemophila* from *Homarus americanus*. (Photograph courtesy of R. Cawthorn, University of Prince Edward Island.)

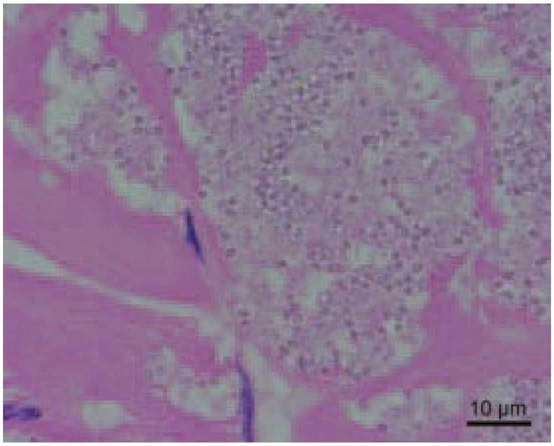


Plate 5.6 Muscle from a western rock lobster, *Panulirus cygnus*, heavily infected with a microsporidian. The musculature of this lobster was an opaque whitish colour when it was captured. Small refractile spores were present throughout most of the muscles in the body.

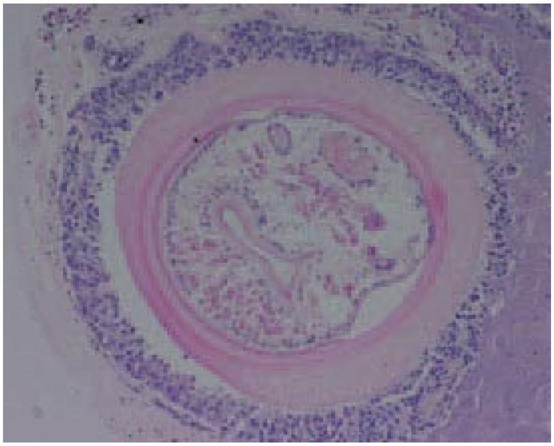


Plate 5.7 Metacercariae of *Thulakiotrema genitale* in the gonad of *Panulirus cygnus* from Western Australia.

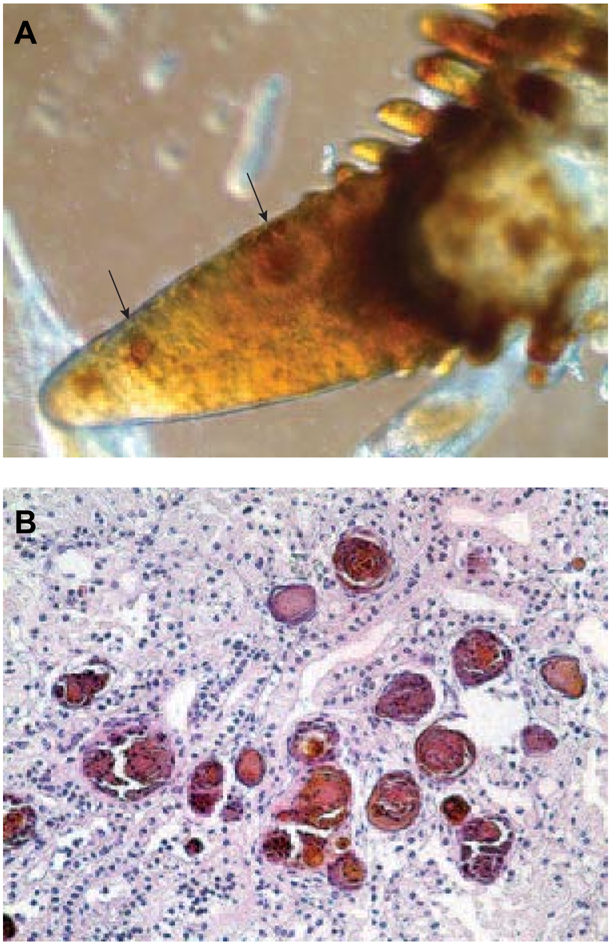


Plate 5.8 Calcinosis in *Homarus americanus* from Long Island Sound, NY. (A) Encapsulated calcium crystals (arrows) within a gill of an affected animal. Fresh preparation. (B) Encapsulated calcium crystals within the antennal gland. Note the displacement of the tissues around the affected area. H&E. (Photographs courtesy of A. Dove, SUNY Stony Brook.)

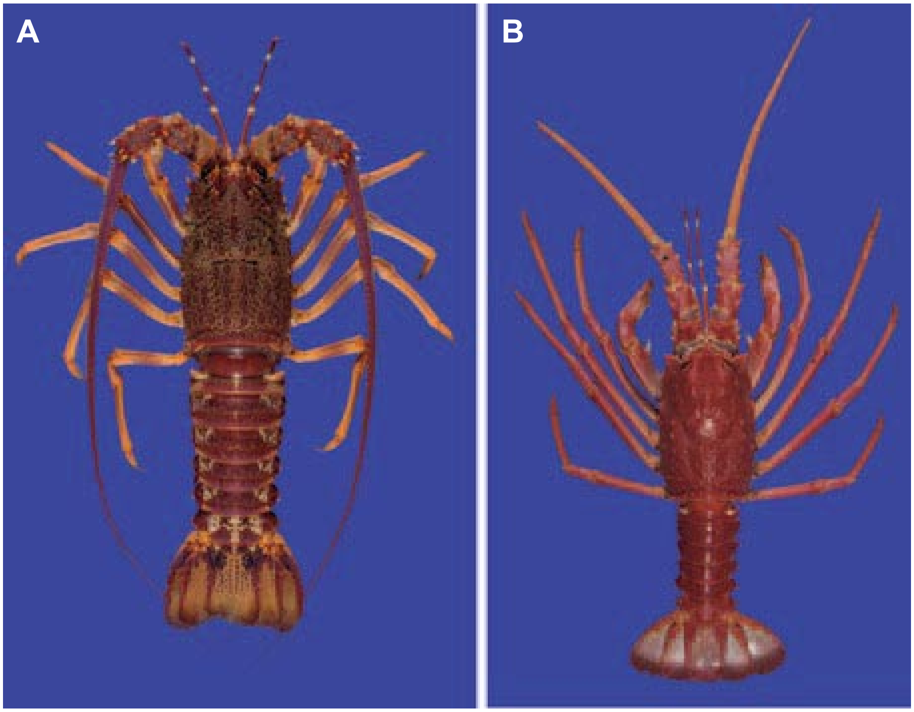


Plate 10.1 Adult males of *Jasus edwardsii* (left), an example of the 'lalandii' subgroup, and *J. caveorum* from the 'frontalis' subgroup. The two subgroups are distinguished most noticeably by the amount of squamal sculpturing on the dorsal surface of the abdomen, more rows of sculpturing being present on the 'lalandii' subgroup lobsters.

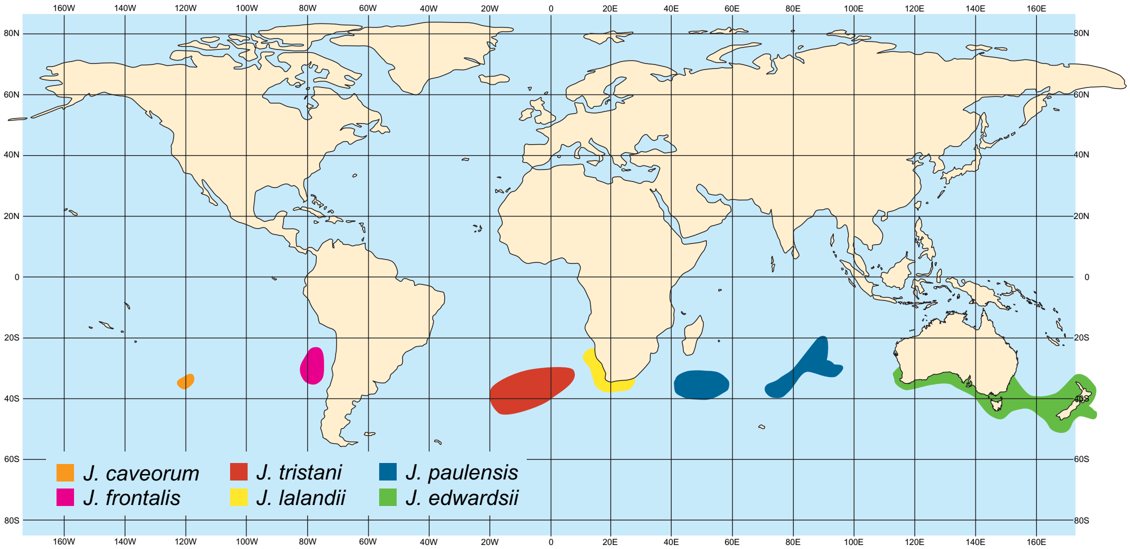


Plate 10.2 Global distribution of *Jasus* species. *J. paulensis* is known to occur south and south-west of Madagascar, but *J. lalandii* may also be there (see text). The extended distribution of *J. paulensis* to the north-east of St Paul and Amsterdam Islands is based on exploratory fishing referred to by Webber & Booth (1988). *J. paulensis* may be occasionally taken at Kerguelen Island (e.g. de la Rue, 1954 in Holthuis, 1991).

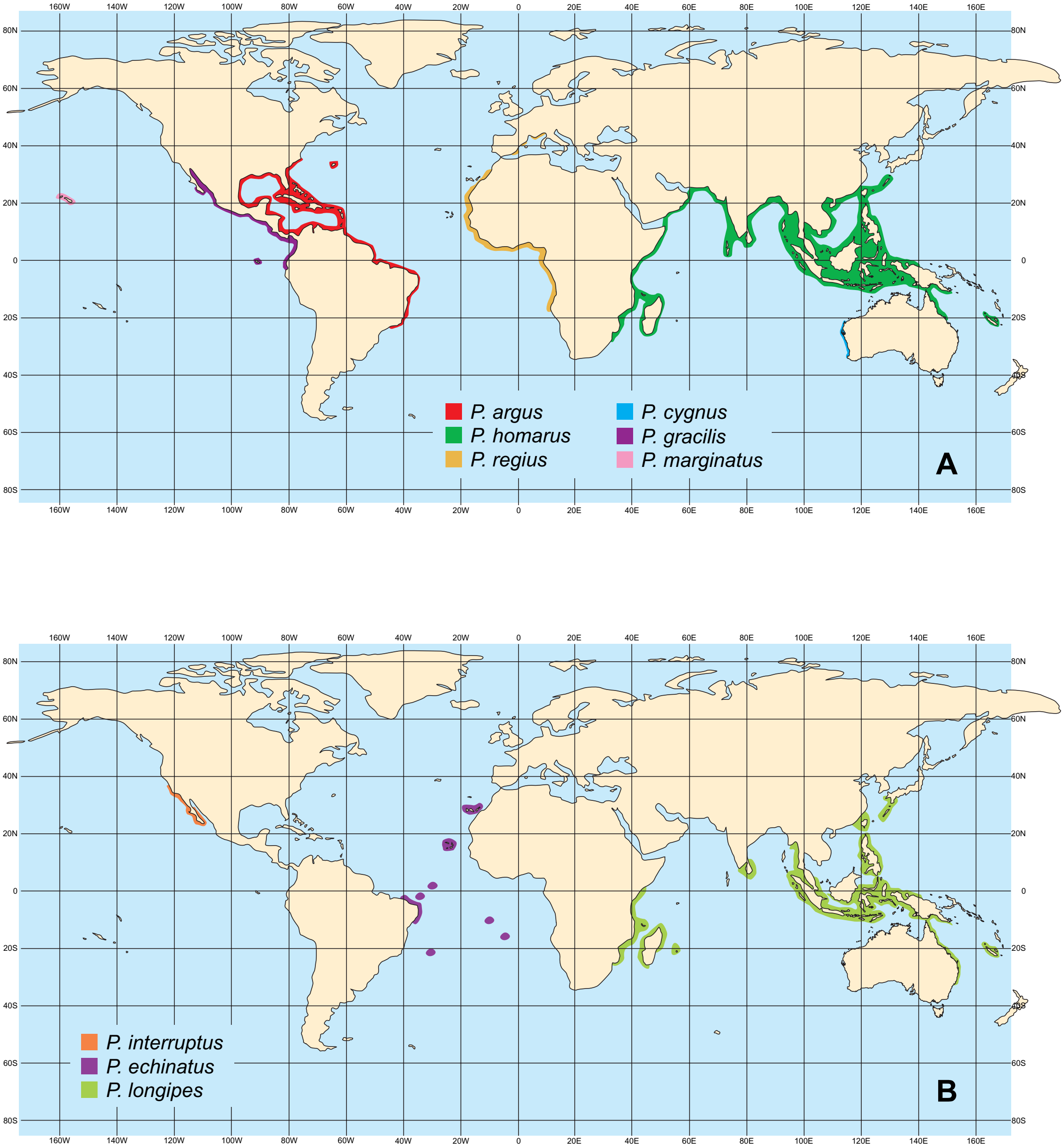


Plate 11.1 Indicative distributions of *Panulirus* species (adapted from Holthuis, 1991).

Plate 11.1 continued overleaf

Plate 11.1 continued

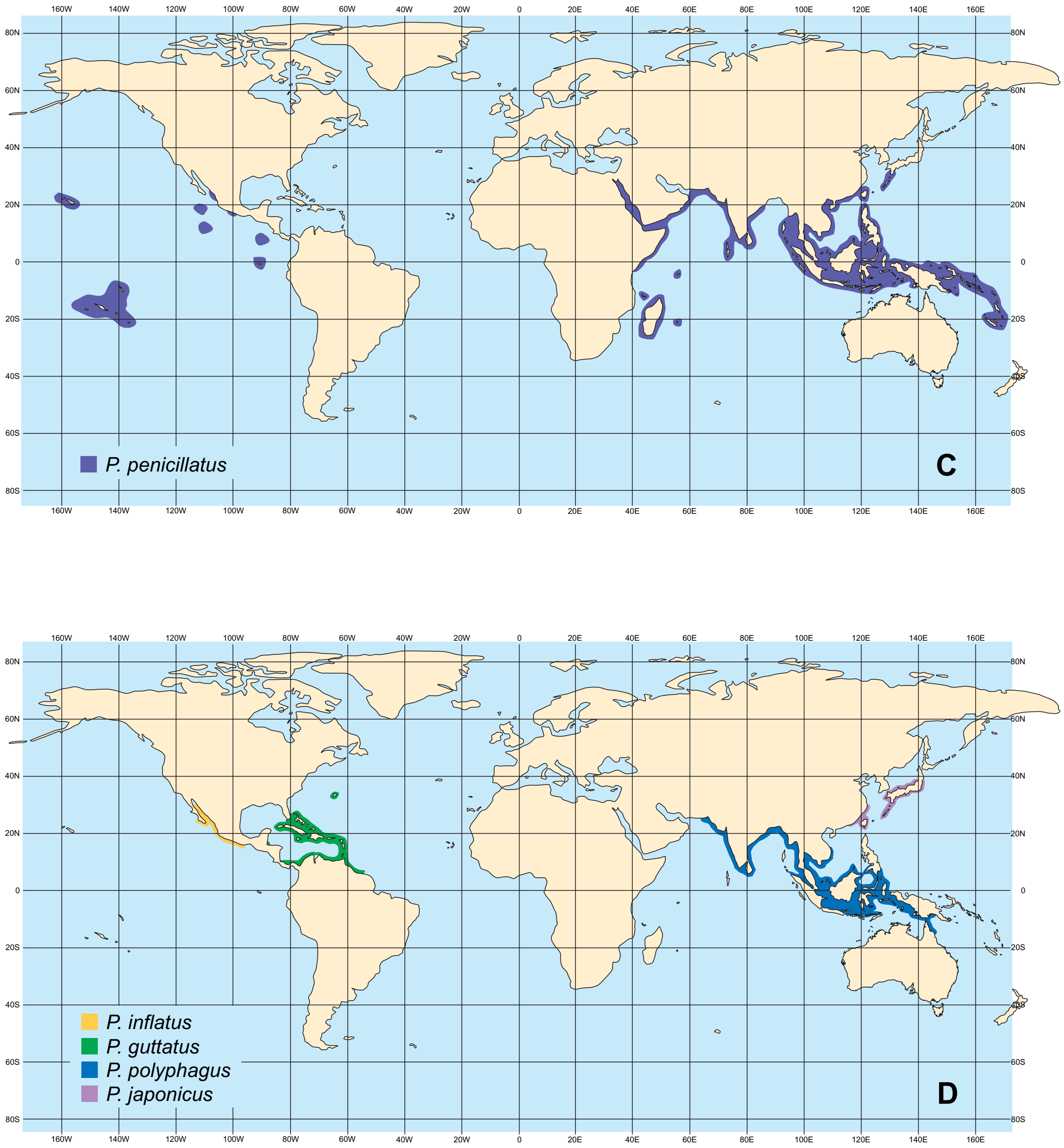
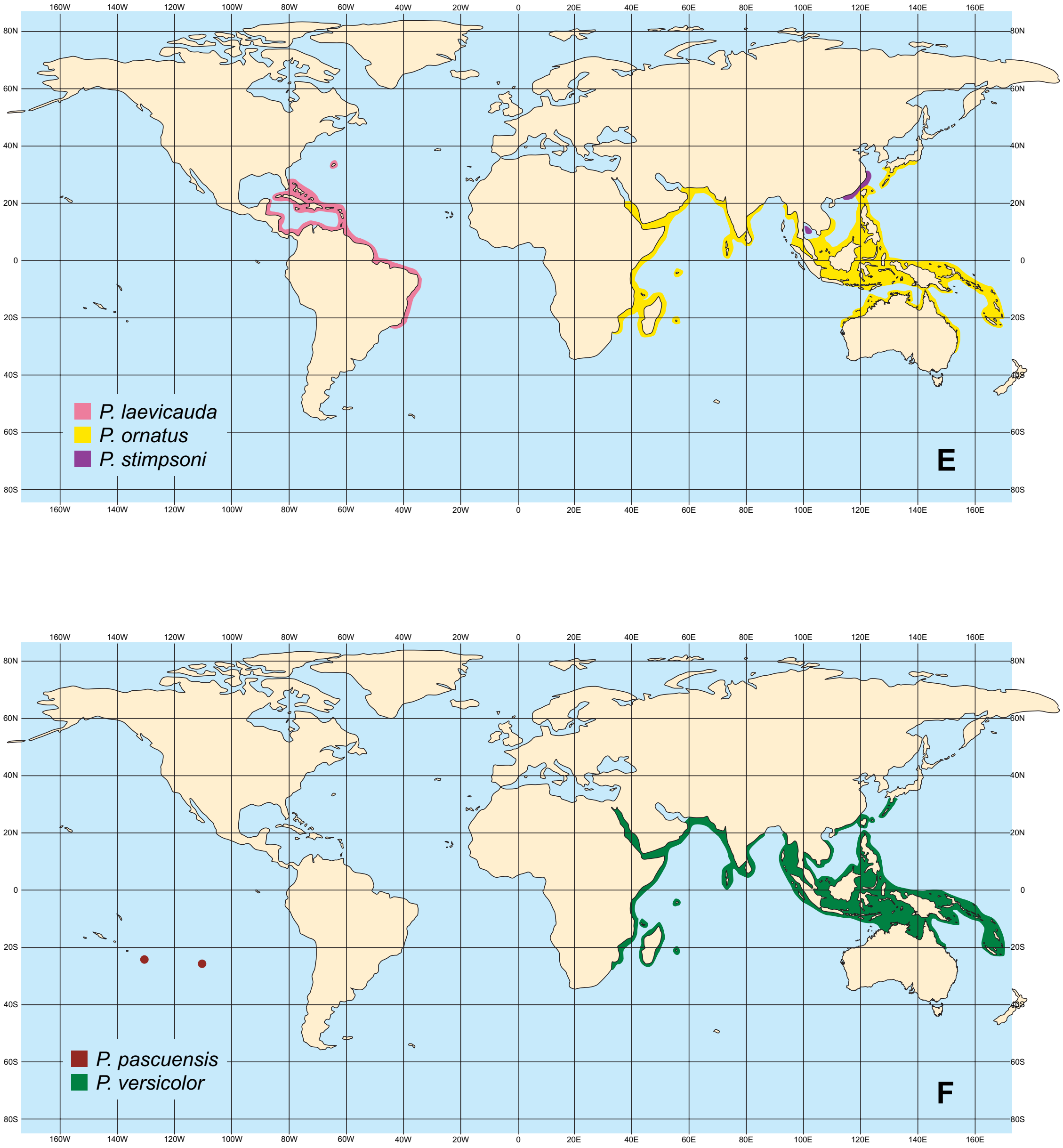


Plate 11.1 continued



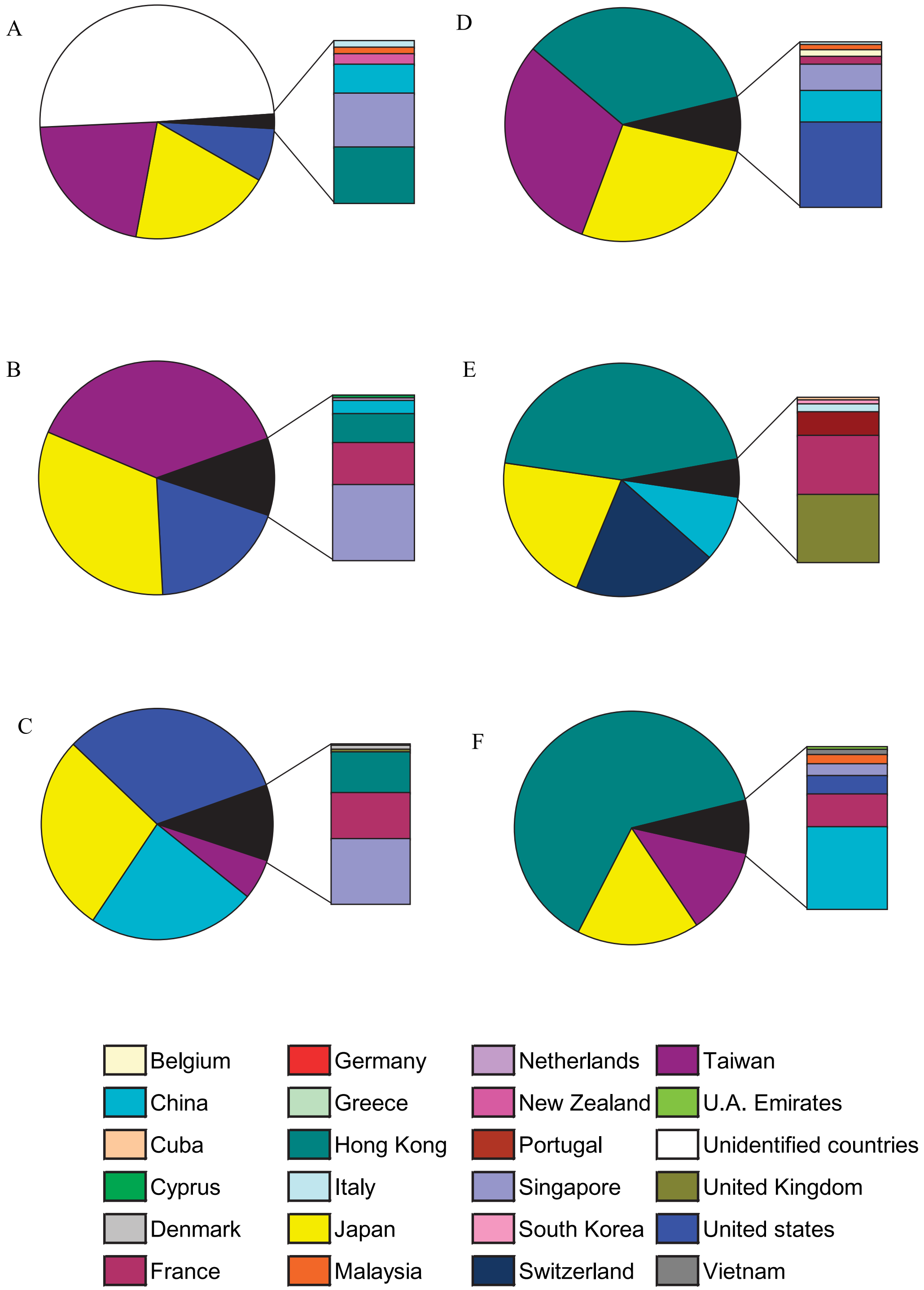


Plate 11.2 Exports of frozen lobster from Australia for (A) 1995, (B) 1999 and (C) 2004, and exports of live lobster for (D) 1995, (E) 1999 and (F) 2004, by percentage of volume exported to each country (data provided courtesy of T. Gibson, Western Rock Lobster Development Association, Perth).

smaller coastal and offshore midwater fishes. Larger phyllosomas have been significant components of the stomach contents of pelagic fishes such as tuna and bramids, many recent reports mirroring the specific examples given by Phillips and Sastry (1980). Scyllarid phyllosomas were found among the stomach contents of a range of fish off New Zealand, from albacore, *Thunnus alalunga*, to sunfish, *Mola mola* (Bailey & Habib, 1982).

Duration of oceanic life

The length of the oceanic development period in nature of both palinurids and scyllarids is seldom well pinned down and may vary between areas and between years. A well-determined estimate of larval duration in the wild requires a short period of egg hatching followed by a brief settlement period, consistent from year to year over the full range of the species, and precise knowledge of the duration of the postlarva from metamorphosis to settlement. Because all these conditions are seldom met, the most precise estimates of larval duration are generally at best, within about ±1 month (e.g. *Panulirus cygnus*), and the least precise about ±6 months (e.g. *Jasus edwardsii*). Laboratory culture might be thought definitive on larval duration, but at least in some species it is little better than a guide. For example, *J. edwardsii* were cultured to settlement in 7–11 months (Kittaka *et al.*, 1988, 2005), but it is not possible to arrive at any larval duration less than 12 months (and more usually 18–24 months) for this species in nature (Booth, 1994; Bruce *et al.*, 2000). Indeed, planktonic development has in many cases been shorter in culture than in nature (see Table 7.1); interestingly, larger volumes of culture water have tended to lead to longer development times (Sekine *et al.*, 2000). In some species, larval culture may indicate the general scale of minimum periods of larval development, the larvae in nature being able to greatly extend this, perhaps through such behaviour as mark-time moulting (Gore, 1985); the few examples of these 'giant' larvae known to date are probably of *Parribacus* (Holthuis, 1985), one of the earlier scyllarid genera.

Despite these problems in estimating larval duration, perhaps the most obvious difference between the palinurids and scyllarids is the range in estimated length of larval life (and actual larval durations under culture). Most palinurids for which there are data have estimated larval durations in nature of 6–12 months (but longer for *Jasus* spp. – up to 24 months) (Table 7.1), and all disperse well offshore. But among the Scyllaridae there is a wider range of estimated larval lifespans, from 1 month to at least 9 months. Many of the small adult scyllarid species have brief, inshore development whereas other, mainly larger scyllarids such as *Arctides*, *Scyllarides* and *Parribacus* have much longer development times, with dispersal offshore sometimes being more extensive than seen among palinurids (Table 7.2). The extent of dispersal is further discussed later.

Warm-water species tend to have shorter larval lives than cool-water ones. Also, among the palinurids, the more recent *Panulirus* species (e.g. *P. versicolor*) may have shorter larval lives than the more primitive species (e.g. *P. argus*) (Baisre, 1994; McWilliam, 1995), but more data are required to be sure. Larval durations among the palinurids of up to about 24 months (for *Jasus edwardsii*) may well be the longest for any invertebrate.

Consistent with the variation in larval duration is a similar variation in the number of instars. For example, among the palinurids there are 6–9 instars in the relatively short-lived *Palinurus elephas* phyllosomas, and around 17 for the much longer-lived *Jasus edwardsii* (Table 7.1). Similarly, in the scyllarids there are four instars in *Thenus* spp. to at least 13 estimated for an *Arctides* sp. (Table 7.2). However, the picture is complicated by a likely temperature effect: for species with similar larval durations, warmer-water species tend to undergo more moults. For example, in culture, during their approximately 10-month larval life, subtropical *Panulirus japonicus* go through almost 30 instars whereas the warm temperate *Sagmariasus verreauxi* have only 17.

Larval behaviour and ecology

The vertical position of phyllosomas in the water column is probably related, at least generally, to the isolume, and is also being affected by levels of moon illumination (Phillips *et al.*, 1981; Yeung &

McGowan, 1991). But the nature and extent of diurnal vertical migration – which presumably brings larvae nearer shallow food sources at night and delivers them into areas of less predator pressure during the day – is not easily estimated in such sparsely distributed zooplankters, and the extent of these migrations seems to vary between species. Among the palinurids, for example, mid- and late-stage *Panulirus cygnus* larvae have a maximum daytime distribution of 60–140 m whereas at night they are close to the surface (Phillips & Pearce, 1997). On the other hand, mid- and late-stage *Jasus edwardsii* apparently migrate little (Bradford *et al.*, 2005). Scyllarids also vertically migrate diurnally (e.g. *Crenarctus* (previously *Scyllarus*) *bicuspidatus* – Phillips *et al.*, 1981), although the wider range of swimming abilities apparent within this family, and the shallow waters in which several species at all stages of larval development are found, means that it is certainly not always extensive. Neither the phyllosomas, nor the nisto, of *Thenus orientalis* have fully developed pleopods (this only occurs in the adult) so only their pereiopods can operate in weak, larval swimming (Barnett *et al.*, 1984). Their larval morphology may limit their vertical migrations, thus keeping them out of surface waters and putting constraints on an otherwise wider dispersal off the shelf – for it would appear that this species is adapted for spending the whole of its life cycle in shelf waters. Furthermore, in both families the extent of vertical movement can vary with stage of development, this difference in turn being crucial to larval offshore dispersal and return (discussed further below). Typically, because they are smaller and more limited in swimming ability, earlier stages show less extensive vertical migration than later stages (Phillips *et al.*, 1981; Wada *et al.*, 1985; Yeung & McGowan, 1991). The extent of diel vertical migration may also be influenced by hydrological conditions. For example, *Chelarctus* (previously *Scyllarus*) *cultrifer* phyllosomas were observed by Minami *et al.* (2001) to be near the surface at night, within the mixed layer, whereas during the day their upper distribution was at the base of the mixed layer (*c.* 60 m depth).

Larval culture has shown that phyllosomas of some palinurid species swim in a distinctive spiralling and looping pattern (Kittaka, 1994) that leads to more extensive vertical movement than horizontal. Indeed, horizontal swimming alone is insufficient to effect return to coast of species that have become widely distributed. It is likely that shoreward transport is achieved more passively, the larvae being carried in that direction in the particular stratum in which they spend most time. However, there may also be some directed swimming: final-stage larvae of *Jasus edwardsii* off the east coast of New Zealand were closer to shore than mid-stage ones, suggesting that the older phyllosomas are able to swim horizontally, perhaps using their well-formed pleopods to help them move out of the eddy and shoreward (Chiswell & Booth, 1999).

A noteworthy feature of the ecology of scyllarid phyllosomas is their sometimes close association with medusae – which appears not to have been observed among palinurid phyllosomas. There have even been several reports of scyllarid phyllosomas, usually late and particularly final stages, 'riding' medusae (and possibly salps and ctenophores). Scyllarid genera that have been observed closely associated with gelatinous zooplankton include *Ibacus*, *Scyllarides*, *Thenus*, *Scyllaru*s, and *Petrarctus* and *Eduarctus* (both previously *Scyllarus*) (see Booth *et al.*, 2005 for references). Medusa-riding does not appear to be accidental or entirely intermittent: for example, among 402 individual *Aurelia aurita* examined, Herrnkind *et al.* (1976) found 80 to have an associated *Scyllarus* sp. larva.

Spatial scale of recruitment mechanisms

The marked difference between the two families in the range in length of larval life is consistent with concomitant differences in the range in extent of phyllosoma dispersals. Palinurids invariably disperse well offshore, in line with their long larval durations. On the other hand, among the scyllarids, *Parribacus*, *Scyllarides* and *Arctides* – large lobsters with long larval lives – generally have far more extensive larval distributions than do many small scyllarine species with short larval lives (Table 7.2). Indeed, it has been recently shown that some scyllarines complete their larval development within the lagoons formed by coral island barrier reefs (Coutures, 2000). Nevertheless, even some of the very small scyllarines disperse widely; this, together with wide dispersal in many large scyllarids, means that the rule of thumb for palinurids that their larvae are seldom taken beyond the latitudes of the adult distribution (George & Main, 1967) does not necessarily apply to scyllarids.

There have been no data to support the hypothesis (Pollock, 1990, 1992) that the larvae of *Jasus* and *Panulirus* circulate entire ocean basins and then recognise their home environments and metamorphose (Polovina & Moffitt, 1995). Indeed it was concluded from widespread sampling that behavioural strategies or physical mechanisms mean that most *Jasus* larvae that recruit to benthic populations are not carried far (>1000 km) from parent grounds (Booth & Ovenden, 2000). Exceptions may be *J. edwardsii* larvae transported across the Tasman Sea to New Zealand (Chiswell *et al.*, 2003), and possibly *J. tristani* larvae carried from near Tristan da Cunha to the Vema Seamount (Lutjeharms & Heydorn, 1981 – although there may be a local recruitment mechanism in effect at Vema, as there must be for the other island and seamount populations of *Jasus* such as *J. frontalis*.

Interaction of ocean processes and larval behaviour

If phyllosomas are not widely distributed in ocean basins, then mechanisms (physical and/or behavioural) must exist for them not to be taken great distances from parent grounds. Even those species with the shortest larval development periods (*c.* 4 weeks, Table 7.2) have the potential to become widely dispersed without them. Recent work has reinforced the likely role of the oceanography – in particular local eddies, gyres, countercurrents, and wind drifts – in preventing at least some phyllosomas of both palinurids and scyllarids from being carried vast distances from shore and in effecting their later return toward shore (e.g. Booth, 1986; Phillips *et al.*, 1991; Yeung & McGowan, 1991; Booth, 1994; Polovina & Moffitt, 1995; Sekiguchi, 1997; Chiswell & Booth, 1999; Yoshimura *et al.*, 1999, 2002; Bruce *et al.*, 2000; Inoue *et al.*, 2000, 2001; Dennis *et al.*, 2001; Griffin *et al.*, 2001; McGarvey & Matthews, 2001; Sekiguchi & Inoue, 2002; Yeung & Lee, 2002; Inoue & Sekiguchi, 2005). Attachment to gelatinous zooplankton could provide late phyllosoma stages of some scyllarids with an indirect way of remaining relatively close to shore. The vertical distribution of larvae appears crucial to their retention and return shoreward, as referred to earlier, with their horizontal direction of movement presumably being affected by position in the water column. For early larval stages, and for species whose larvae at all stages of development migrate little, small vertical migrations may lead to relatively restricted larval dispersal (e.g. Yeung & McGowan, 1991). However, generalising is difficult: it is likely that the particular lobster species being considered, its developmental stage, and the local oceanography – and the interactions of these – are crucial to the dispersal, retention, and later return of larvae.

Alongshore coastal currents can influence the levels of postlarval settlement, but it is not known whether they act on the larvae, the postlarvae, or both, or perhaps it is the abundance of the predators or prey of the larvae/postlarvae that is being affected. Oceanographic modelling of the 9–11 month larval phase of *Panulirus cygnus* suggested that the Leeuwin Current may affect the survival of the larval and/or puerulus stages, *ergo* the level of puerulus settlement, through non-advective processes such as water temperatures of primary production. The ocean climate, in turn linked to the oceanography, is known to be important in palinurid larval recruitment. For example, El Niño years bring lower settlement of *P. cygnus* in Western Australia (Phillips *et al.*, 2000; Caputi *et al.*, 2001; Clarke & Li, 2004) and often higher settlement of *Jasus edwardsii* on the east coast of New Zealand (Booth *et al.*, 2000), again the precise mechanisms being unclear. No similar data are yet available for scyllarid species.

7.2.2 Puerulus and nisto

The puerulus is a single moult stage, 6–12 mm CL in shallow-water species (see Booth & Kittaka, 1994), but about 20 mm CL in deep-water *Projasus parkeri* (cf. Webber & Booth, 1988). The puerulus has appendices internae on the pleopods, which are lost in the postpuerulus. Similar morphology between species of the same genus makes identification of pueruli difficult; body proportions, spination, and colour are widely used (Baez, 1979; Nonaka *et al.*, 1980; Cooke & MacDonald, 1981; Shanmugham & Kathirvel, 1983; Aoyama, 1987; Sekiguchi, 1990b), and biochemical genetic techniques may help (Espinosa *et al.*, 1990). Adults and pueruli sometimes have key features such as spination in common (e.g. *P. parkeri*; Webber & Booth, 1988). The duration of the puerulus stage in nature is poorly known, but it is probably related to the width of the continental shelf and may be species-specific, and it generally exceeds that found in laboratory culture (Table 7.1).

Although referred to as primarily 'surface-dwelling', 'planktonic', and 'nektonic' (Serfling & Ford, 1975; Phillips, 1981; Phillips & McWilliam, 1986; respectively) the puerulus stage of several *Jasus* and *Panulirus* spp. spends much of its time on the seafloor during the day and later settles over a wide depth range. The puerulus in at least these species is therefore better described as a stage alternating between pelagic (night) and demersal (day) life. In culture, pueruli alternated swimming with resting on the bottom (Kittaka, 1988, 1990, 1994; Kittaka & Ikegami, 1988; Kittaka & Kimura, 1989; Yamakawa *et al.*, 1989).

The puerulus of some species of *Jasus* and *Panulirus* is known to be a non-feeding stage that relies exclusively on energy stored during the preceding larval phase (Lemmens, 1994a, b; Jeffs *et al.*, 1999; 2001a, b; Booth, 2002; Nishida, 2002; Hayakawa & Nishida, 2005). These pueruli swim across the continental shelf to the coast and settle in shallow water, moulting to become benthic juveniles. Presumably other species of these two shallow-water genera have the same, or similar, non-feeding habit and shelf-crossing behaviour, although the distances they generally swim may vary between species, the width of the continental shelf, and their competency to swim from wherever their phyllosomas metamorphose to their specific settlement sites on continental shelved, coral reefs and seamounts, etc. The processes involved in cross-shelf movement by the puerulus are poorly understood largely due to their cryptic morphology and behaviour, and their relatively low abundance in the pelagic environment (Phillips *et al.*, 1978; Butler & Herrnkind, 2000). However, laboratory studies of *Jasus edwardsii* pueruli have confirmed that they are nocturnal and rest under stones or bury themselves shallowly in sand during the day (Hayakawa & Nishida, 2005).

Metamorphosis to postlarva

For the shallow-water scyllarid lobsters, the location of metamorphosis of individual species is unknown but is likely to be variable with some species moulting to the nisto at, or beyond, the shelf break, with others metamorphosing inshore on the shelf, e.g. the very small scyllarine, *Eduarctus martensii* (see Rothlisberg *et al.*, 1994) and perhaps *Thenus orientalis* (see Barnett *et al.*, 1984).

In the shallow-water palinurids, there is evidence on the possible locations and stimuli for metamorphosis to the puerulus, but there are different opinions as to the interpretation of this evidence. The usual capture of pueruli within the shelf break has led to early and repeated conclusions that metamorphosis takes place mainly near the shelf break (Lesser, 1978; Phillips, 1981; Pollock, 1986; Booth & Stewart, 1992; Pearce *et al.*, 1992; Booth, 1994; Pearce & Phillips, 1994; Phillips & Pearce, 1997; Yoshimura *et al.*, 1999; Bruce *et al.*, 2000; Dennis *et al.*, 2001; Jeffs *et al.*, 2001a). Consequently this led to the earlier conclusions that features of the shelf-break region, such as contact by final-stage phyllosomas with the seafloor (Booth, 1980; Booth & Phillips, 1994) or with lower salinity water over the continental shelf, were likely stimuli for metamorphosis. McWilliam and Phillips (1997, see foot of p. 788) consider that metamorphosis of *P. cygnus* and other palinurids is not a stimulus-response event triggered by some external factor but results from the culmination of sustained nutrition and energy-reserve levels through later larval development. Phillips and Pearce (1997) and earlier studies of the *P. cygnus* larvae, found the late-stage phyllosomas more abundant in the richer slope waters adjoining the shelf break, rather than further out to sea in more oligotrophic waters. From this, McWilliam and Phillips (1997) inferred that the metamorphosis occurs mainly in this location, and is probably associated with the attainment of some critical level of stored energy in the final larval instar, since the puerulus is a non-feeding stage. They also invoked the results of larval culture studies and observations of Kittaka (1994) that metamorphosis occurred after development through a certain number of instars, 'which seemed to be influenced by a combination of water temperature, nature of the food and feeding rate'.

On the other hand, attaining a threshold of energy reserve is thought unlikely to be a stimulus in *Panulirus ornatus* or *Jasus edwardsii* (Dennis *et al.*, 2001; Jeffs *et al.*, 2001a). Perhaps the answer lies in the suggestion of Jeffs *et al.* (2001a) that metamorphosis may be 'a programmed developmental process'. This too could be mediated by a combination of factors including age, sustained and adequate nutrition and amenable temperatures, throughout the larval phase in all three families.

Three other studies provide alternative evidence of the location of metamorphosis in palinurids and all three suggest that metamorphosis is not associated with the physical characteristics of the shelf break. The location of metamorphosis of *P. cygnus* was inferred from the capture of 19 cast exuviae of final-stage phyllosomas at more than 161 km (ranging from 215–400 km) from the shore of Western Australia and well beyond the shelf at around 45 km offshore (Ritz, 1972). Three metamorphosing final stage phyllosomas of *P. japonicas* were caught in the Kuroshio Current at 54 and 63 km from the coast of Japan in water more than 400 m deep, i.e., beyond the shelf (Yoshimura *et al.*, 1999). Jeffs *et al.* (2001a) inferred the location of metamorphosis of *J. edwardsii* based on the presence of soft carapaces in 33 out of 260 pueruli caught in an extensive offshore survey east of New Zealand. These recently metamorphosed pueruli were captured between 24 and 216 km offshore (mean of 92.4 km ± 7.8 s.e.) and all were well beyond the shelf (740–3622 m deep). Analyses showed there was no relationship between the distribution of the recently metamorphosed pueruli and their stored energy levels, water depth, distance offshore, phytoplankton biomass, sea surface temperature, salinity or the distribution of late-stage phyllosomas. However, there was an indication that metamorphosis could be associated with the inshore margins of oceanic eddies, i.e. richer frontal regions (McWilliam & Phillips, 1983).

In the scyllarid *Thenus orientalis* (Barnett *et al.*, 1984), the entire larval period is spent over the shelf. This does not mean that it could not metamorphose off the shelf should some larvae be offshore. But since the nisto of *Thenus* does not develop functional pleopods, nor appendices internae with cincinnuli, it only moves by flexion and tailflaps – and probably does not have the capacity to reach the shelf from very far offshore.

Movement to settlement sites

The patterns of movement by the nistos of slipper lobsters are also poorly understood although the nistos of a number of species are known to be competent swimmers in the same manner as palinurid pueruli (Lyons, 1970). Again, there are few field or laboratory data or observations on the movements or swimming capacity of the scyllarid nisto – for any species. However, there are some data on duration of the nisto stage for five scyllarid species (representing three of the four families). These range from 5–6 days in *Petrarctus* (formerly *Scyllarus*) *demani*, to 14–24 days in *Ibacus peroni* (Booth *et al.*, 2005); the extent of offshore distribution of their late-stage larval ranges from oceanic to intermediate and coastal (Table 7.2). In *Thenus orientalis*, the only strictly coastal species, whose larvae, like the adults, are also distributed in shelf waters (Barnett *et al.*, 1984), the cultured nisto lasted 7 days before settling. Most of the information presently known about early development, behaviour and ecology of the scyllarid phyllosomas and nistos, has been well covered in Booth *et al.* (2005).

In contrast, there is a considerable amount of information about the onshore movement of the pueruli of shallow-water palinurids. Direct observations of active pueruli have only been made at night time, and they have most often been seen actively swimming in straight lines within centimetres of the surface or on occasions with their antennae emergent in calm conditions (Phillips & Olsen, 1975; Serfling & Ford, 1975; Calinski & Lyons, 1983; Jeffs & Holland, 2000). Offshore pelagic surveys using zooplankton nets have caught pueruli in their greatest numbers near the surface at night and for some species, rough sea conditions appear to concentrate the pueruli in surface waters (Ritz, 1972; Phillips *et al.*, 1978). Inoue *et al.* (2002) reported the stranding of some pueruli of *P. longipes bispinosus* which had been washed ashore after a storm, and also described this puerulus. During the day, the pueruli are in deeper waters or absent from the water column (Phillips *et al.*, 1978; Phillips & Pearce, 1997; Yoshimura *et al.*, 1999). However, in *P. cygnus*, there is a strong indication that the initial onshore movement of pueruli is undertaken at greater depths, later moving to surface waters once well within shelf waters (Ritz, 1972; Phillips *et al.*, 1978). The pueruli of a number of species are almost exclusively found during the dark new moon period, probably to avoid detection by predators (Acosta *et al.*, 1997; Acosta & Butler, 1999), whereas the pueruli of other species have no lunar periodicity to their activity (Hayakawa *et al.*, 1990; Butler & Herrnkind, 2000). Also, lunar periodicity does not seem to affect the numbers of pueruli of *S. verreauxi* recruiting on seaweed collectors (Montgomery & Kittaka, 1994; Montgomery & Craig, 2003).

Offshore surveys of the distribution of pueruli strongly suggest that their movement is directed onshore rather than being dispersed at random or by prevailing ocean currents (Ritz, 1972; Chiswell & Booth, 1999). For example, the distributions of mid- and late-stage phyllosomas, and pueruli of *J. edwardsii* sampled offshore of New Zealand demonstrated that the distribution of the mid-stages was consistent with passive drift in the dominant ocean gyre of this region (Chiswell & Booth, 1999). However, late-stage phyllosomas were significantly displaced inshore, consistent with shoreward directed movement of 4–6 cm s^{-1}, and pueruli at 8–10 cm s^{-1}. These findings suggest that both pueruli and late-stage phyllosomas are directing their movement shoreward from considerable distances offshore (>50 km). This movement is likely to involve a combination of active onshore swimming and the use of natural onshore advection or passive processes, such as wind-driven surface currents (Butler & Herrnkind, 2000).

The evidence for active onshore swimming has been inferred from measured short-distance swimming speeds (ranging from 6–46 cm s^{-1}) and high rates of endogenous energy consumption which both correspond closely with theoretical estimates of the timing of onshore movement and calculated energy budgets (Lemmens, 1994a, b; Jeffs *et al.*, 1999, 2001a, b, 2002; Jeffs & Holland, 2000). The evidence for passive onshore transport of pueruli consists of correlations between the timing of arrivals of settling pueruli and natural phenomenon such as onshore winds, current patterns, and rainfall (Phillips & Pearce, 1991; Caputi & Brown, 1993; Caputi *et al.*, 1995a, b; Acosta *et al.*, 1997; Eggleston *et al.*, 1998; Yoshimura *et al.*, 1999). These studies have consistently shown relatively weak correlations between onshore advective physical processes and the arrival of settling pueruli on the coast, or have produced conflicting results. For example, coastal wind patterns known to produce onshore currents explained up to half the variation in the abundance of settling *P. argus* pueruli over six years in the Bahamas (Eggleston *et al.*, 1998), but other studies in the Florida Keys have found both a marginal correlation and no correlation at all between the two variables (Acosta *et al.*, 1997; Yeung & McGowan, 2001). Correlations between the abundance of settling pueruli and weather and/or current patterns have been found in other palinurid species, but in all cases they fail to provide the high level of correlation that might be expected if pueruli were making extensive use of advective physical processes for their onshore movement (Hayakawa *et al.*, 1990; Caputi & Brown, 1993; Pearce & Phillips, 1988; Caputi *et al.*, 1995b; Booth *et al.*, 2000; Caputi *et al.*, 2003).

The directed onshore movement of final-stage phyllosomas and pueruli strongly suggests that they are capable of orienting toward the coast over extensive distances (>50 km), however, it is unclear what orientation cues are used. Underwater sound emanating from the coast, such as from breaking waves, has been widely suggested as a shoreward orientation cue (Phillips & Penrose, 1985; Phillips & Macmillan, 1987; Booth, 1989; Macmillan *et al.*, 1992; Jeffs *et al.*, 1997). A number of recent field studies have confirmed that underwater sound is an important orientation cue in larval and post-larval crabs and fishes, but lobster species have not been examined (Tolimieri *et al.*, 2000, 2004; Leis *et al.*, 2002; Jeffs *et al.*, 2003; Simpson *et al.*, 2004). A number of other potential orientation cues including water chemistry, magnetic fields, celestial and hydrodynamic cues have been identified, and it is most likely that pelagic palinurid stages use a mix of orientation cues that may change in importance with increasing proximity towards inshore settlement areas or with changing circumstances (Jeffs *et al.*, 2005).

7.3 Clawed lobsters

All but a few of the 43 species of marine clawed lobsters (Nephropoidea) inhabit deep water, and little is known of their biology. We will focus on the only three species whose larval biology is fairly well known, *Homarus gammarus*, *H. americanus* and *Nephrops norvegicus*. Early life history characteristics, behaviour, and larval supply will be of primary interest. Much has been written, and there have been several reviews (Cobb & Wahle, 1994; Ennis, 1995; Cobb *et al.*, 1997). While providing general background information, we focus primarily in this chapter on findings since those papers appeared.

7.3.1 Development

Both *Homarus* spp. and *Nephrops* have a brief (measured in hours) prelarval stage that swims poorly if at all, and remains within the clutch of eggs before moulting to the first zoeal stage. Female *Homarus* release larvae in batches at night by pleopod fanning. Timing of the larval release rhythm is endogenous in *H. gammarus* (Ennis, 1973; Brandford, 1978) and in *Nephrops* (Naylor & Atkinson, 1976). The larvae of these three clawed lobsters pass through three zoeal instars. Metamorphosis follows the final instar, producing a pelagic postlarva that is very similar to the adult in appearance.

The three zoeal larval stages and the postlarva of *Homarus* and *Nephrops* are illustrated in Figs. 7.2 and 7.3. Development is similar in each species. There is a large rostral spine present in all species at all three stages; abdominal spines are present in all species but much-exaggerated in *Nephrops*. The zoea swims erratically, using thoracic appendages. The primary anatomical difference is the greatly extended abdominal spines of *Nephrops* zoea. Their appearance suggests they are an anti-predator adaptation.

The larvae of all three species are approximately the same size, and larger than most larval crustaceans. Effects of female size on the size of larvae at hatching appear to be minimal in *H. americanus*, although primiparous females produce smaller larvae than do others (Ouellet & Plante, 2004). The larvae of *Homarus gammarus* are indistinguishable from those of *H. americanus* but 20–40% larger (Gruffydd *et al.*, 1975). Larvae hatched from rapidly developing eggs of *H. gammarus* had much greater lipid reserves than did those hatching from more slowly developing eggs (Wickins *et al.*, 1995).

The duration of each larval stage depends primarily upon temperature (MacKenzie, 1988, Ennis, 1995, Dickey-Collas *et al.*, 2000a). The larval period (the beginning of stage I to the end of stage III) raised at several temperatures (10–20°C) in the laboratory ranged from 11–54 days in *H. americanus*, (MacKenzie, 1988). Estimates from field sampling ranged from 16–28 days in the warmer waters of the Magdalen Islands (Ouellet & Allard, 2002). Laboratory estimates range from 43–90 days for the larval period of *Nephrops* (Dickey-Collas *et al.*, 2000b). *Nephrops* larvae are difficult to culture and mortality is high. Diet appears to play an important role (Rotllant *et al.*, 2001). The estimates of stage duration for the larvae of this species continue to need to be refined (Dickey-Collas *et al.*, 2000b). Larvae of *Homarus americanus* in the wild grow faster (data comparison in Ennis, 1995) than do those in culture. Wild *H. americanus* postlarvae are usually considerably larger than their cultured counterparts at metamorphosis (Hudon & Fradette 1988; Rooney & Cobb, 1991). Larvae growing at warmer temperatures, during the middle to the end of the season, are smaller, probably as a result of a decreased intermoult interval (Templeman, 1936; Ouellet & Allard, 2002).

Larval growth rate can be measured in field-captured larvae as increase in protein over time (mg protein d^{-1}) in a population (Ouellet & Allard, 2002) or by RNA : DNA ratio analyses (Juinio &

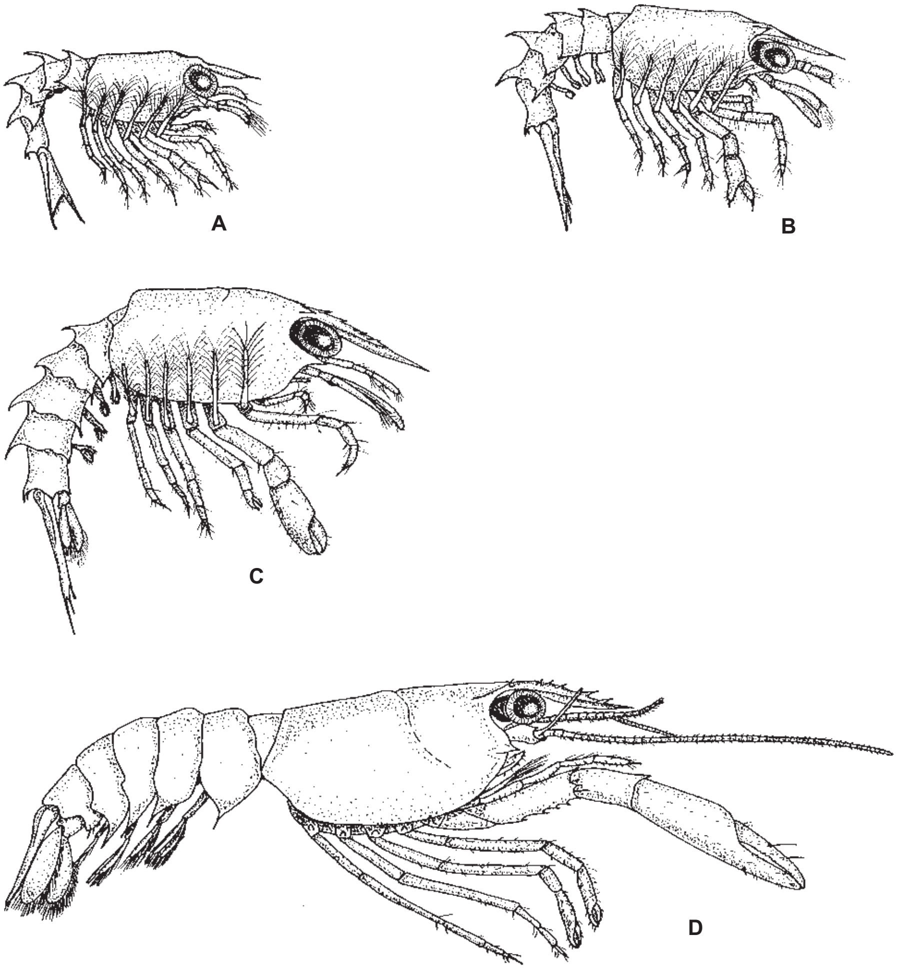


Fig. 7.2 The three larval stages and the postlarva of *Homarus americanus* (from Charmantier *et al*. 1991).

Cobb, 1994). Nutritional status may be assessed by determination of lipid (e.g. triacylglycerols) normalised by total protein (Ouellet & Allard, 2002). It is important to hold constant the moult stage of the individuals as growth varies over the moult cycle.

Metamorphosis occurs at the moult from the last zoeal stage to the postlarval stage (reviewed by Charmantier, 1991). It involves: a change in body plan, so the postlarva resembles the juvenile and adult stages; a change in behaviour, e.g. swimming by use of the pleopods rather than the thoracic appendages; and a change in habitat, from the pelagic realm to benthic. The several parts of metamorphosis do not all occur simultaneously. While the forward swimming behaviour begins immediately after moulting, the behaviour for going from surface to bottom during settlement does not appear until about day four of the postlarval stage of *H. americanus* (Cobb *et al.*, 1989a). The metamorphic moult generally occurs at night, this appears to be timed by an endogenous rhythm (Waddy & Aiken, 1999).

In a number of invertebrates, the size and age at metamorphosis and the timing of settlement affects subsequent size, condition and risk of predation of the juvenile stages (Pechenik *et al.*, 1998; Morgan, 2000). This seems to be true in clawed lobsters as

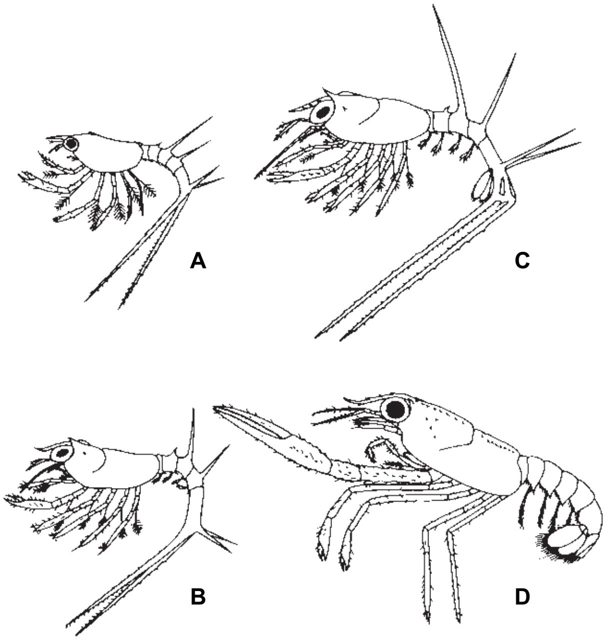


Fig. 7.3 The three larval stages and the postlarva of *Nephrops norvegicus* (from Farmer, 1975).

well. Ouellet and Allard (2002) sampled larval *H. americanus* at three nearby locations in the Magdalen Islands (southern Gulf of St Lawrence) for three years and found both spatial and temporal (seasonal) variation in growth and condition. At the end of the season, the size of stage III larvae had declined from its peak in midseason. This decline was reflected in the size at metamorphosis of postlarvae produced from the smaller stage III larvae. In the laboratory, Niedbalski (1998) fed larvae of *H. americanus* different amounts of food to determine if this affected size and age at metamorphosis. As total food supply increased, age at metamorphosis decreased and size increased. A critical point in development was found between larval stages II and III, after which the developmental rate is set. Changes in food concentrations beyond the critical point may alter size at metamorphosis, but not age.

The size and timing of metamorphosis is not trivial. Larger size and earlier habitat transition confer a survival advantage in many species with complex life cycles (Wilbur, 1980). In *H. americanus*, larvae that metamorphosed and settled early in the season were 30–50% larger and two or three instars further advanced than late-season settlers when winter set in (James-Pirri *et al.*, 1998). The size advantage may result in a lower risk of predation (Wahle, 1992) for the larger (earlier-settling) individuals.

7.3.2 Behaviour

With a few exceptions, the behaviour of the larvae and postlarvae of clawed lobsters has been little studied. Nevertheless, larval behaviour is of great importance to understanding the mortality, distribution and recruitment of this brief but critical phase of the lobster's life cycle. In this section we review some of the behavioural studies and, in some cases, draw inferences from indirect measures such as net sampling.

The three larval stages of *Homarus* swim, apparently aimlessly, by beating the endopodites of the third maxillipeds and the thoracic appendages (Herrick, 1895; Ennis, 1995). After metamorphosis to the postlarval stage, swimming is accomplished by beating the abdominal pleopods with the tail outstretched so the postlarva moves rapidly forward. The claws are held either together in a streamlined posture, or apart during slower swimming, perhaps in a feeding mode.

Despite the 'aimless' nature of larval swimming noted by Herrick (1895), some directionality is possible, allowing the larvae to maintain position in the water column and undergo diel vertical migrations. The vertical distribution of larvae in the water column varies among the species of clawed lobster. *Homarus gammarus* larvae are rare in the neuston during night and day, but numbers increase dramatically at dawn and dusk implying vertical migration upwards at the beginning and end of the day. (Nichols & Lovewell, 1987; Tully & Ceidigh, 1987). Sampling the neuston layer alone is not adequate to quantitatively assess the abundance of the larval stages of *H. gammarus* although postlarvae are found primarily at the surface. The larvae of *Nephrops* are generally found in the mixed layer above the thermocline. Daily vertical migrations have been reported (Hillis, 1974;

Lindley *et al.*, 1994) but *Nephrops* larvae are generally sampled with oblique net tows, thus accounting for larvae at all depths. The postlarvae of *Nephrops* appear to be rarely captured (Dickey-Collas *et al.*, 2000a). The larval stages of *H. americanus* are concentrated near the surface, particularly in shallow, nearshore areas (Cobb & Wahle, 1994). However, offshore, where the water is deeper (and clearer), larvae are distributed down to 20–30 m. Stage I *Homarus americanus* larvae migrate vertically in offshore waters (Harding *et al.*, 1987) and although found much closer to the surface inshore, are more abundant in night time surface tows than daytime tows (Ennis, 1995). Nearly all postlarvae are found at the surface at all times of day both inshore and offshore. Rooney and Cobb (1991) speculated that the postlarvae are near the surface so that they can use celestial cues for orientation in directional swimming.

The postlarvae of *H. americanus* swim using their pleopods at very nearly 10 body lengths per second (18 cm s^{-1}). In a flume, the postlarvae swam more during the day than at night (Rooney & Cobb, 1991). In the field, when swimming direction was observed, most of the postlarvae were swimming northward or eastward (Cobb *et al.*, 1989b). Other crustacean larvae (e.g. barnacles, Walker, 2004) also swim as fast relative to body size, and the postlarvae of *Panulirus cygnus* swim up to 46 cm s^{-1} on its cross-shelf migration (Phillips & Olsen, 1975). Such rapid swimming, if directional, must have implications for the final distribution of settlement. The northward swimming of *H. americanus* postlarvae in the southern New England part of their range takes them shoreward (Katz *et al.*, 1994) and towards shallow nursery cobble areas. The swimming behaviour of *H. americanus* postlarvae in other parts of the range has not been investigated, nor has it been investigated for the other species of clawed lobster.

Little is known about the feeding behaviour or diet of larvae in the field. In the laboratory, lobster larvae appear to be omnivorous. Herrick (1895) described stomach contents of *H. americanus* to include crustacean parts, algae, and amorphous matter 'in large masses'. Based on an examination of the contents of the foreguts of 800 field-captured *H. americanus* postlarvae, Juinio and Cobb (1992) found that other larval crustaceans, copepods, and insect parts made up by far the largest proportion of prey. Newly-ingested prey was more prevalent at night, primarily due to the addition of copepods to the crab megalopae that were ingested in equal amounts over the 24-hour period. Thus, feeding appears to take place day and night suggesting that vision may not play an important role in prey capture. Larval and postlarval feed is of great importance to those who need to raise larvae. Generally, an enriched brine shrimp (*Artemia*) diet has proven to be the most successful (e.g. Conklin, 1995; Rotllant, 2001).

Metamorphosis comprises a change of body shape, changes in behaviour, and changes in habitat. The habitat shift is accomplished by a behavioural change. *H. americanus* postlarvae, the metamorphic stage, swim near the surface, as mentioned above. If an individual encounters the bottom, exploration and shelter inspection, and burrow digging begins as soon as the day after moulting. Starting about three or four days after the metamorphic moult, surface swimming is accompanied by diving behaviour and bottom searching behaviour develops (Cobb *et al.*, 1989a). Thus, if an individual happens to be in shallow water, it is behaviourally competent to take advantage of it and start benthic life immediately. However, if the bottom is not near, the pelagic to benthic transition will not start until two or three days later. Thus the ontogeny of bottom seeking and bottom use provides flexibility in the timing of the transition. Any structured habitat that provides preformed shelter appears to be favoured over unstructured habitat by newly-settled *H. gammarus* (Linnane *et al.*, 2000) which may explain why the postlarvae of *H. americanus* generally choose cobble habitat to settle in (Wahle & Steneck, 1991). Cobble habitat is usually found in shallow, nearshore areas. A cue to bottom-seeking postlarvae that may indicate deep (less suitable) water is the thermocline. Boudreau *et al.* (1991, 1992) found in laboratory studies that few *H. americanus* postlarvae would pass through a sudden change in temperature. A more gradual gradient allowed more to go through the thermocline. The possibility that the thermocline inhibits settlement leads to the suggestion that settlement would occur primarily in shallower water. This, of course leaves unanswered the question of how offshore deep areas are repopulated.

7.3.3 *Factors affecting larval distribution*

There are no wide-ranging synoptic studies that describe larval distribution and abundance. Many individual small to mesoscale sampling programmes have been directed at determining the abundance of larvae, and to determine mechanisms of recruitment. It is clear that consistent differences in abundances among locations do occur, a result of the actions of advective processes, differential mortality, or size of the breeding stock. In this section, we examine two case studies on the effects of advective processes and larval behaviour on settlement distribution of recruits: *Nephrops* in the Irish Sea and *H. americanus* in the Gulf of Maine.

Two mud patches in the Irish Sea are the locations of important populations of *Nephrops norvegicus*. A small patch lies on the eastern side of the sea, just off the Cumbrian coast; a much larger one occupies about half of the northern part of the western Irish Sea (Fig. 7.4). Both lie deeper than 100 m and low tidal energy allows the deposition of mud sediments suitable for the *Nephrops* habitat. Early observations (Hill, 1990; Hill & White, 1990) of the population in the western Irish Sea suggested that the mud patch could be recruitment-limited in some years due to horizontal advection away from the natal grounds. In other years, with more moderate winds generating weaker geostrophic currents, it was hypothesised that there would be enough larval recruits to the area for density-dependent mortality to occur. More recently, a summertime cyclonic gyre overlying the deep, cold water was described (Hill *et al.*, 1996).

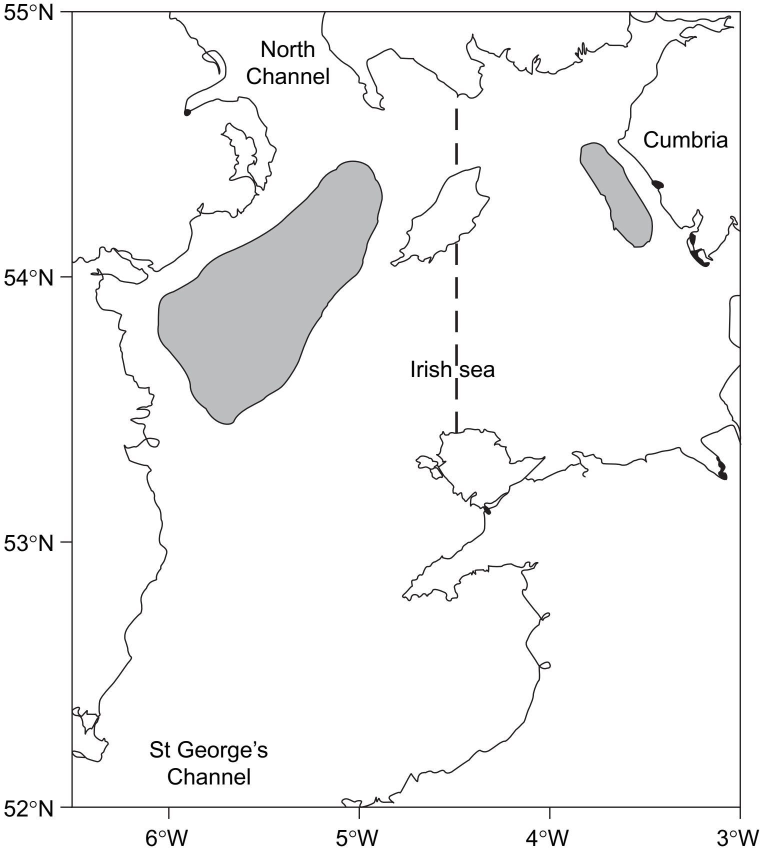


Fig. 7.4 The Irish Sea, showing the location of the 'mud patches', habitat for *Nephrops norvegicus*.

The gyre is driven by density gradients as the surface waters warm. *Nephrops* larvae are released in March and April and spend 40–60 days in the upper 40 m, corresponding to the time of maximum intensification of the gyre. As the stratification strengthens, the circulation around the mud patch increases in velocity and the gyre becomes less 'leaky'. The distribution of larvae corresponds well with the areas of maximum stratification (the potential energy anomaly field). The degree of vertical migration by the larvae probably affects the retention ratio of several species (Emsley *et al.*, 2005). If the *Nephrops* larvae metamorphose and postlarvae settle in the same area, the gyre is a likely retention mechanism, re-supplying the population in the western Irish Sea mud patch (Hill *et al.*, 1996).

Dickey-Collas *et al.* (2000a) used earlier high-speed plankton tow data to estimate the production of *Nephrops* larvae in the west and east Irish Sea. Estimates of the annual production of stage I larvae were $327 \cdot 10^9 \text{m}^{-2}$ in the west and $17 \cdot 10^9 \text{m}^{-2}$ in the east. The production on the eastern side of the sea is about 5% of that of the western side, which is congruent with the relative size of the mud patches on either side – the patch in the east is about 5% of the area of that in the west. In contrast, estimates of the annual production of stage III (premetamorphic) larvae were $75 \cdot 10^9 \text{m}^{-2}$ in the west and $1 \cdot 10^9 \text{m}^{-2}$ in the east (about 1%). This suggests that advection or mortality (or both) are greater in the eastern side of the sea than in the western side.

The larvae of *Homarus americanus* are found along the east coast of North America from Newfoundland to New Jersey. Variation in abundance occurs on both a micro and a mesoscale. In southern New England, larval density drops markedly offshore and postlarvae are rare at the edge of the continental shelf, 200 km from the coast (Katz *et al.*, 1994). In the Gulf of Maine, on the other hand, postlarvae are equally as numerous 50 km from the coast (Incze *et al.*, 2000) as they are in nearshore waters. Along the coast of Maine, variations in density of newly settled lobsters varies greatly, from below the limits of detection at the eastern end (Mount Desert and Jonesport), to as much as two individuals per square metre at the western end (Palma *et al.*, 1999; Steneck & Wilson, 2001). In seven adjacent fishing areas along 190 km of coast in Nova Scotia, Miller (1997) found persistent differences in the abundance of postlarvae and of fishery recruits. At an even smaller scale, Wahle and Incze (1997) observed differences in postlarval supply and newly-settled lobsters on either side of a narrow island. A 'supply shadow' of lower abundance of pelagic postlarvae on the island's downwind side was reflected in lower numbers of settlers. This supply shadow can be observed at a scale of tens of metres on either side of a narrow point (J. Cobb, personal observations).

As the western Irish Sea case made clear, the advective environment is critical for the delivery of competent larvae to nursery sites. A model of the transport of *H. americanus* larvae in the Gulf of Maine (Incze & Naimie, 2000) coupled physical and biological factors in an attempt to explain the broad scale spatial variability in larval supply. They wished to link conceptually sources of larvae (reproduction) and sinks of settlers (recruitment). The sources were mature females in offshore waters, 20–200 m deep, located by trawl surveys. Advection was modelled using a three-dimensional numerical circulation model, coupled to surface temperature that determined the duration of each stage (MacKenzie, 1988). Model larvae were 'hatched' at intervals along each of ten transects at locations around the Gulf. The Gulf has a cyclonic residual circulation with highest velocities south of Nova Scotia and along the coast of eastern Maine (Incze & Naimie, 2000). Larval transport in this area was estimated to be on the order of 200 km, suggesting larvae hatched there are exported with little replacement. This may explain the low settlement rates seen in the eastern Gulf. Another result from the model exercise was recognition of the importance of the summertime sea breeze in helping to transport postlarvae to shallow nurseries. Larvae 'hatched' on Georges Bank were generally retained on the bank, which has a gyral circulation of its own (Fig. 7.5).

A recent study by Harding *et al.* (2005), also in the Gulf of Maine, identified the locations of sources of newly-hatched larvae and timing of hatching, suggested potential oceanographic transport mechanisms, and modelled outcomes of larval transport. Larval sources appear to be associated with water depths of less than 100 m on Browns and Georges Banks. Early-stage larvae were more abundant over Georges Bank, and late-stage larvae and postlarvae more abundant off the Bank. The larvae on Georges Bank are more advanced developmentally than those over Browns Bank; in fact, if the gyre on Georges Bank is leaky it could be a source of the postlarvae found on Browns Bank. It also seemed plausible that late stage larvae north of Georges Bank may have come from warmer areas in the Gulf riding plumes of water off Georges Bank, or carried by occasional strong winds. The trajectories of larval drift that would result in postlarvae found off Georges Bank were hindcast with a three-dimensional circulation model (Fig. 7.5). Most of the origins were in the middle of the Gulf, in areas deeper than 100 m, not a plausible outcome to the authors. Instead, they suggest, more likely are a few model trajectories that originate off Penobscot Bay or off Cape Cod. This does not agree with Incze and Naimie's (2000) results, but both studies make a good case for advection of larvae away from their natal area. It is also true that the development of coupled biological–circulation models is still in its larval stage; much more needs to be learned about both the biology and the oceanography of the system.

These models and similar observations (e.g. Harding & Trites, 1988) suggest that much of the Gulf of Maine population of *H. americanus* acts as a metapopulation with source–sink dynamics such that many subpopulations are likely to be repopulated annually by larvae hatched upstream. The coastline is complex and convoluted, and the possibility of local retention around headlands and islands is yet to be tested (Incze & Naimie, 2000). These studies also reinforced the premise behind

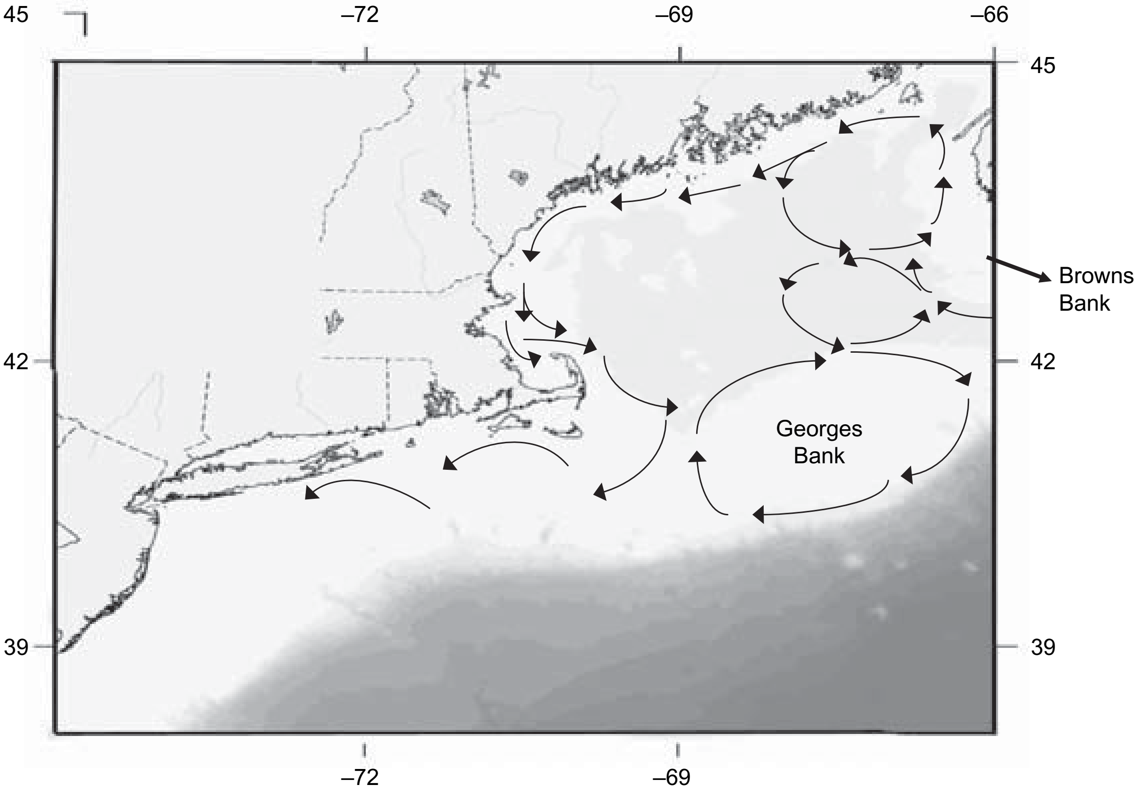


Fig. 7.5 Generalised summer circulation pattern (surface residual drift) in the Gulf of Maine, USA.

Fogarty's (1998) analysis of the *H. americanus* population south of Cape Cod in which he assumed that a subpopulation located at the edge of the continental shelf is the source of at least some of the larvae recruited to the nearshore subpopulation. This metapopulation analysis indicated that with a modest subsidy of larvae to the inshore population from offshore the inshore subpopulation could be sustained even in the face of extremely high fishing mortality. That such subsidy is possible was suggested by a hydrodynamic and biological model incorporating directional swimming of postlarvae (Cobb *et al.*, 1989b) developed by Katz *et al.* (1994).

Advective processes are not the only influence on the supply of postlarvae to populations. Larval mortality also is likely to play an important role. Herrick (1895) mentions that when liberating about 25 000 stage I larvae from his hatchery in shallow water, 'a lot of small cunners made their appearance and snapped up the larvae . . .'. Boudreau *et al.* (1993) showed that postlarvae avoid the source of odour of cunner in a Y maze. The cunner (*Tautogolabrus adspersus*) is a bottom-dwelling fish; predators of pelagic larvae include mackerel and herring (Ennis, 1995) and presumably other planktivorous fishes, but predation on larval lobsters has been given little attention.

Postlarvae descending to the bottom to settle may run a gauntlet of predators as they make the transition from neustonic to benthic habitat. Norden (2003) tested the hypothesis that predation was equal at all depths by tethering *H. americanus* postlarvae at intervals from surface to a rocky reef at the bottom. Mortality was nearly 100% at the bottom and negligible near the surface. Fish predators captured on similar tethers were concentrated near the bottom. Norden suggested that the dark coloration of postlarvae, which makes them quite visible at the surface, is an adaptation for camouflage once arriving at the bottom.

7.4 Conclusions

The planktonic life of relatively few palinurid or scyllarid species has been investigated in detail but some conclusions can be drawn regarding larval recruitment strategies, including similarities and differences between them. In both families, the long-lived phyllosoma larval phase is the key to dispersal of the species. Most phyllosomas appear to feed mainly on fleshy foods and to migrate diurnally – to a greater or lesser extent according to species and stage of development – between surface and deeper waters in a perpetual cycle of seeking food and avoiding predators. Shallow-water palinurids invariably have long-lived, widely-dispersed larvae, some of the survivors of which return to the vicinity of the shelf break to metamorphose. In contrast there is much more variety in the length of larval life and the concomitant extent of dispersal among the scyllarids.

In both families, changing vertical migratory behaviour with development, and the prevailing oceanographic features such as eddies and countercurrents, are probably important in larval dispersal, retention, and return. It would seem that both palinurid and scyllarid phyllosomas have continued to evolve from the time of the development of the present prevailing current systems, so enabling them to exploit the plankton for food and the currents for transport and dispersal. However, adaptation to current regimes as different as those within lagoons and in the deep sea suggests different specialisation among the scyllarids to that among the otherwise similar palinurids.

The three larval and postlarval stages of clawed lobsters, while short in contrast to other parts of the life cycle of clawed lobsters, are a critical period. Strength of recruitment to the benthic population depends on the supply of pelagic larvae, determined by mortality and advection. There are still significant gaps in our knowledge of important aspects of the larvae and postlarvae of *Homarus*, despite a century of study (Nicosia & Lavalli, 1999), and relatively little is known about the biology of *Nephrops* larvae. The potential for aquaculture of *Homarus* has produced a great deal of information about dietary requirements. However, the natural diet, particularly at the time of transition from surface to bottom, is little known. Studies of larval condition suggest differences from one location to another, but longer-term consequences are unclear. Behaviour clearly plays an important role in determining direction and distance of larval transport. The larvae of the three species considered here appear to behave differently regarding diel changes in depth. As three-dimensional models of circulation begin to be used, knowledge of depth distribution and swimming behaviour become very important. Source–sink dynamics of clawed lobster populations are beginning to be considered. The role of molecular genetics will be an important one in answering questions such as whether the gyre over the mud patch in the Irish Sea creates a closed population of *Nephrops*, or what proportion of *H. americanus* postlarvae settling in coastal southern New England are from the offshore population. Studies such as these, and others, are important to fisheries biologists as they attempt to make predictive the relationship between spawning stock and recruitment. Finally, the contrast in larval biology between spiny and clawed lobsters should prove fertile ground for the consideration of larval adaptations and evolution.

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Chapter 8

Juvenile and Adult Ecology

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8.1 Introduction

The ecological dynamics that shape the benthic life of all lobsters are largely circumscribed by the settlement of postlarvae, the structure and availability of nursery habitats, prey availability and growth, predation risk, disease, patterns of movement, social and reproductive behaviours, and their interaction with humans and a changing environment. During the first synthetic effort to assess clawed and spiny lobster ecology, nearly three decades ago (Phillips & Cobb, 1977; Cobb & Phillips, 1980), these issues were identified as important directions for research. The great advances since then have come about for numerous reasons but foremost, the integration of basic life-history, ecology studies with applied fishery research, the application of field experimental and quantitative methods in a hypothesis testing framework, and the emergence of sophisticated computer-assisted modelling. In addition, more species have come under scrutiny by comparable methods, thus supplying the breadth necessary for recognition of general principles and of special cases. A sufficient knowledge of lobster ecology now exists so that in a single chapter we can proffer a synopsis of an array of ecologically relevant issues pertaining to lobsters, although much remains to be done.

In this chapter, we focus on the ecological processes that drive recruitment, the acquisition of shelter and food, predator–prey relationships, movement and migration, and in the case of spiny lobsters, sociality. Growth, reproduction, behaviour, and disease all play important roles in the ecology of spiny and clawed lobsters, but all are covered in depth in other chapters in this volume (Chapters 1, 2, 3 and 5 respectively) so our treatment of these subjects is minimal. Many species of lobster are also of commercial importance, and those species and the fisheries for them are highlighted in Chapters 9–14. We discuss the ecology of spiny and clawed lobsters separately, so as to emphasise the processes most important, or best known, for each. We also stress recent findings and attempt to avoid repeating detailed topical information provided in recent comprehensive reviews (see Factor, 1995; Phillips & Kittaka, 2000). We apologise for undoubtedly overlooking some of the pertinent literature, particularly that appearing in publications that are not peer-reviewed and therefore not widely distributed, and those written in languages other than English. Still, the information readily available on the ecology of juvenile and adult lobsters is voluminous and relevant whether one is interested in natural history, ecology, or fishery management.

8.2 Spiny lobsters

There are more than 45 species of spiny lobsters (Palinuridae), which are widespread and inhabit temperate and tropical seas worldwide, from the intertidal zone to depths approaching 1000 m (Holthuis, 1995). The different genera do not generally co-occur; their distributions are defined in broad terms by latitude and water depth (George & Main, 1967; Cobb & Wang, 1985; Fig. 8.1). Often, only one or a few species of spiny lobster co-occur in a particular region (e.g. *Palinurus elephas* in the

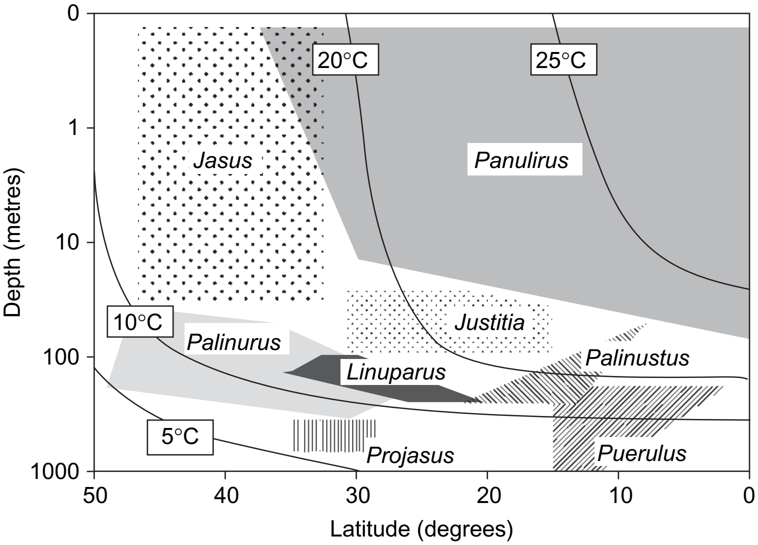

Fig. 8.1 Approximate geographic distribution of spiny lobster genera as a function of water depth, latitude, and water temperature (adapted from George & Main, 1967).

Mediterranean; *Panulirus argus* and *P. guttatus* in the northern Caribbean), but where multiple species of spiny lobster co-occur they are generally segregated by habitat (e.g. the seven genera that co-occur in southern Africa; Berry, 1971). The morphologies of spiny lobster are quite similar and provide little insight into the varied ecological dynamics among the many species. Morphological features that reflect ecological differences are often minor or are obvious functional specialisations, including: sub-chelate or enlarged anterior pereiopods for prying and manipulating prey, elongate and gracile legs on migratory forms, and robust antennae on species often exposed to piscine predators. Otherwise, few morphological cues signify the particular combination of depth, hydrographic conditions, habitat, sociality, predators, or prey that define the ecology of each species. Yet, those ecologies can be remarkably different, spanning lifestyles that include shallow, semi-social, residential dwellers on coral reefs to gregarious, migratory species that live on open, particulate substrates at >300 m depth. Indeed, the versatile palinurid body design has successfully accommodated a broad range of benthic circumstances.

The benthic existence of spiny lobsters is preceded by an extraordinarily long (up to 24 months), oceanic larval phase followed by a brief (few weeks) stint as a fast-swimming, non-feeding postlarval phase, which links the offshore life cycle to its inshore, benthic component (see Chapter 7). The postlarvae of some species settle in crevices, others in architecturally complex vegetation. All have evolved chemical and tactile mechanisms that allow them to locate locally available microhabitats that provide both refuge and prey for the succeeding life stage: the early benthic phase juvenile. Early benthic phase juveniles are the benthic phase most vulnerable to predation and they suffer high mortality from an array of fishes and motile invertebrates (e.g. crabs and octopus), despite mitigating adaptations including use of physical refuges, overdispersed distributions, camouflage, cryptic behaviour, and nocturnality. As they grow, benthic juveniles increasingly attain a 'size refuge' from predation and many species of spiny lobster undergo ontogenetic changes in their use of shelters and habitats. All large juvenile and adult spiny lobsters are nocturnally active predators of the benthos, and all aggregate to some degree in appropriately sized crevices for daytime shelter. The large juveniles and adults of many species are nomadic, or participate in seasonal or ontogenetic migrations among habitats, but other primarily reef-dwelling species are philopatric and dwell within the intricately structured confines of coral or rocky reefs throughout their benthic existence. Unlike the solitary clawed lobsters, benthic spiny lobsters also exhibit an ontogeny in sociality; abruptly changing from the asocial early benthic phase juvenile to the gregarious, social large juveniles and adults. Beyond these generalities, species differ strikingly in the details of their ecology that reflect unique evolutionary solutions to conditions in dissimilar ecological circumstances.

8.2.1 Limits to recruitment

Postlarval availability and settlement

Phyllosoma abundance, coastal advective processes, and puerulus behaviour, condition and mortality all influence the supply of pueruli to coastal nurseries. The processes are reviewed elsewhere (see reviews by Butler & Herrnkind, 2001 and Chapter 7), so here we focus on the importance of postlarval supply as a factor that potentially limits the recruitment of juvenile spiny lobsters. Settlement of many palinurid species is estimated by sampling of pueruli and recently-molted early-benthic juveniles on collecting devices ranging from artificial seaweed (Witham *et al.*, 1968, Phillips, 1972) to artificial crevices (Booth 1979; Booth *et al.*, 1991). Phillips and Booth (1994) provide a thorough review of the design, use, and effectiveness of these devices. Some have attempted to measure settlement in natural crevices or vegetated habitats (Marx & Herrnkind, 1985a; Booth & Bowring, 1988: Yoshimura & Yamakawa, 1988, Fitzpatrick *et al.*, 1989; Jernakoff, 1990; Herrnkind & Butler, 1994; Butler & Herrnkind, 1997; Butler *et al.*, 1997; Diaz *et al.*, 2001 among others), but the high crypticity and low density of newly-settled palinurids has prevented common use of such techniques. Few studies have demonstrated that the catch of postlarvae on artificial collectors indeed reflects postlarval planktonic abundance and local settlement density (Herrnkind & Butler, 1994, Phillips *et al.*, 2003).

Most research employing postlarval collectors is primarily intended to establish predictive statistical relationships between relative postlarval abundance (i.e. catch of postlarvae on collectors) and catch in the commercial fishery (or pre-recruits to the fishery), which are of obvious importance for fishery management (Booth & Bowring, 1988; Breen & Booth, 1989; Cruz *et al.*, 1995a; Gardner, 2001). To date, the most successful of these programmes is that for *P. cygnus* in Western Australia. There, puerulus settlement is strongly correlated with juvenile abundance on nearby reefs (Jernakoff *et al.*, 1994) and with the commercial fishery catch four years later (Phillips, 1986; Caputi *et al.*, 1995, 2003). Despite widespread attempts to duplicate the Western Australian model, only a few have shown promise (*P. argus* in Cuba, Cruz *et al.*, 1995b; *Jasus edwardsii* in Tasmania, Gardner *et al.*, 2001), partly because time-series are too short or spatial coverage insufficient. In other cases, the lack of a strong, consistent correlation between postlarval supply and recruitment to later juvenile or adult stages is probably real, reflecting the additional importance of post-settlement processes in regulating recruitment.

Several investigations have sought to correlate the local supply of postlarvae, as measured on collectors, with the subsequent recruitment of juvenile or adult spiny lobsters at specific locations with mixed results. Puerulus settlement in Western Australia is strongly correlated with juvenile abundance on nearby reefs (Jernakoff *et al.*, 1994), just as it is with fishery catch, a proxy for adult abundance (Caputi *et al.*, 1995). In New Zealand, inter-annual patterns in postlarval supply and the abundance of juveniles two to three years later are positively correlated at some sites but not at others (Breen & Booth, 1989; Booth *et al.*, 2001). In Cuba, the relationship between the catch of postlarval *P. argus* caught on collectors and the abundance of juvenile lobsters dwelling in artificial structures several months later is inconsistent from year to year (Cruz *et al.*, 2001). Varying post-settlement mortality due to hurricanes and variation in the amount of available settlement habitat (seagrass and macroalgae) are the explanations offered by the authors. Variability among sites in the strength of the relationship between *P. argus* postlarval supply and juvenile or adult abundance is a recurring theme in the Bahamas (Lipcius *et al.*, 1997; Eggleston *et al.*, 1998) and in Florida (Butler & Herrnkind, 1992a, b, 1997; Field & Butler, 1994; Forcucci *et al.*, 1994), because of complex interactions between the local availabilities of settlers and of nursery habitat. Sites with abundant settlement habitat (e.g. red macroalgae) and shelters for juveniles (e.g. sponges) generally attain the highest levels of settlement, but settlement is locally unpredictable even at the most 'optimal' sites, presumably because of small-scale variability in the arrival of pueruli.

Nursery habitats and demographic bottlenecks

In the past two decades, we have become increasingly familiar with the natural settlement habitat of many species of spiny lobster (see Herrnkind *et al.*, 1994; Butler & Herrnkind, 2001). Still, the sparseness, small size, and crypticity of pueruli and early-benthic phase as well as the complex topography of the microhabitat in which they reside, make the early life stages of nearly all spiny lobsters challenging to study. In general, the natural habitats that newly settled pueruli and early-benthic phase juveniles seek are either dense vegetation (e.g. red or brown macroalgae, seagrass) (*P. argus*: Marx & Herrnkind, 1985a; Herrnkind & Butler, 1986; *P. interruptus*: Serfling & Ford, 1975; Engle, 1979; Castaneda-Fernandez *et al.*, 2005) or small holes in rocks or reefs scaled to their body size (*P. cygnus*: Jernakoff, 1990; *P. echinatus*: Vianna, 1986; *Palinurus elephas*: Diaz *et al.*, 2001; *P. homarus*: Kuthalingam *et al.*, 1980; *P. japonicus*: Yoshimura & Yamakawa, 1988: Norman *et al.*, 1994; Norman & Morikawa, 1996; *P. ornatus*: Berry, 1971; Dennis *et al.*, 1997; *P. versicolor*: George, 1968; *Jasus lalandii*: Pollock, 1973; *P. guttatus*: Sharp *et al.*, 1997; *Jasus edwardsii*: Kensler, 1967; Lewis, 1977; Booth & Bowring, 1988; Edmunds, 1995; Butler *et al.*, 1997; Booth, 2001). Lobsters are not unique in this respect. A recent meta-analysis of >200 papers describing the relative roles of seagrass and other habitats as nursery grounds concludes that structure *per se*, rather than the type of structure, was the most important determinant of the value of a habitat as a nursery (Heck *et al.*, 2003).

After settlement, and a variable period of time spent dwelling within vegetation or in small holes, juveniles attain a transitional size (typically >15–20 mm CL) at which they begin to seek nearby crevice shelters (e.g. rock crevices, holes and ledges; undercut coral heads and sponges) more appropriately scaled to their body size (*P. argus*: Cruz *et al.*, 1986; Eggleston *et al.*, 1990, 1997; Forcucci *et al.*, 1994; Butler & Herrnkind, 1997; Childress & Herrnkind, 1997; Arango *et al.*, 2001; *J. edwardsii*: Edmunds, 1995; Butler *et al.*, 1997; *P. ornatus*: Dennis *et al.*, 1997; Skewes *et al.*, 1997; *P. cygnus*: Jernakoff, 1990; among others). Many studies focusing on *P. argus*, some using natural shelters and others artificial shelters, have shown that appropriately-scaled shelters and aggregations of lobsters increase survival of crevice-dwelling juvenile and subadult *P. argus* that occupy them (Eggleston *et al.*, 1990, 1997; Smith & Herrnkind, 1992; Lozano-Álvarez *et al.*, 1994; Mintz *et al.*, 1994; Arce *et al.*, 1997; Sosa-Cordero *et al.*, 1998; Butler & Herrnkind, 1992a, 1997; Herrnkind *et al.*, 1997, 1999; Losada-Torteson & Posada, 2001; and others). The same can be said for other species wherever the phenomenon has been tested (see Butler & Herrnkind, 2001).

It is therefore not surprising that the local abundance of juvenile lobsters can be limited by the availability of crevice shelters. For example, changes in the availability of natural shelters for juvenile *P. argus* in Florida brought about by a mass die-off of sponges resulted in dramatic declines in juvenile abundance and patterns of shelter use (Butler *et al.*, 1995; Herrnkind *et al.*, 1997, 1999). Similarly, experimental manipulations of artificial shelters designed to mimic small, widely-distributed natural shelters (i.e. sponges and small coral heads) showed that the availability of crevice shelters for juveniles can limit the local recruitment of juveniles (Butler & Herrnkind, 1997; Herrnkind *et al.*, 1997; Briones-Fourzán & Lozano-Álvarez, 2001). Field surveys in the northwest Hawaiian Islands and the Bahamas suggest that the abundances of juvenile *P. marginatus* and *P. argus* are linked to the availability of high relief habitat (Parrish & Polovina, 1994; Lipcius *et al.*, 1997). Although habitat bottlenecks to juvenile recruitment can be shown to exist at some sites and at small spatial scales for these two species (*P. argus* and *P. marginatus*), regional recruitment patterns in Florida, the Bahamas, and Hawaii are tied to both the levels of puerulus supply and habitat structure (Forcucci *et al.*, 1994; Polovina *et al.*, 1995; Polovina & Mitchum, 1994; Butler & Herrnkind, 1997; Lipcius *et al.*, 1997). To generalise, many regions can be viewed as ecological mosaics where the processes that drive local recruitment vary locally depending on spatial and temporal patterns of habitat structure and postlarval supply (Fig 8.2).

In some situations, however, where nursery habitat is less dynamic and perhaps more uniform, there is little evidence for density-dependent regulation of juvenile abundance through habitat bottlenecks. Chittleborough and Phillips (1975) initially proposed that density-dependent processes limited the numbers of early-benthic phase juveniles on nursery reefs. This hypothesis has been revised because puerulus settlement was later found to highly correlate with juvenile abundance on nearby reefs (Jernakoff *et al.*, 1994) and was also highly correlated with commercial catches four years later (Phillips, 1990). A similar situation may exist for *J. edwardsii* along parts of the rocky coasts of Tasmania (Edmunds, 1995) and New Zealand (e.g. Stewart Island; Breen & Booth, 1989) where the settlement of pueruli is correlated with local juvenile abundance a few years later. The situation for all other species is unknown.

Simulation modelling has recently been used to explore the sources of recruitment variability in spiny lobster, and to integrate our understanding of the recruitment process with the growing body of data on benthic habitat structure. Two different types of models have been developed for spiny lobsters: those that are oceanographic in context and those that focus on benthic processes. Several spatially-explicit, biophysical oceanographic models are now available that depict larval release, the oceanic transport of passive or behaviourally active spiny lobster larvae and, in some cases, the arrival of postlarvae to the coast. Models include those constructed for *P. marginatus* in Hawaii (Polovina *et al.*, 1999), *P. argus* in Exuma Sound in the Bahamas (Stockhausen *et al.*, 2000; Stockhausen & Lipcius, 2001), *P. cygnus* in Western Australia (Griffin *et al.*, 2001) and *J. edwardsii* in New Zealand (Chiswell & Booth, 1999). Attempts at validating these models against empirical patterns of postlarval supply have not been altogether successful, but each has yielded insights into the importance of oceanographic features and larval behaviour in influencing larval dispersal and postlarval arrival in coastal nurseries (see Chapter 7).

We are aware of only one simulation model that encompasses the post-settlement ecology of a palinurid lobster, that being a spatially-explicit, individual-based model of *P. argus* recruitment in the Florida Keys (Butler *et al.*, 2001, 2005; Butler 2003). That model uses geographical information system (GIS)-based habitat information and field surveys of habitat structure to depict the benthic landscape, whose biogenic features (e.g. sponges, corals, seagrass) are dynamic and can change in response to environmental factors such as harmful algal blooms and salinity. The effects of spatial and temporal variation in postlarval supply on recruitment are incorporated into the model from either empirical data or theoretical depictions. Model predictions of juvenile recruitment (i.e. abundance of 50 mm CL lobsters) in response to a large-scale environmental disturbance (sponge die-off) were in good accord with predicted changes in recruitment suggested by data from field surveys and fishery catch (Butler *et al.*, 2005). Other simulations support the idea that local variation in habitat availability and postlarval settlement can affect recruitment success (Butler *et al.*, 2001). In particular, those simulations suggested that spatio-temporally variable postlarval supply result in the highest recruitment of juveniles, because the potential for density-dependent regulation in patchily distributed nursery habitat, is diminished by varying levels of postlarval arrival. Model predictions were less sensitive to changes in the spatial depiction of habitat structure than those in postlarval supply, but the most spatially explicit (i.e. fine-grained) and realistic portrayal of habitat structure produced marginally significant differences in recruitment in contrast to more generalised spatial scenarios. These findings parallel a growing body of empirical evidence that in general, postlarval abundance driven by spawning stock and the vagaries of oceanographic survival and transport determine the regional potential for recruitment

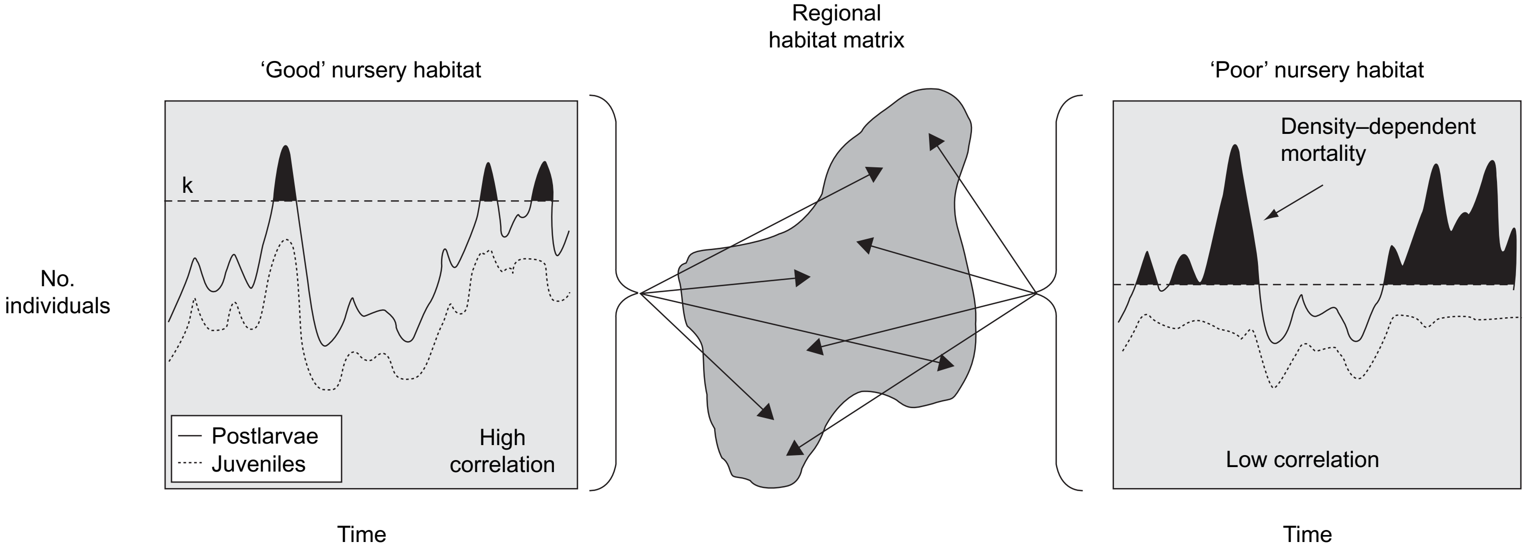

Fig. 8.2 Conceptual diagram of site-specific, nursery habitat-mediated demographic bottlenecks to spiny lobster recruitment within a regional mosaic of habitats. The graph at left shows a time–series relationship between the number of postlarvae arriving (solid line) and the resultant number of juveniles recruiting (lagged by some number of months; dotted line) at a site with 'good' nursery habitat quality or availability. In this situation, the site has a high carrying capacity (k) and post-settlement density-dependent mortality (solid black area) is low, therefore the correlation between postlarval supply and juvenile recruitment is high. The opposite condition is depicted in the graph on the right, where a site with 'poor' habitat quality or availability (i.e. low carrying capacity) results in high post-settlement density-dependent mortality and a poor relationship between postlarval supply and recruitment – a demographic bottleneck. At centre is displayed a hypothetical region wherein habitat quality and postlarval supply vary locally, resulting in a mosaic of ecological regulation of recruitment.

in spiny lobster, modified by local variation in postlarval delivery and the condition of the nursery habitat.

8.2.2 Post-recruitment patterns and processes

The ecological role of sociality

Sociality, common among palinurids, is an important, widespread ecological adaptation (Childress & Herrnkind, 1996; Herrnkind *et al.*, 2001), mediated by sophisticated sensory processes, especially olfaction and behaviour (Zimmer-Faust *et al.*, 1985; Ratchford & Eggleston, 1998). Initially, small juveniles are ineffective at cooperatively defending against predators but they eventually attain sufficient size and defensive ability to reduce predation mortality by co-occupying dens (Butler *et al.*, 1999). Several species (e.g. *P. argus, P. ornatus*) form queues or defensive rosettes while away from crevices, gaining increased vigilance and facilitating active defence against predators, as well as reducing drag during migration.

The general assertion that palinurids widely exhibit sociality belies the range and complexity of social processes represented with the taxon and the large changes in sociality during ontogeny in certain species. Research during the past decade has concentrated on a few species, particularly *P. argus* and *J. edwardsii*. That work includes careful field and captive observations, as well as experiments that reveal both the consequences of sociality in the natural ecological setting (Childress & Herrnkind, 1997; Butler *et al.*, 1999) and the mechanisms of the processes involved (Ratchford & Eggleston, 1998; Childress & Herrnkind, 1994; 2001a, b) (Fig. 8.3). Further inference is available from observations on numerous species including: *P. cygnus, P. guttatus, P. interruptus, P. marginatus, P. japonicus, P. ornatus, Palinurus elephas, and J. lalandii* (Lindberg, 1955; Berrill, 1976; MacDonald *et al.*, 1984; Holthuis, 1991; Yoshimura & Yamakawa, 1988; Childress & Herrnkind, 1996; Dennis *et al.*, 1997; Butler *et al.*, 1999; Butler & Herrnkind, 2001; Herrnkind *et al.*, 2001; Lozano-Álvarez & Briones-Fourzán, 2001). Because *P. argus* and *J. edwardsii* differ ecologically and biologically, they represent disparate points along the palinurid spectrum.

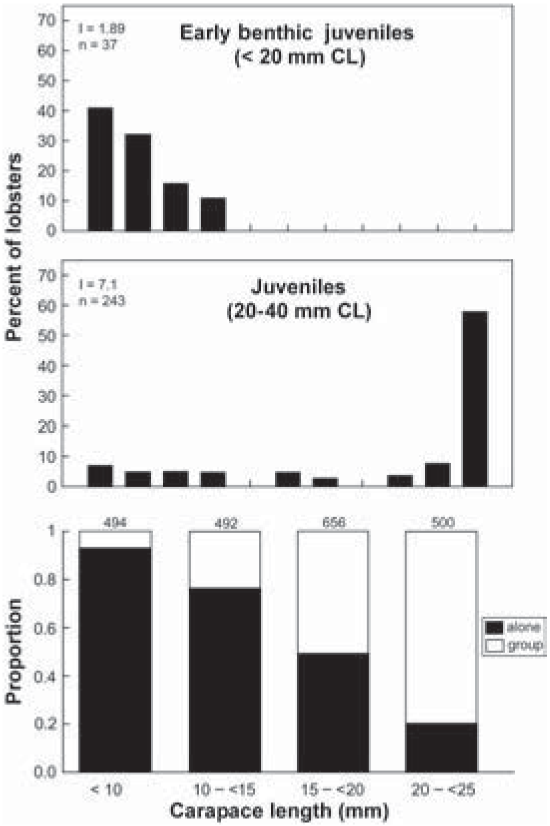

Fig. 8.3 A number of palinurid lobsters are initially solitary and cryptic. Sociality and the tendency to congregate in dens occurs during an ontogenetic shift later in the juvenile period. *Jasus edwardsii* in New Zealand (top two panels) and *Panulirus cygnus* in Western Australia (bottom panel) den in large groups after about 20 mm CL (adapted from Butler *et al.*, 1999 and Jernakoff, 1990, respectively).

Palinurid postlarvae typically settle in a dispersed pattern within complex habitats and the early benthic phase juveniles are asocial, display outline-disruptive colouration, and remain in refuge or forage in darkness within centimetres of shelter (see Butler & Herrnkind, 2001). Asocial behaviour, which maintains large inter-individual distances, reduces mortality by forcing the predators of these vulnerable stages to hunt for each solitary individual over a large area in highly cryptic habitat (Butler *et al.*, 1997). For example, early juvenile *P.*

argus placed together in contiguous vegetation, move apart within a day while those in small patches surrounded by open substrate remain residential but probably suffer higher predation (Herrnkind & Butler, 1986).

The onset of sociality, the point at which individuals begin to seek out conspecifics, occurs abruptly at about 20 mm CL in *P. argus* and *J. edwardsii*, and general observations suggest that the same is true in most palinurids (Marx & Herrnkind, 1985a; Butler *et al.*, 1999). This change in social behaviour coincides, in *P. argus*, with an ontogenetic habitat switch from initially remaining in vegetation at all times to diurnal dwelling in sponge, coral, or rock crevices (Andree, 1981; Childress & Herrnkind, 1996). In the case of *J. edwardsii*, *P. japonicus*, *P. elephas*, *P. guttatus* and other species with hole-dwelling early benthic phase juveniles, the shift in habitat is less dramatic as they simply vacate small holes to occupy larger rocky crevices nearby (Yoshimura *et al.*, 1994; Sharp *et al.*, 1997; Butler *et al.*, 1999, Diaz *et al.*, 2001). Emergence of the adult markings and gradual loss of the post-settlement pattern as well as strong social facilitation of behaviour, including queuing, begin in *P. argus* at this size (Childress & Herrnkind, 1999). Limited information from other species suggests similar shifts (Butler *et al.*, 1999).

With this shift in habitat use and sociality, cohabitation of dens becomes prevalent, altering juvenile spatial distribution according to the distribution of larger crevices (Butler *et al.*, 1999). At the same time, social juveniles begin to produce a waterborne odour that attracts other juveniles during the pre-dawn hours (Zimmer-Faust *et al.*, 1985; Childress & Herrnkind, 1996; Ratchford & Eggleston, 1998; Butler *et al.*, 1999; Nevitt *et al.*, 2000). This odour 'guides' shelter-seeking individuals from several metres away to a crevice, which the resident is usually willing to share (Childress & Herrnkind, 2001a). Orienting to a den already occupied by a conspecific is theoretically beneficial in two ways. First, it reduces exposure time, thus decreasing the probability of a predator encounter in the open. Second, it makes group defence against predators possible (Butler *et al.*, 1999). At the initial social shift size, juveniles are probably too small to benefit from cooperatively defending against predators (Childress & Herrnkind, 1997) but, hypothetically, may gain if their den mates are larger and capable of repulsing a predator (Butler *et al.*, 1999). In *P. argus*, juveniles choose either solitary dens or tightly-packed dens depending on the nature of the predator, shelter availability, and shelter dimensions (Eggleston & Lipcius, 1992). This presumably applies generally to spiny lobsters and may explain why patterns of aggregation among juvenile spiny lobsters vary despite the fact that all are social. For example, rocky crevices of appropriate dimensions to house large aggregations of juvenile lobster are common along the New Zealand coast where the majority of juvenile *J. edwardsii* are found clustered together in dens (Butler *et al.*, 1999). In Florida, dens for juveniles are widely scattered and most are only small crevices, thus only about half of the juvenile *P. argus* are found sheltering by day in groups (Behringer, 2003; Fig. 8.4).

Another factor that alters patterns of den co-occupancy for *P. argus* in Florida is the presence of a newly-discovered viral disease (Shields & Behringer, 2004). Field observations and labora-

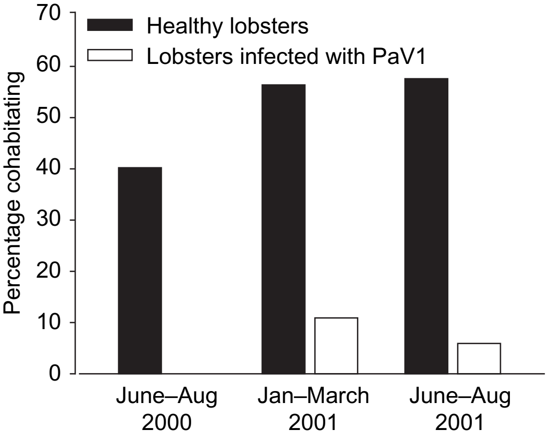

Fig. 8.4 Sociality in spiny lobsters can be altered by pathogens, as shown in this figure depicting patterns of den cohabitation by healthy and PaV1 virus infected juvenile (20–55 mm CL) *P. argus* in the Florida Keys during three census periods. Note the solitary nature of infected lobsters, which occurs because healthy lobsters avoid cohabitation with diseased conspecifics (adapted from Behringer, 2003).

tory experiments confirm that healthy lobsters can somehow detect when others are infected and will not cohabit with them, resulting in an increase in the frequency of solitary inhabitants (Fig. 8.4) – the only confirmed instance of disease avoidance by any animal in nature. Whether other species of spiny lobster respond similarly to conspecifics that are diseased or in poor health is unknown. However, such behaviour, along with characteristics of available shelter and predator risk, may also explain why normally social species are often found alone.

For at least one species, *P. guttatus*, social aggregations appear to be of lesser importance. *Panulirus guttatus* is an obligate inhabitant of coral reefs in the Caribbean, where it rests by day in small groups in deep, inaccessible crevices, emerging only well after dusk to forage solitarily on the reef close to shelter (Briones-Fourzán, 1995; Sharp *et al.*, 1997; Robertson, 2001; Acosta & Robertson, 2002). Although *P. guttatus* will co-occupy dens with conspecifics, as well as with *P. argus*, it is more aggressive toward conspecifics and relies less on communal defence from predators than does *P. argus* (Lozano-Álvarez & Briones-Fourzán, 2001). *Panulirus guttatus* attains sexual maturity by 40 mm CL (Sharp *et al.*, 1997; Robertson & Butler, 2003), about the same size at which juveniles of *P. argus* and *J. edwardsii* first benefit from active social defence. That is, cryptic behaviour in a sheltered habitat, rather than large size and sociality, serves as a deterrent to predation for *P. guttatus* and presumably other species that are obligate dwellers of coral reefs.

Large juveniles and non-reproductive adults of most palinurids commonly co-occupy dens, exhibiting higher proportions of multiple than of solitary occupancy (Atema & Cobb, 1980; MacDiarmid, 1994; Eggleston & Lipcius, 1992). The actual number and frequency of solitary and co-occupant lobsters may vary with locality and with season. In adult *P. argus*, for example, the frequency of multiple den occupants ranges from ~45% to 98% (Herrnkind *et al.*, 2001). Local occupants at any time are a mixture of long-term residents of one to three dens (used interchangeably) in the vicinity and transients, either immigrants or past residents that have been elsewhere and returned (Herrnkind *et al.*, 1975). Many of the occupants can re-orient themselves and return back to a den even after being displaced several hundred metres to a kilometre away (Herrnkind & McLean, 1971; Nevitt *et al.*, 2000; Boles & Lohman, 2003). This ability suggests selective and repeated use of known shelters for months by old adults. In this case, co-occupancy of dens might be a by-product of the attractiveness of a large den, or social attraction by chemical signals from a den's residents, or some combination of the two. Displacement by aggression also influences the den occupancy pattern, presumably when den space is rare or the residents enforce a dominance hierarchy (Berrill, 1975, 1976). Both tolerant and antagonistic social interactions interact with den features and predation to produce the observed local distributions and residential patterns.

Intensive field experiments using scaled artificial shelters, which provide space for multiple occupants, reveal a complex relationship among physical dimensions of a shelter, lobster density (local numbers), lobster size distribution, type and number of predators, and whether the predators are actively feeding (Eggleston *et al.*, 1990; Eggleston & Lipcius, 1992). That is, the number and size of den co-occupants change when one or more of the above conditions is substantially altered. When the choice is among smaller crevices, juveniles co-den until a nurse shark is introduced and attacks, causing a switch to solitary den use (Childress, 1995). Lobster social rearrangement in dens in the presence of predators hypothetically reduces predation risk, but the degree of benefit from having more or fewer co-residents has not been determined (Childress & Herrnkind, 1997).

Direct evidence from the field and from observations in large tanks, as well as indirect inferences from information provided by fishers, indicates that several palinurids congregate to travel over open terrain (Herrnkind 1980). Head-to-tail queues of up to 60 lobsters, which form a radial, outward facing group when attacked, were first described in *P. argus* (Herrnkind & Cummings, 1964) but are now documented or strongly inferred for *P. ornatus*, *P. marginatus*, *P. cygnus*, *Palinurus delagoae*, and *J. edwardsii* (Herrnkind *et al.*, 2001). Although benefits remain to be fully tested in any species, these behaviours yield theoretical anti-predatory advantages of dilution, vigilance, and cooperative defence, in addition to drag-reduction (i.e. locomotory efficiency) during queuing (Herrnkind *et al.*, 2001). In New Zealand, large *J. edwardsii* regularly gather in radial pods well away from shelter, leave to forage nightly, and then regroup afterward (Kelly *et al.*, 1999). The pods seem to have few predators although at spawning, gravid females release larvae while using their antennae to parry fish attacking the egg mass or spawn. Without shelter or enhanced defence, even large spiny lobsters in some habitats are subject to debilitating injury and death from triggerfish, octopus, and large sharks (Kanciruk, 1980). That is, they cannot out-swim the predator, yet the armoured spiny carapace alone is insufficient to resist either octopus or carapace-crushing predators.

Movement and migration

Migration is common among shallow-water palinurids, although some non-migrating species exist (Fig. 8.5). For example, the spotted lobster, *P. guttatus,* settles on crevice-rich reefs and remains there through adulthood, isolated by open substrate from neighbouring reefs (Briones-Fourzán, 1995; Sharp *et al.*, 1997; Robertson, 2001). Most widely-distributed, large-growing species collectively exhibit a wide range of ontogenetic, seasonal, reproductive, or episodic population movements. Palinurid migrations reflect changing ecological conditions of the benthic life stage during ontogeny and eventual movement to oceanic sites for larval transport. That is, pueruli settle into shallow nursery microhabitats distant from spawning reefs. Newly-hatched larvae must access oceanic currents that then transport the phyllosoma stages offshore to return them later near the coastal nursery. In several palinurid species, whose larvae settle far down current from the spawning site, the benthic stages make long migrations to counter the larval transport (Herrnkind, 1980, 1983; Booth, 1986; Pitcher *et al.*, 1992, Groeneveld, 2000; Groeneveld & Branch, 2002)(Fig. 8.5).

Maturing adults of most well-studied palinurid species exhibit either an incremental ontogenetic migration culminating in mating and spawning in distinct adult habitats, or seasonal inshore–offshore movements for mating or foraging. The track may be relatively short, a few kilometres as in *P. interruptus* and *J. edwardsii* that live on narrow coastal shelves, or scores of kilometres, as is the case for *P. argus*, *P. ornatus*, and *P. cygnus* that recruit nearshore but must cross wide coastal shelves to reach oceanic currents. During gradual ontogenetic migration, juvenile *P. argus* use corridors of food-rich habitat, particularly shallow seagrass meadows, within which individuals move about nomadically in a spatial pattern dictated by the location of prey and shelter (Cox *et al.*, 2001; Briones-Fourzán *et al.*, 2003). That is, lobsters cluster where cover is located adjacent to feeding habitat although these sites may be hundreds of metres apart (Herrnkind *et al.*, 1975). That is particularly so for juvenile and subadult lobsters. In Belize, for example, *P. argus* are significantly more abundant around mangrove and coral islands surrounded by seagrass than those surrounded by sand or rubble (Acosta & Butler, 1997; Acosta, 1999). Furthermore, immigration and emigration rates of lobster were nearly four times greater for islands surrounded by seagrass than rubble, demonstrating the importance of vegetated habitats as corridors for movement by juvenile lobsters (Herrnkind & Butler, 1986; Acosta 1999).

Although movement by pre-adults onto reefs for reproduction peaks in Florida and the Bahamas during the late winter just prior to reproduction in spring, gradual offshore movement by nomadic juveniles also takes place throughout the year (Herrnkind, 1980; Gregory & Labisky, 1996). Movement is largely nocturnal and solitary, rather than in groups. One of the most detailed studies of movement in adult palinurids comes from a recently-completed eight year mark–recapture study of >1300 *J. edwardsii* in northern New Zealand (Kelly & MacDiarmid, 2003). That study confirms that large adults show greater site fidelity than smaller individuals, and that movement varies markedly with season. In Western Australia, *P. cygnus* undergoes a marked physiological transition to the migratory phase signified by the moult from the typical red carapace to the white phase (Melville-Smith *et al.*, 2003). In contrast to *P. argus*, migratory white *P. cygnus* move continu-

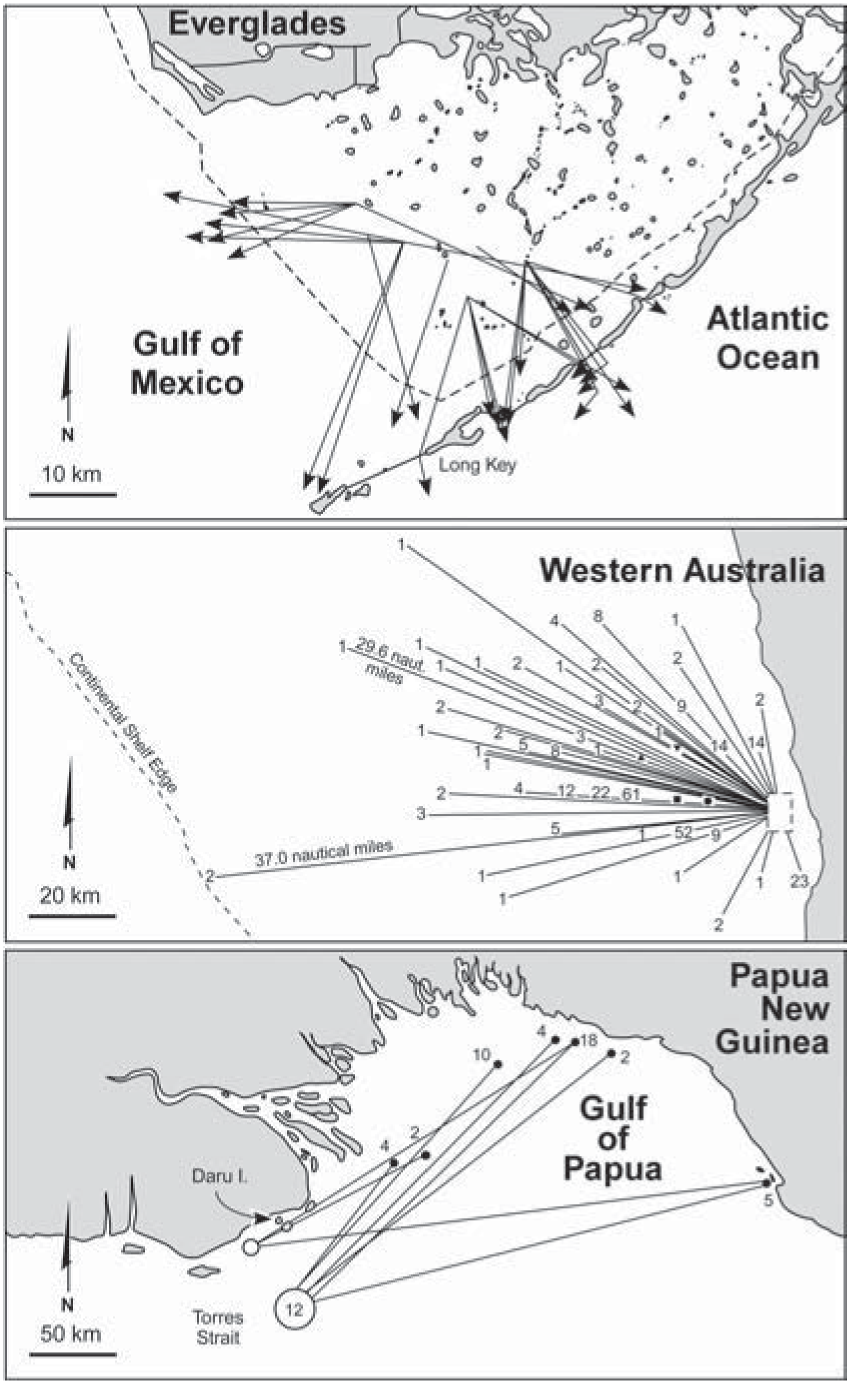

Fig. 8.5 Examples of migratory movements from nursery areas to reproductive or spawning areas, at different scales, based on tag return data. (Top) *Panulirus argus* in Florida settle and grow in expansive shallow vegetated habitats then move ~20–30 km to reef sites, especially bordering the Atlantic Ocean (adapted from unpublished data, Florida Department of Natural Resources, 1980). (Centre) *Panulirus cygnus* grow nearshore then have to move 40–50 km offshore to the shelf edge to spawn (adapted from Phillips, 1983). (Bottom) Maturing *Panulirus ornatus* move several hundred kilometres across the Gulf of Papua to release larvae that drift back westward to settle along the northeast Australian coast (adapted from Prescott *et al.*, 1986).

ously over long distances, across deeper, less prey-rich habitats (Phillips, 1983).

Some of the longest migrations, in both duration and distance, take place in species (or populations of particular species) whose nursery habitats and spawning sites lie far apart along the streamline of the larval transport current (Herrnkind, 1980, 1983; Booth, 1986, Pitcher *et al.*, 1992). That is, the benthic life phase must travel back to the spawning point to assure that the cycle is completed. Among such long distance migrants, *P. ornatus* settle and grow up in coastal reef areas on the west side of the Gulf of Papua then, as maturing pre-adults, they initiate a mass migration hundreds of kilometres eastward (Bell *et al.*, 1987). They mate during this time then spawn on the other side of the Gulf in concert with the seasonal shift in winds and ocean currents that deliver the larvae back to the nursery region (Pitcher *et al.*, 1992). Evidence is mounting that deep water South African *Palinurus delagoae* and *P. gilchristi* make a long ontogenetic upcurrent migration over months and years, theorised to counter phyllosomal drift after spawning (Groeneveld, 2000; Groeneveld & Branch, 2002).

The localised, brief but spectacular non-reproductive mass 'migrations' by *P. argus* are probably rapid evasive movements from areas of disturbance (subject to rapid cooling and high turbulence) to more stable sites (Herrnkind, 1985). In the northern Caribbean and Bahamas, *P. argus* abruptly begin to march in single-file queues both day and night across open substrata, resting for several hours in the open in radial rosettes or filling and overflowing crevices along the route (Herrnkind *et al.*, 2001). The movements are triggered by autumnal storms, sometimes by hurricanes, well after the preceding spawning season and several months before peak spring spawning; egg-bearing females or even those with developing ovaries are rare among these migrants (Herrnkind, 1980; Kanciruk, 1980). In Bahaman populations, about half of the migrants are immature size but off north-eastern Yucatan, nearly all are mature (Herrnkind, 1985). Although tag–recapture evidence shows that some individuals return within the following year to the shallow feeding habitats near the tagging site, no instances of a mass return movement *per se* have been documented. Lobster mortality during episodic severe cooling in juvenile habitats suggests the selective advantage of leaving shallow areas of rapid cooling and high turbulence (Herrnkind, 1980, 1985). These highly-oriented movements may also promote the redistribution of individuals into new habitat. Boles and Lohman (2003) provide compelling evidence that lobsters can accurately navigate during such movements. *Panulirus argus* possesses both a magnetic directional compass and a geographic position sense. The latter capability, equivalent to vertebrate navigation (e.g. birds, sea turtles), hypothetically serves long-distance migration and homing in palinurids.

Competition

With the exception of intraspecific competition for mates (see Chapter 2), competition among spiny lobsters for shelter or food in the wild is not well documented and is presumably rare. Certainly, in some instances palinurids aggressively compete over food (Kanciruk, 1980), over a den following foraging (Berrill, 1975), and among adult males as they establish harems (MacDiarmid, 1989), but these agonistic displays of interference competition are typically for localised resources and are of short duration, in keeping with the social nature of palinurids. Although experimental enhancement of shelter availability in the wild often results in greater numbers of lobsters in an area (see Section 8.2.1 on limits to recruitment), no evidence indicates that a density-dependent depression of growth results (Ford *et al.*, 1988; Behringer & Butler, in press). In Western Australia, Ford *et al.* (1988) found that lobster survival was higher on rocky reefs where densities were experimentally reduced, but they did not account for the potentially confounding effects of immigration and emigration. Results from a recent study of juvenile *P. argus* in Florida also failed to find evidence of intraspecific competition (Behringer & Butler, in press). In that study, lobsters were marked and recaptured over several seasons and years on sites that naturally varied in shelter and lobster density, and on sites where shelter (and thus lobster density) was experimentally manipulated. High densities had no effect on lobster nutritional condition, mortality, or disease incidence, even though residency of lobsters on a site increased with density.

Evidence for interspecific competition between lobster species, or between lobster and other taxa is largely circumstantial and confounded by predatory interactions. Instances of non-overlapping use of habitats by different species of lobster in sympatry, implies the evolution of habitat segregation, but this 'ghost of competition past' (*sensu* Connell, 1983) has no experimental confirmation. Furthermore, some species actually share dens (e.g. *P. argus* and *P. guttatus*) and in such cases, intraspecific agonism is more common than interspecific aggression (Lozano-Álvarez & Briones-Fourzán, 2001). Spiny lobsters might conceivably compete with other taxa (e.g. predacious gastropods, crabs and fish) for prey or shelter when those resources are limiting, but we know of no published accounts of such competition. Where lobsters occur, there are octopuses. Beyond their role as predators of lobsters, octopuses also require the same crevice shelters and prey (e.g. molluscs and crustaceans) as spiny lobsters and thus could compete with lobsters for those resources (Berger & Butler, 2001), but experimental evidence indicates that predation indeed dominates the lobster–octopus interaction, mitigated to some degree by the presence of alternative prey and group defence by lobsters (Lear, 2004).

Predation

During benthic life, palinurids are subjected to a wide variety of predators, mainly piscine (but also octopus, as noted above), and they experience the highest relative mortality during their early life stages (Butler & Herrnkind, 2001; Phillips *et al.*, 2003). For example, pueruli and early benthic phase juvenile *P. argus* are vulnerable to pelagic and benthic predators, especially in coral reefs (Acosta & Butler, 1999). A year after settling, juvenile *P. argus* in Florida will have suffered 96–99% mortality (Herrnkind and Butler, 1994: Sharp *et al.*, 2000). A large fraction of that predation on juveniles happens at the transition from the initial fully alga-dwelling stage to the crevice-dwelling stage at ~15–25 mm CL (Fig. 8.6) (Butler & Herrnkind, 2001).

Rapid growth to a large size serves as an important mechanism for predator avoidance. Among crustaceans, palinurids include some of the largest and fastest-growing species. Growth rate, both generally and within a species, seems to be dictated by the local temperature regime and the nutritional quality and abundance of prey (Mayfield *et al.*, 2000; Butler & Herrnkind, 2001; Chapter 1). Most spiny lobster species attain 1–10 kg in weight and overall lengths of 30–50 cm (excluding antennae). Some, including *P. ornatus* and *P. argus,* reach a weight of one kilogram only 2–4 years after settlement (Olsen & Koblick, 1975; Trendall *et al.*, 1988; Sharp *et al.*, 2000). Maximum size is not correlated with thermal regime because several temperate species attain large size (45–60 cm total length (TL); *J. edwardsii, Sagmariasus verreauxi, Palinurus elephas, P. interruptus*), whereas numerous warm water species do not (25–30 cm TL; *P. guttatus, P. laevicauda, P. regius, P. echinatus*). Large spiny lobsters can be defensively formidable while fending off piscine predators by antennal whipping and thrusting, especially when bunched tightly together in a den or in radial rosettes in the open. Very large (5–15 kg), well-armoured adults probably have very few non-human predators, especially in recent decades because fishing has reduced the abundance of large fishes and sharks. In fact, large spiny lobsters will move about solitarily over open terrain or reefs during the day, especially large males during the breeding season.

The primary determining factor that mitigates predator success is abundant crevice shelter adjacent to good foraging, which reduces the exposure time of the vulnerable juveniles. Sparse, dispersed shelter or prey creates the population bottleneck effect theorised by Caddy (1986), in which growing individuals must move about to locate ever-decreasing numbers of appropriately-sized shelters. Although sites differ in predator risk, tethering studies confirm an extremely high probability of predation on exposed juveniles in nursery habitats (Herrnkind & Butler, 1986; Eggleston *et al.*, 1990; Smith & Herrnkind, 1992; Childress & Herrnkind, 1994; Mintz *et al.*, 1994; Lipcius *et al.*, 1998; Briones-Fourzán *et al.*, 2003). Field studies suggest a similar process in *P. cygnus* (Howard, 1988) and *J. edwardsii* (Butler *et al.*, 1999) juveniles.

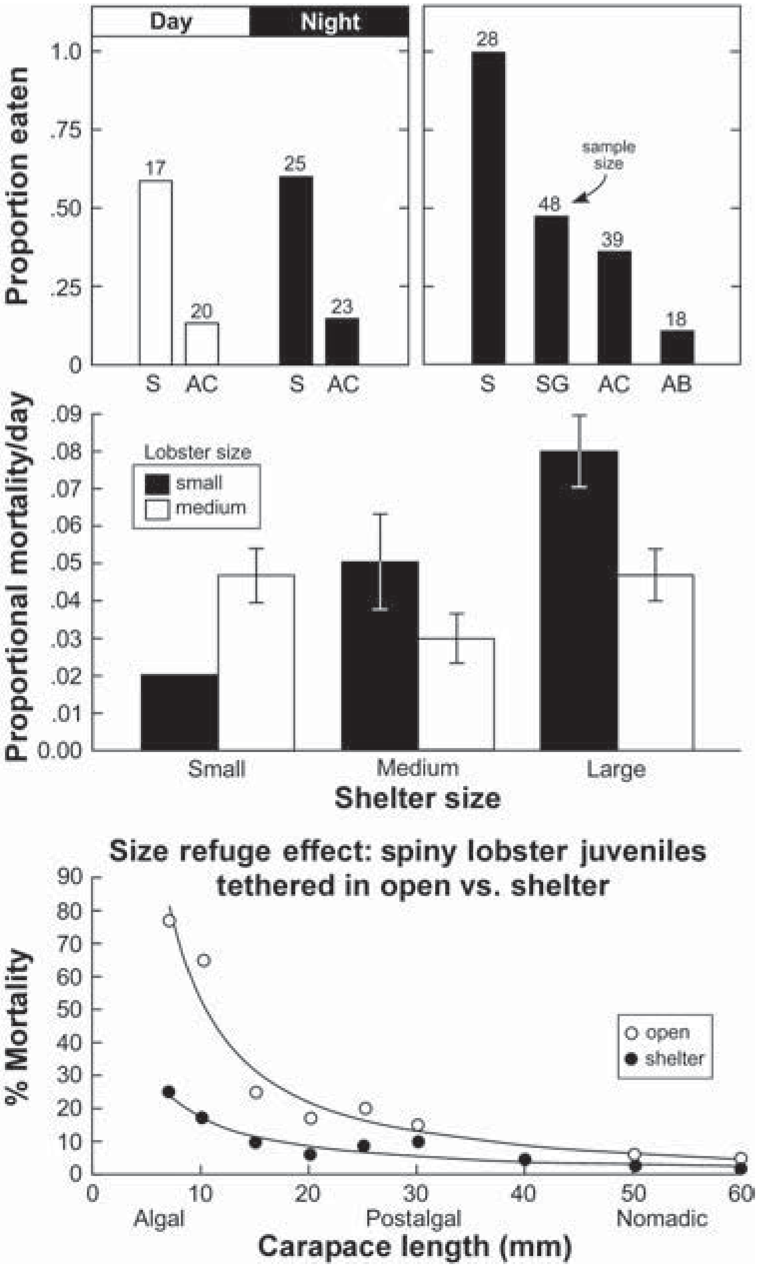

Fig. 8.6 Predation risk in spiny lobsters, especially the early benthic phases, depends greatly on size and shelter features. (Top) Exposed algal phase juvenile *Panulirus argus* (7–11 mm CL) suffer high predation compared to those in structure (S, sand; SG, seagrass; AC, algal clump; AB, algal bed) at all times of day (adapted from Herrnkind & Butler, 1986). (Centre) Relative survival of sheltered juvenile *P. argus* depends on the relationship between shelter size (artificial 'casitas') and lobster size (small lobsters 35–45 mm CL; medium lobsters, 46–55 mm CL) (adapted from Eggleston *et al.*, 1990). (Bottom) Shelter from predators is exceedingly important during the algal and early postalgal period in *P. argus* (<25 mm CL)(composite tethering data from Smith & Herrnkind, 1992; Eggleston *et al.*, 1990).

Shallow-dwelling tropical species face the most diverse predator array (Howard, 1988; Smith & Herrnkind, 1992), although temperate species may suffer similarly high mortality from less diverse yet highly abundant predatory species (Wahle & Steneck, 1992; Butler *et al.*, 1999). The predators' tactics include active nocturnal and diurnal hunt and chase, ambush, probe-and-grab, and others cued by visual, hydrodynamic, and chemical cues. All palinurids, in turn, exhibit a combination of evasion ('avoidance of predatory encounters') and escape ('survival of a predatory encounter') tactics that reduces predation mortality (Barshaw *et al.*, 2003). The most ubiquitous tactic is sheltering in interstices, which either reduces the chance of being encountered or protects the inhabitant from attack once discovered. A second near-universal tactic is adoption of solitary nocturnal foraging, which reduces the risk from visual predators. Staying within shelter and emerging only in darkness is especially characteristic of juveniles. Palinurids also use chemical cues to detect and avoid encounters with certain predators, such as octopods (Berger & Butler, 2001), but are unable to detect others (e.g. red grouper, *Epinephalus morio*; Schratweiser, 1999) by the same means.

The number and size of predators can predictably alter the abundance or size of local spiny lobsters. Field measures and experimental evidence show that octopuses cause juvenile *P. argus* to move from nearby dens or to select dens well away from an octopus lair (Berger & Butler, 2001). Red groupers and Nassau grouper, *E. striatus*, also cause reduced local abundances of small lobsters either by direct predation or by influence on den choice and residency by the lobster (Eggleston *et al.*, 1997; Schratwieser, 1999). Eggleston *et al.* (1997) found greater juvenile lobster abundances on artificial patch reefs from which groupers had been removed. The community-level influence of increasing numbers and size of large lobster predators has become an important facet of marine reserve design.

Pathogens

Evans *et al.* (2000) recently reviewed the few known diseases of spiny lobsters, and this subject is covered for both spiny and clawed lobsters in Chapter 5. We therefore only touch on the matter of disease in spiny lobsters as it relates to their ecology in the wild – a brief discussion indeed, because almost nothing is known. Most reports of disease come from laboratory or aquaculture conditions, where handling stress and inappropriate water quality probably exacerbate the incidence and severity of infection. Remarkably few natural diseases appear to be fatal. Shell disease from chitinoclastic bacteria causes lesions around the tail and uropods of several species (Iversen & Beardsley, 1976; Sindermann & Rosenfield, 1976; Booth, 1988; Porter *et al.*, 2001), and some helminths use spiny lobsters as intermediate hosts (Deblock *et al.*, 1990). Infections by *Vibrio* spp., bacteria, protozoans, and fungi also occur in lobsters held in captivity (Bach & Beardsley, 1976; McAleer, 1983; Kittaka & Abrunhosa, 1997; Diggles *et al.*, 2000). The recently-discovered pathogenic viral disease (PaV1) infecting *P. argus* in Florida (the first report of a viral disease in lobsters), is one of the few known to occur at high incidence in nature and it is nearly always lethal (Shields & Behringer, 2004). It affects the ecology of *P. argus* in other ways as well (Behringer, 2003). Susceptibility to PaV1 disease declines with ontogeny, with early benthic phase juveniles and small crevice-dwelling juveniles being the most susceptible. Furthermore, the spatial distribution of juvenile lobsters is altered where the disease is prevalent, because healthy individuals can identify diseased conspecifics and will not cohabit with them (Fig. 8.4). The occurrence of PaV1 in other areas of the Caribbean is not known, but pandemics of several shrimp viruses have spread widely across the tropical and subtropical regions of the world with catastrophic results to the aquaculture and fisheries for penaeid shrimps.

Human and environmental effects

> 'When one tugs at a single thing in nature, one finds it attached to the rest of the world.'
> – John Muir, American naturalist (1838–1914)

The ecology of spiny lobsters does not operate in isolation from the large-scale environmental changes that periodically affect marine communities, nor is it immune to the reverberations of human activity. Often, the two are intermingled; therefore ascribing the impact on lobsters to one or the other can be difficult. Because spiny lobsters are the targets of valuable fisheries worldwide, the influence of fishing on their ecology has received the most scrutiny. Wahle (1997) summarised and expounded on a discussion of the consequences of fishing on lobsters held at the Fifth International Conference and Workshop on Lobster Biology and Management in Queenstown, New Zealand in

1997. The points raised there are still relevant today and few are unique to lobsters. The most immediate and obvious impact of fishing is the culling of large individuals from the population, followed by reductions in population density under more severe levels of fishing. Commensurate with those changes in population structure, theoretically, come alterations in population dynamics, including: reductions in average size at maturity and per capita fecundity, increases in growth (due to intraspecific competitive release), mating system anomalies, and potential changes in genetic structure. The first of these changes has been realised in various populations around the world (DeMartini *et al.*, 1993; Pollock, 1995; Chubb, 2000). As far as we know the others have not, except in limited circumstances or under laboratory conditions. For example, the disproportionate loss of large male spiny lobsters could limit fertilisation success through sperm limitation as demonstrated in experiments on *J. edwardsii*, *P. argus*, and *P. guttatus* (MacDiarmid & Butler, 1999; Robertson, 2001; Heisig 2003). Other potential effects of fishing on spiny lobsters include: reduced growth and increased susceptibility to disease due to handling stress and injury, loss of habitat caused by destructive fishing gear, enhanced food availability in the form of bait, competitive or predatory release as a result of fishing of other species, and incidental mortality of lobsters as by-catch in non-targeted fisheries, among others (Jennings & Kaiser, 1998).

Spiny lobster populations are also buffeted by environmental changes – some natural, and some not – that compound the effects of fishing. The National Research Council (1994) and the US Ocean Commission (2004) categorise the problems facing our seas similarly: (1) pollution and eutrophication, (2) habitat destruction (primarily coastal and benthic habitats), (3) over-exploitation of fishery resources, and (4) climate change. Although degraded water quality is a ubiquitous problem and laboratory studies show that juvenile spiny lobster are sensitive to it (Herrnkind *et al.*, 1988; Field & Butler, 1994; Booth & Kittaka, 2000), few published reports address the impact of poor water quality on lobsters in nature. The most dramatic and well-documented events are the periodic mass mortalities of *J. lalandi* observed along the southwest coast of South Africa (see Cockcroft, 2001). Episodes of hypoxia caused by blooms of dinoflagellates at times corresponding with severe El Niño events, are the culprits. In the 1990s, over 2000 t of dead lobsters were stranded along the coast. Similar hypoxic events in the past are hypothesised to have resulted in the local extirpation of spiny lobster from certain isolated islands in South Africa, where lobster populations have never recovered. In response to the loss of a higher trophic level predator (i.e. lobsters), the communities on those islands are believed to have achieved an 'alternative stable state' (*sensu* Sutherland, 1974) where predatory gastropods dominate the benthos (Barkai & McQuaid 1988).

Phytoplankton blooms also wreaked havoc on lobsters in south Florida in the 1990s. The ultimate cause of the phytoplankton blooms that blanketed portions of south Florida in the early 1990s cannot be pinpointed with precision, yet compelling circumstantial evidence suggests that a series of hot, dry summers coupled with diversion of freshwater within the Everglades from Florida Bay sparked the problems to come (Fourqurean & Robblee, 1999). In short, changes in the flow and quality of freshwater emanating from the Everglades resulted in the overproduction of seagrass throughout much of the western basin. Density-dependent declines in the health of seagrasses coupled with high temperature and an outbreak of a pathogenic slime mould (*Labyrinthula* sp.) resulted in the die-off of thousands of hectares of seagrass. The release of nutrients from decaying seagrass and the suspension of sediments in the water column is thought to have fuelled the subsequent and repeated harmful algal blooms, which persisted for months. The blooms loomed over hundreds of kilometres of seagrass and tropical hard-bottom habitat, and at times were swept out to sea threatening the coral reefs (Butler *et al.*, 1995; Philips *et al.*, 1999). The cyanobacterial blooms triggered a massive mortality of sponges, resulting in the decimation of the sponge community over much of the affected region (Butler *et al.*, 1995; Herrnkind *et al.*, 1997; Lynch & Philips, 2000). In turn, the rapid loss of seagrass and sponges resulted in a reconfiguration of nursery habitat for spiny lobster on a grand scale.

Approximately 20% of the area used by *P. argus* as a nursery in Florida was destroyed, and the result was significant local declines in lobster recruitment (Herrnkind *et al.*, 1997).

8.2.3 Effect of spiny lobsters on benthic community structure

Lobsters are simultaneously predators and prey throughout their benthic life. Gut-content analysis on many species shows the ubiquitous presence of molluscs, crustaceans, echinoderms, and other invertebrates, but also coralline and fleshy algae (Joll & Phillips, 1984; Herrnkind *et al.*, 1987; Edgar 1990; Jernakoff *et al.*, 1993; Díaz-Arredondo & Guzmán-del-Próo, 1995; Lozano-Álvarez, 1996; Cox *et al.*, 1997; Mayfield *et al.*, 2000; Castaneda *et al.*, 2005). Prey size generally increases with lobster growth, reflecting changes in mandible size and other constraints to handling, accessibility, and durophagy. Throughout life, palinurids are highly opportunistic foragers and consume the same types of prey, although the size and species composition may vary widely with habitat (Briones-Fourzán *et al.*, 2003). Although we know much about the array of prey consumed by lobsters in various habitats, less is known about the effects of lobsters on prey communities.

The large size, predatory habits, and often great local abundance of spiny lobsters suggests that their impact on benthic prey communities should be profound, yet evidence of their influence on prey community structure appears limited largely to rocky, temperate ecosystems. The most extensive evidence that spiny lobsters alter prey communities with cascading effects on benthic community structure comes from studies of *P. interruptus* in southern California. Tegner and Dayton (1981) found that *P. interruptus* together with a predatory fish (sheepshead; *Semicossyphus pulcher*) controlled the abundance and distribution of two species of sea urchin (red sea urchin, *Strongylocentrotus franciscanus*; purple sea urchin, *S. purpuratus*). The grazing activities of the urchins, in turn, altered the abundance of giant kelp (*Macrocystis pyrifera*), the defining species in California kelp forests. Later modelling studies suggested that predation by *P. interruptus* also probably controls the bimodality in size structure observed in red sea urchins that dwell in different habitats that vary in accessibility to lobster (Botsford *et al.*, 1994). Predation by *P. interruptus*, along with that by octopuses and whelks, also controls the joint distribution of bivalve and gastropod prey on rocky reefs in Southern California (Schmidt, 1982, 1987), resulting in 'apparent competition' between prey that is in fact due to dissimilar patterns of predation. Other investigations of *P. interruptus* demonstrated its similar role in structuring sessile benthic communities via its consumption of a competitively dominant mussel (Robles *et al.*, 1995; Robles 1997), although physical disturbance (i.e. wave surge) and prey recruitment patterns moderate lobster impacts. A similar picture has emerged in temperate, subtidal rocky communities on the opposite side of the globe in South Africa and New Zealand.

In South Africa, predation by *J. lalandii* and *P. homarus* alters the abundance and size structure of their mussel, urchin, and gastropod prey, whose availability may limit lobster growth (Newman & Pollock, 1974; Pollock, 1979; Griffiths & Seiderer, 1980; Berry & Smale, 1980; Barkai & McQuaid, 1988; Mayfield *et al.*, 2000). Much as in southern California, predation by lobsters and fishes on these benthic invertebrates is thought to have cascading effects in the ecosystem, including impacts on macroalgal community structure and abalone recruitment (Branch, in prep.). A peculiar role reversal has also been reported in South Africa on isolated islands long devoid of lobsters (Barkai & McQuaid, 1988). On those islands, predatory whelks freed from lobster predation, after low dissolved oxygen events had decimated the lobsters, have reached extraordinary densities and have assumed benthic predatory primacy. Lobster immigrants to those islands are quickly consumed by marauding whelks, which prevent the re-establishment of lobster populations in the area.

Studies in New Zealand also suggest that lobsters *(J. edwardsii)* together with predatory fishes control the abundance of sea urchins that in turn alter macroalgal structure in subtidal rocky communities (Andrew & MacDiarmid, 1991; Shears & Babock, 2002). For example, when urchins (*Evechinus chloroticus*) were removed from urchin barrens dominated by crustose coralline algae, those areas were transformed into macroalgal-dominated habitat within 12 months. Indeed, macroalgal-dominated areas are more abundant in marine protected areas where lobsters and large fishes abound (Babcock *et al*., 1999).

Each of these studies is one step removed from actually manipulating predator abundance (lobster or fish) experimentally so that the response of the community without confounding influences can be observed. Nonetheless, their observations provide compelling evidence of top-down control of community structure by spiny lobster in rocky subtidal temperate ecosystems. In contrast, there is little evidence to indicate that palinurids have the same defining effect on benthic community structure in tropical or soft-sediment habitats. Predation by spiny lobsters can reduce prey densities and alter prey-size structure and species composition in seagrass and soft-sediment habitats adjacent to dens where lobsters are aggregated, but the effects are localised and diminish with distance from the den (Joll & Phillips, 1984; Jernakoff, 1987; Jernakoff *et al*., 1987; Edgar, 1990; Nizinski, 1998). The prey that spiny lobsters seek in seagrass and soft-bottom habitats are presumably sufficiently cryptic and sparse that lobsters cannot pinpoint them, and so lobsters must forage over wide areas in search of prey, and the severity of their predatory activities is diminished.

8.2.4 Spiny lobsters and marine protected areas

Marine protected areas (MPAs) have taken marine science by storm in the past decade. Their potential for preserving ecosystem biodiversity and their utility as management tools for protecting unique or sensitive habitats, species, or cultural sites is real and generally unquestioned, but many are less sanguine about their appropriate design or usefulness in fishery management. Ironically, spiny lobsters are often touted as a success story in the burgeoning literature on MPAs. In a 1997 review of the effects of marine reserves on spiny lobster populations, Childress (1997) concluded that the evidence was convincing that palinurid abundance, mean size, and spawning-stock biomass are typically greater within MPAs where removal of lobster is prohibited than in surrounding fished areas. He also noted that the magnitude of this difference was a function of the size of the MPA, the suite of habitats encompassed by the MPA, and the movement patterns of the lobsters. Those themes recur in recent studies, which continue to yield evidence that the population abundance, individual size, and egg production of palinurid lobsters generally increase in no-take MPAs.

Some of the best recent examples come from studies of *J. edwardsii* in New Zealand. Using linear models, Kelly *et al*. (2000) estimated the temporal patterns of change in lobster population structure at a series of marine reserves that differed in age. Their results show that change can indeed be rapid. Lobster density increased by ~4% per year in shallow areas (<10 m) and ~10% in deeper regions of the MPAs. The size of lobsters observed in the reserves increased by an average of 1.14 mm CL per year, and by coupling patterns in size and abundance, the authors estimated that lobster biomass increased by ~5% per year in shallow areas and ~11% per year in deeper reserve areas. Egg production increases mirrored those of biomass. Strikingly similar patterns in MPA effects on *J. edwardsii* were observed by other researchers using similar methods at another MPA (Tonga Island MPA) in New Zealand (Davidson *et al*., 2002). Five years after establishment of the Tonga Island MPA, the abundance of *J. edwardsii* had increased by 22% (~4% per year), and change was greater at deeper sites. Lobsters were nearly three times more abundant in the MPA than in adjacent fished sites, they were 19–28 mm CL larger (shallow–deep sites, respectively), large males were an order of magnitude more abundant, and fecundity in the MPA was nearly nine times greater than that in the fished area. These results are consistent with the findings of earlier studies conducted in the same region (Cole *et al*., 1990; MacDiarmid & Breen, 1993).

Similar differences in spiny lobster population structure or egg production between MPAs and fished areas have been noted in studies of other palinurid species in Spain (*Palinurus elephas*; Goñi *et al*., 2001), Florida (*P. argus*; Bertlesen & Cox, 2000; Bertelsen & Mathews, 2001), and

France (*P. elephas*; Secci *et al.*, 1999) among others. In fact, *P. elephas* has been identified as an important indicator species for measuring the success of MPAs in the Mediterranean (Mouillot *et al.*, 2002). Not every MPA in the world has experienced the same blossoming of spiny lobster populations, however. Notable exceptions are studies of MPA effectiveness in Florida and the Bahamas where the small size of MPAs, habitat differences between MPAs and fished sites, or lack of enforcement and resultant poaching within MPAs have precluded the development of noticeable differences in *P. argus* populations (Lipcius *et al.*, 2001; Bertelsen *et al.*, in press). Although commercial fishing is undeniably the primary cause of differences in lobster population attributes between MPAs and unprotected areas, substantial recreational fisheries also contribute to this difference in some areas (Davis, 1977; Eggleston & Dahlgren, 2001).

Despite recent advances, we are still uncertain whether the effects documented within MPAs produce any measurable impact on spiny lobster populations outside the reserves. For lobsters, as well as other species subject to fishing, this is one of the most pressing issues related to MPAs – and also perhaps the most difficult one to answer. The long larval period of palinurid lobsters poses a formidable obstacle to empirical investigation of the benefits of MPAs to recruitment and population replenishment outside of reserves. Simulation modelling has thus far been the tool of choice for building at least a heuristic understanding of the potential importance of larval and postlarval retention and transport in MPA design (Stockhausen *et al.*, 2000; Griffin *et al.*, 2001; Lipcius *et al.*, 2001; Stockhausen & Lipcius, 2001). There is little or no empirical evidence to support the idea that the build-up of lobsters and spawning stocks within MPAs has had any impact outside the reserves.

Even the importance of adult 'spill-over' into adjacent fisheries is questionable (Chiappone & Sealey, 2000; Kelly *et al.*, 2002). In perhaps the best study to date of adult lobster movement and spill-over, Kelly and MacDiarmid (2003) detailed how size-specific differences in male and female lobster movements contribute to population build-up within MPAs. During their eight year mark–recapture study of *J. edwardsii* in Leigh Marine Reserve in northern New Zealand, over 20% of the over 1300 adults they tagged were re-sighted on a small, 15 ha rocky reef in the reserve. Philopatry increased with size for females and among the larger males (>130 mm CL), but adult lobsters also participated in seasonal movements back and forth across the reserve boundary and were thus susceptible to capture by the fishery (i.e. spilled over). These same patterns were evident in the adjacent fishery catch. More large individuals were indeed captured by the fishery adjacent to the Leigh MPA, but the catch was seasonally variable – more so than in nearby fished populations (Kelly *et al.*, 2002). That seasonality, together with differences in the catch of smaller, legal-sized lobsters, resulted in non-significant differences in catch-per-unit-effort (i.e., kg /trap haul) of *J. edwardsii* between areas adjacent to reserves and those further away.

Rates of movement, MPA area and habitat structure, and fishing intensity along the MPA boundary are all critical factors governing the spill-over from MPAs, as well as the equilibrium density of spiny lobsters within MPAs. Acosta (2002) examined these factors in detail using a simple logistic rate model and empirical data for *P. argus* and queen conch from an isolated MPA (Glover's Atoll) in Belize. The model predicted that the lobster population within the MPA would increase 2.5 fold within five years of MPA establishment, in close agreement with the observed data. Changes in the modelled reserve size led to predictable changes in lobster population size, but changes in fishing intensity along the MPA border resulted in equally dramatic changes in lobster density in the MPA because of nomadic foraging by adult *P. argus* outside the reserve.

Research on spiny lobsters in MPAs is still in its infancy, but the need for new tools for better management of lobster populations subject to fishing could not be direr. Like the majority of fishery stocks worldwide, lobster stocks are nearly all fully- or over-exploited (National Research Council, 1994; US Ocean Commission, 2004). In southern California, for example, the fishery for *P. interruptus* began in the late 1880s when landings in only 260 traps was about 105 000 kg annually with lobsters averaging 150 mm CL (Dayton *et al.*, 1998). By 1976, it took 19 000 traps to land an equivalent biomass of lobsters that by then averaged only about half (88 mm CL) their former size. That fishery is virtually non-existent today. Yet lobsters may be good model organisms for studying the efficacy of MPAs as tools for fishery replenishment. Their long larval period sets an upper bound on the potential for long-distance oceanic dispersal of marine organisms, yet the vertical migratory behaviour of palinurid larvae and the remarkable swimming and olfactory responses of the pueruli (see Chapter 7) leave open the seemingly unlikely possibility of local retention and recruitment. Similarly, adult lobsters, although capable of extraordinary excursions, are often place-bound. Yet benthic lobsters are also more tractable than fishes, so more studies of adult spill-over from MPAs are certain to appear soon. Coming to grips with these possibilities is likely to require a melding of approaches, including modelling, molecular genetics, and some ingenious empirical studies.

8.3 Clawed lobsters

Clawed lobsters (Homaridae) are phylogenetically diverse (Chapter 4), abundant, and ecologically important in coastal zones and continental shelves of the temperate to subarctic regions of the North Atlantic (Fig. 8.7A). The most abundant species are *Homarus americanus*, *H. gammarus* and *Nephrops norvegicus*. Based on commercial landings, that reflect the magnitude of relative abundance, *H. americanus* is the most abundant, *N. norvegicus* next, and *H. gammarus* a distant third (Fig. 8.7B; FAO, 2004). *Nephrops* and *H. gammarus* are distributed from northern Norway (Lofoten Islands) south to the Atlantic coast of Morocco and throughout much of the Mediterranean (Holthuis, 1995). In contrast, *H. americanus* has greater landings over a relatively small geographic range from northern Newfoundland south to the mid-Atlantic coast of North America (Holthuis, 1995).

Direct, *in situ* measurement of clawed lobster population densities scale with their fisheries-dependent abundances (i.e. Fig. 8.7B). Average population densities of *H. americanus* range between one and two per square metre (Fig. 8.8A, B) over hundreds of kilometres of the US coast of Maine (Steneck & Wilson 2001). In contrast, *H. gammarus* is so rare, that we could find no published population densities from the field. The population density of *N. norvegicus* is also lower than that of *H. americanus*, though its landings are high (Fig. 8.7B) because it is distributed in sedimentary habitats over vast areas of the continental shelf (Chapman, 1980; Tuck *et al.*, 1997; Maynou *et al.*, 1998) (Fig. 8.7A) from 20–800 m (Holthuis, 1995). Its maximum population densities range between 0.006/m^2 in the Mediterranean near Spain (Maynou *et al.*, 1998) to 0.125/m^2 for Scotland (Chapman & Rice, 1971). These population densities are one to three orders of magnitude lower than those reported for *H. americanus* in Maine, USA (Fig. 8.8B; Steneck & Wilson, 2001).

Although good ecological observations have been made on *N. norvegicus* (e.g. Chapman & Rice, 1971; Chapman, 1980; Cobb & Wahle, 1994), our knowledge of the ecology of *H. americanus* is far greater. The American lobster is abundant and occurs within depths that are easily studied. In contrast, the average depth of occurrence for *N. norvegicus* is 300–400 m (Maynou *et al.*, 1998), a range that is difficult and expensive to study. For these reasons, *H americanus* has received the most attention in ecological research, and its treatment therefore dominates our review.

There are numerous physiological and behavioural similarities shared by clawed lobsters beyond their obvious large chelipeds, which they use for prey capture and mate selection. For example, clawed lobsters are solitary crevice dwellers that defend their space against others of their species and each other (Cobb, 1971). They carry developing eggs for nearly a year, before the eggs hatch at about 10°C (18–12°C, *H. americanus*, Aiken & Waddy, 1989; 5–15°C, *H. gammarus*, Tully *et al.*, 2001; 7–11°C, *N. norvegicus*, Thompson & Ayers, 1989). They all have relatively short larval durations: three larval stages before they metamorphose into postlarvae (reviewed by Cobb & Wahle, 1994). Once they become established in benthic habitats, they pass through three ecological phases (early benthic, adolescent and reproductive phases; *sensu* Cobb & Wahle, 1994). The timing and duration of each phase varies geographically

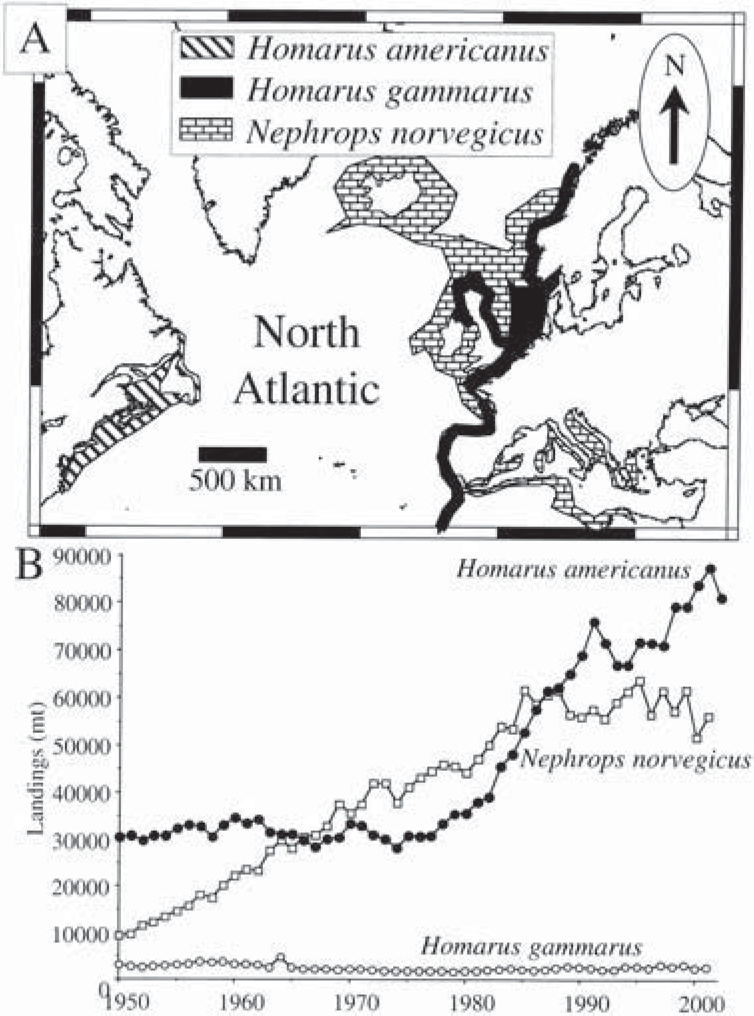

Fig. 8.7 (A) The North Atlantic distribution of American lobster *Homarus americanus* (US and Canada), European lobster *H. gammarus* and the Norway lobster *Nephrops norvegicus* (Holthuis, 1995). (B) Landings for all three species since 1950. Open squares are *H. americanus*, open circles are *H. gammarus*, and closed squares are *N. norvegicus*. (Data from FAO (2004), National Marine Fisheries Service and Canada Department of Fisheries and Oceans.)

and oceanographically among and within the three species (e.g. Wahle *et al.*, 2004). Despite these similarities, these species differ strikingly in patterns of distribution, abundance, agility (their propensity to move), habitat use, and key aspects of the ecology of the habitats in which they live.

8.3.1 Limits to recruitment

Several studies concluded that successful settlement to the benthos drives the demography of lobsters (e.g. spiny: Butler & Herrnkind, 1997; Parrish & Polovina, 1994; and clawed: Cobb & Wahle, 1994). For the American lobster, settlement and early benthic phase (juveniles <40 mm CL) subpopulations are strongly bound to the interstices of their cobblestone shelter (Steneck, 1989; Wahle & Steneck, 1991). Their strong habitat-selection behaviour for small shelter-providing substrata (Able *et al.*, 1988; Wahle & Steneck, 1991) at the time of settlement coupled with the demonstrably low post-settlement mortality measured in the field (Wahle & Steneck, 1992; Palma *et al.*, 1999; Wahle *et al.*, 2004) may explain why successful settlement drives the demography of this species today (Palma *et al.*, 1999; Steneck & Wilson, 2001). As lobsters grow, their dependency on shelters for protection declines (Wahle & Steneck, 1991; Wahle, 1992),

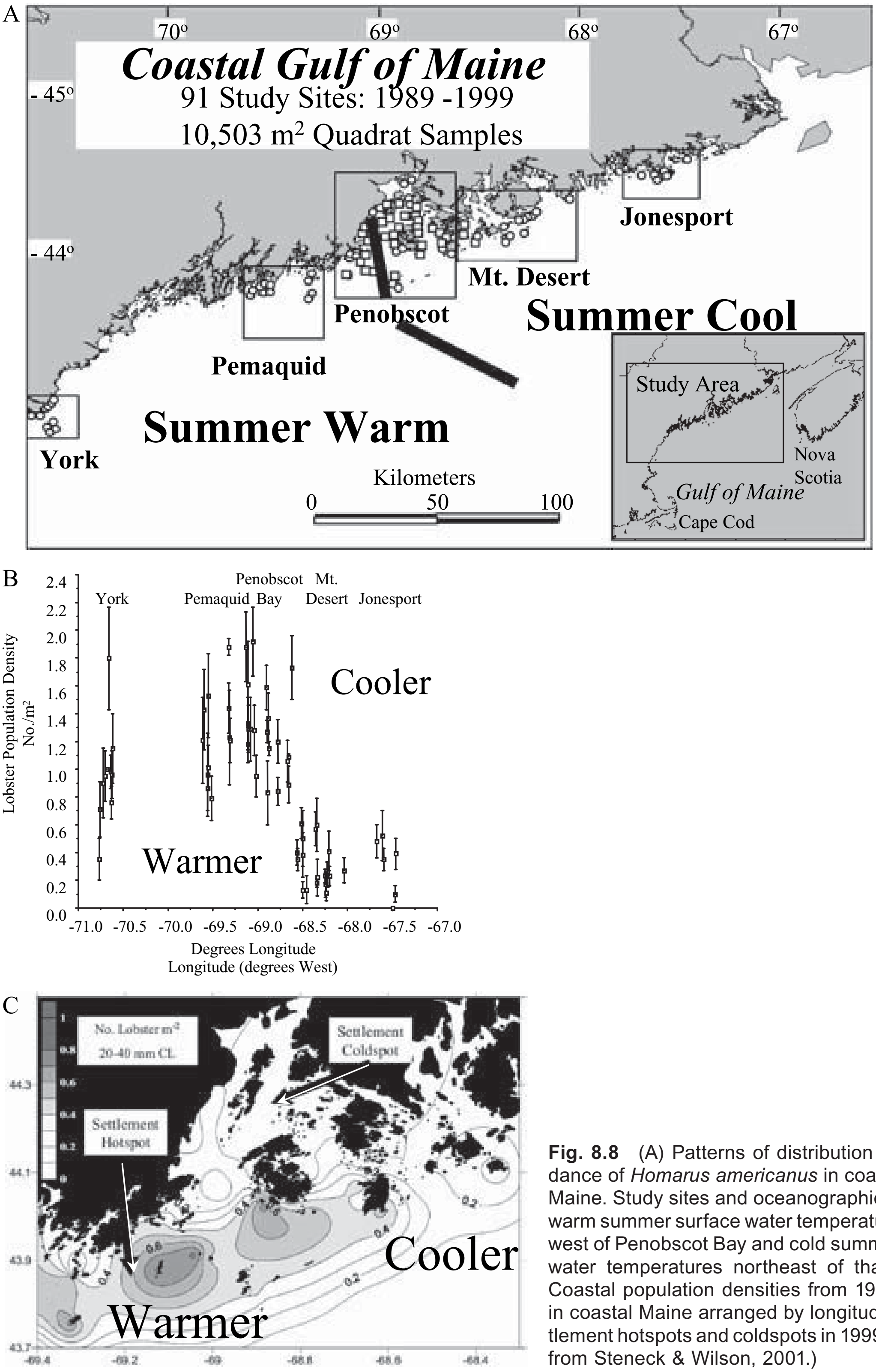

Fig. 8.8 (A) Patterns of distribution and abundance of *Homarus americanus* in coastal Gulf of Maine. Study sites and oceanographic feature of warm summer surface water temperatures southwest of Penobscot Bay and cold summer surface water temperatures northeast of that bay. (B) Coastal population densities from 1989 to 1999 in coastal Maine arranged by longitude. (C) Settlement hotspots and coldspots in 1999. (Adapted from Steneck & Wilson, 2001.)

and their annual migration range increases (Krouse, 1980). Specifically, young of the year lobsters remain only a metre or two from where they settled (Incze *et al*., 1997; Palma *et al*., 1999).

Recruitment to the benthos may therefore be the gateway to population growth among at least some clawed lobsters. Successful settlement for lobsters requires three sequential steps (Fig. 8.9): (1) available competent larvae (which requires sufficient broodstock, larval production and connectivity via oceanographically driven dispersal), (2) the larval behaviour contributing to its propensity to settle, and (3) available nursery habitat (i.e. microhabitats where post-settlement mortality is low). Most of what we know about clawed lobster recruitment comes from studies of *H. americanus* in the Gulf of Maine. The Gulf of Maine is a good laboratory in which to study lobster ecology because larvae

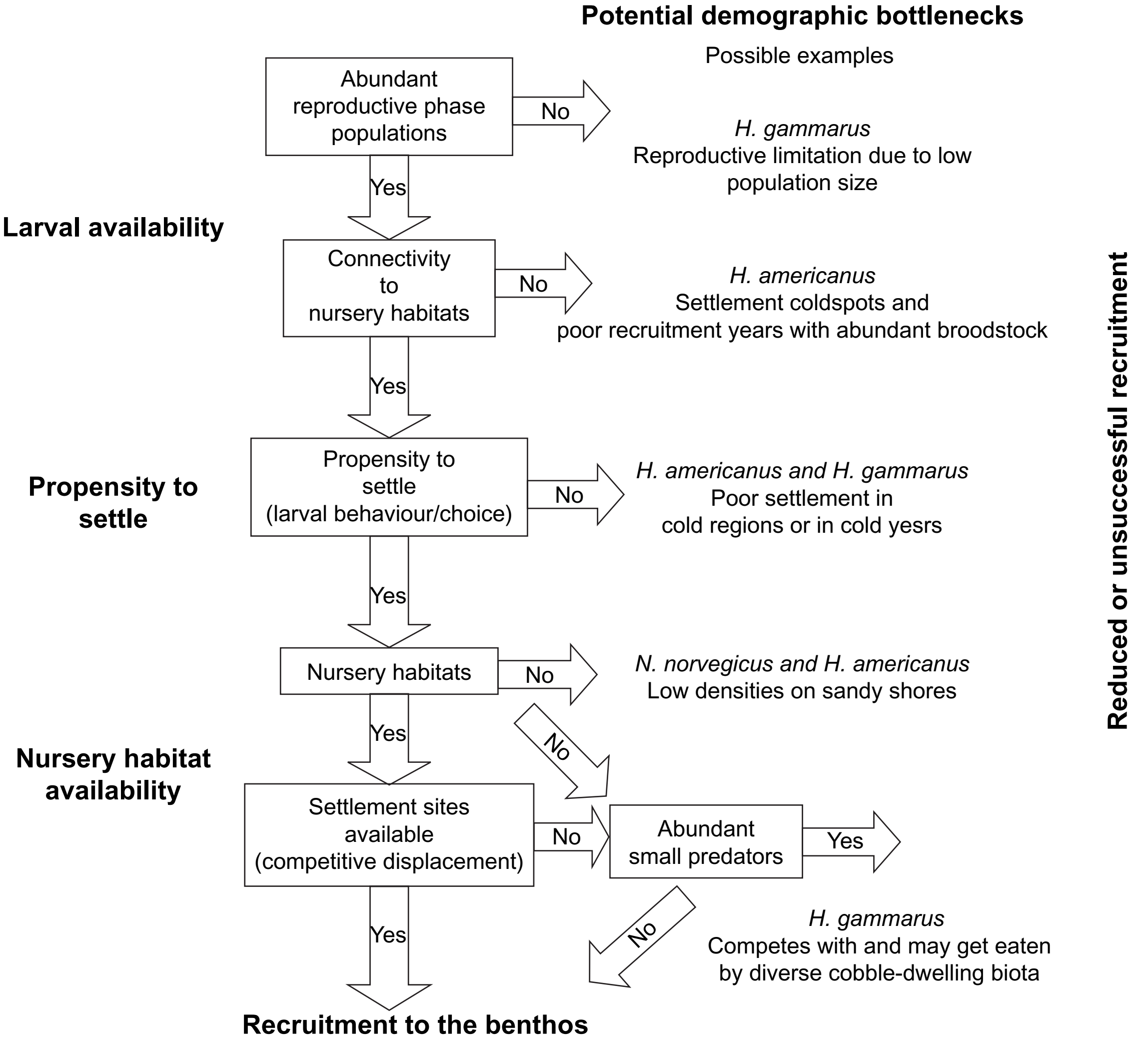

Fig. 8.9 Conceptual model of variable demographic bottlenecks for clawed lobsters leading to recruitment limitation. Three sequential steps related to larval availability, propensity to settle and available nursery habitats lead to recruitment to the benthos. Arrows to the right represent possible bottlenecks. Examples of those bottlenecks are given to the right of the arrows.

and young of the year lobsters are abundant and easy to sample (Incze & Wahle, 1991; Wahle & Steneck, 1991; Miller & Reeves, 2000).

Postlarval availability and settlement

The abundance of larvae and settlement to the benthos are invariably greatest in outer coastal habitats and decline up estuaries and in deep embayments (Palma *et al.*, 1999; Steneck & Wilson, 2001). At very coarse levels, therefore, connectivity must exist between outer coastal regions where larvae and postlarvae develop (Incze *et al.*, 1997) and nearshore shallow (Wilson, 1999) nursery habitats. Oceanographic control of lobster larval transport and availability for settlement is evident at several scales. For example, larval 'shadows' occur on the lee sides of small islands, where wind-driven advection significantly reduces settlement (Incze & Wahle, 1991; Palma *et al.*, 1999). The absence of available larvae for settlement is also thought to create settlement 'cold spot' patches up estuaries such as Maine's Penobscot Bay, (Fig. 8.8C, Steneck & Wilson, 2001) and elsewhere (Palma *et al.*, 1999). Advection of larvae and postlarvae offshore into deep-water regions probably causes considerable pre-settlement mortality (Incze & Naimie, 2000; Wahle, 2003) and may explain why lobster settlement in the Gulf of Maine declined from 1995 to 2000 (Wahle *et al.*, 2004) despite reproductive populations in the region increasing over that same period of time (ASMFC, 2000; Steneck, 2006). Larval mortality as a result of oceanic transport away from nursery habitats has also been reported for *H. gammarus* (Nichols & Lovewell, 1987) and *Nephrops* (White *et al.*, 1988; Hill, 1990; Cobb & Wahle, 1994) of the western Irish Sea. Simple passive advection by ocean currents (Incze & Namie, 2000) together with wind-driven surface currents, may explain a considerable proportion of the variance in settlement, but long-distance directional swimming by postlarvae could also affect larval availability (Fig. 8.9) (Katz *et al.*, 1994). Nevertheless, arrival of postlarvae in waters over potential nursery grounds does not alone assure successful settlement.

Once competent postlarvae arrive at a potential settlement site, their propensity to settle is controlled by several factors that operate hierarchically (Boudreau *et al.*, 1990). Water temperature controls larval development and possibly recruitment of postlarvae to the benthos (Cobb & Wahle, 1994) by limiting the diving behaviour of pelagic postlarvae (Boudreau *et al.*, 1990, 1991; Annis, 2004). Although laboratory studies by Boudreau *et al.* (1990, 1991) concluded that compressed temperature gradients with depth (i.e. thermoclines) exceeding 6°C will limit settlement of American lobsters, other studies concluded that a specific temperature or 'thermal threshold' mediates settling behaviour among postlarvae (Annis, 2004). Annis (2004) followed sounding postlarvae in the field and observed that water temperatures of 12°C or more limited their diving. This is the same temperature that Huntsman (1923) hypothesised controlled recruitment along the north shore of the Gulf of Maine. Similarly, Wilson (1999) found a marked increase in lobster settlement both in areas and at depths having temperatures warmer than 11.5°C. This result conformed to observations from large regional studies that found high rates of settlement in warm stratified water in Maine (e.g. west of Penobscot Bay, Maine, Fig. 8.8A, C; Steneck & Wilson, 2001) but low settlement in eastern Maine where water is cold but not stratified (Wahle & Steneck, 1991; Cobb & Wahle, 1994). These observations do not contradict the laboratory findings of Boudreau *et al.* (1992) because all of their control chambers in which the highest rates of lobster settlement were observed were warmer than the 12°C threshold temperature. Nevertheless, several lines of evidence point to seawater temperatures as controlling the propensity to settle in American lobsters (Fig. 8.8).

Olfactory cues may also contribute to recruitment success among settling lobsters. Laboratory studies on the behaviour of competent American lobster postlarvae with respect to odour plumes, found that at the time of settlement, they swim toward adult lobsters, other postlarvae and benthic algae, but away from potential predators (Boudreau *et al.*, 1993). This behaviour is likely to increase post-settlement survival by attracting lobsters to the shallow photic zone where water warms during the summer months and their growth rates will be high (Wahle *et al.*, 2004) but will allow them to avoid predators (Wahle, 1992; Boudreau *et al.*, 1993). This illustrates the rather elaborate metre-scale habitat selection behaviour evident in this species at the time of settlement.

Nursery habitats and demographic bottlenecks

Lobster settlement is largely limited to shallow, cobble, nursery grounds (Wahle & Steneck, 1991; Cobb & Wahle, 1994) where early benthic phase lobsters live for the first several years of their lives. Because this substrate comprises no more than 2–10% of coastal substrates in Maine (Kelley, 1987) it has been described as the primary 'demographic bottleneck' for the American lobster (Wahle & Steneck, 1991; Wahle, 1992; Cobb & Wahle, 1994). As such, this substrate at this life history phase may set the carrying capacity for this species.

Little is known about recruitment to the benthos by European lobster, *H. gammarus*, because they are exceedingly rare. Newly-settled, young of the year and early benthic phase lobsters have never been found subtidally (Mercer *et al.*, 2001). This, despite experienced researchers using techniques proven effective for *H. americanus* (e.g. Wahle, 1998) and a large team of European researchers sampling broadly in four countries (Norway, Ireland, UK and Italy) (Linnane *et al.*, 2001; Mercer *et al.*, 2001; and discussed below). A few early benthic phase and adolescent phase European lobsters (20–50 mm CL) were found in an intertidal zone near a source of fresh water (Linnane *et al.*, 2000a, 2001), but little can be concluded from that rare encounter. It does indicate, however, that European lobsters can live in the intertidal zone but that they do so at a small fraction of the densities common for American lobsters in that zone (Cowen *et al.*, 2001). For example, the four-year study by Cowen *et al.* (2001) reported 1934 lobsters from 4490 quadrates from New England, or an average density of $0.4/\mathrm{m}^2$ with maximum site averages exceeding one per square metre.

Observations of laboratory-reared European lobsters indicates that their settlement and early post-settlement ecology is similar to that of *H. americanus*. They preferentially select cobble habitat and sustain themselves by suspension feeding (Linnane *et al.*, 2000b). Theories advanced to explain why European early benthic phase lobsters have not been found include simple rarity of the species, avoidance of sampling gear, preference for habitats distinct from those of juvenile and adult lobsters, and preference for specialised nursery grounds that are yet to be sampled. Although Mercer *et al.* (2001) favoured the last thesis, others argued simply that they are too rare to be detected (Wahle, 1998). Overall population density estimates of early benthic phase European lobsters, based on landings, range from 0.01 to $0.001/\mathrm{m}^2$ (R. Bannister & S. Lovewell personal communication in Mercer *et al.*, 2001). If these estimates were correct, then suction sampling of areas between 100 and $1000\,\mathrm{m}^2$ per site would be necessary (although admittedly impractical on the high side). To date, a total area of $94.5\,\mathrm{m}^2$ has been suction sampled among four countries (Ireland, $23\,\mathrm{m}^2$; UK, $6.5\,\mathrm{m}^2$; Norway, $41\,\mathrm{m}^2$; Italy, $24\,\mathrm{m}^2$), and some sampling was devoted to substrates such as *Zostera* eelgrass (Norway), which are generally considered poor settlement and early benthic phase habitats (Cobb & Wahle 1994). In comparison, $280\,\mathrm{m}^2$ of cobble substrate is sampled annually at seven locations as part of Maine's lobster settlement monitoring programme.

Clearly, newly-settled and all subsequent phases of European lobsters are much less abundant than their American counterparts (e.g., Fig. 8.7B). Accordingly, larval availability is likely to be relatively low because of the low densities of reproductive-phase populations. European lobsters may therefore be reproductively limited; the demographic bottleneck limiting their overall density may be at the first step of the recruitment sequence (Fig. 8.9). Despite low larval availability however, the other steps may also be important for recruitment. Recent advances in methods for aging European lobsters (Sheehy *et al.*, 1999) allow high-resolution cohort analyses, which can determine interannual variations in recruitment strength (Sheehy & Bannister, 2002). Analysis by these methods showed that onshore winds (driving larval availability) and local sea temperatures at the time of settlement (affecting the propensity to settle) correspond to reconstructed annual settlement strength for *H. gammarus* (Sheehy & Bannister, 2002).

Table 8.1 Regional comparison of decapod populations from suction sampling of cobblestone habitat at 5–10 m depth. (Europe data from Linnane *et al.* (2001) and Mercer *et al.* (2001). Gulf of Maine data from Steneck – unpublished data from Damariscove Island, Maine 2003.)

	Gulf of Maine	Norway	Ireland	UK	Italy
Lobster (no./m^2)	1.5	0	0	0	0
Decapod density (no./m^2)	8.6	146.5	86.5	85.5	32
No. decapod families	4	12	14	13	12
No. decapod species	5	17	32	15	20
Dominant genus/family	*Homarus*	*Galathea* sp.	Porcellanidae	Porcellanidae	*Alpheus*
No. m^2 quadrats	40	74	46	13	48

Experimental and field evidence indicate that early post-settlement processes such as competition and predation may also be important to recruitment of this species. For example, tethering studies showed that attack rates on small, unprotected lobsters were very high (Ball *et al.*, 2001; Mercer *et al.*, 2001), as they are for the American lobster (Wahle & Steneck, 1992), but competition for interstitial space among cobblestones is likely to be much greater for European than for American lobsters (Wahle, 1998). Suction samples of cobblestone nursery habitats yielded densities of decapods nearly an order of magnitude greater in Europe than at a rich site in the Gulf of Maine (Table 8.1). The diversity of decapod families and species were also considerably higher in Europe than that found in America.

Interactions between these two early post-settlement processes could have synergistic effects. Settling lobsters select the habitat into which they recruit by probing spaces with their claws and exploring entry into small shelters. The high density of other decapods in Europe (Table 8.1) may lead to much longer searches for unoccupied shelters by European than by American lobsters and therefore higher per capita predation rates on them. In contrast, American lobsters more often encounter vacant cobblestone habitats resulting in rapid occupation of predator-free refuges (Wahle & Steneck, 1992).

Recruitment dynamics for *N. norvegicus* differ from those of *Homarus* spp. because it lives in deeper water and recruits to and lives in cohesive mud habitats (Chapman & Rice, 1971; Cobb, 1977; Cobb & Wahle, 1994). Larval availability in the western Irish Sea is related to the biophysics of oceanographic connectivity, which are under climatological control (Hill, 1990; Hill & White, 1990). Relatively little is known about the settlement behaviour of *N. norvegicus* (see Cobb & Wahle, 1994), but they are thought to be most abundant in fine sediment near the lower limit of the photic zone (Chapman, 1980), where visual predators are probably less effective (Cobb & Wahle, 1994). In contrast to *H. americanus*, *N. norvegicus* is believed to settle into small holes in the same habitat where adults live.

Bottleneck variability

The limits to recruitment described above are reasonable proximate explanations for the differences we see today in the abundances of clawed lobsters. The series of events leading to successful recruitment may be 'pinched' at any of several successive nodes, with significant demographic consequences (Fig. 8.9). Demographic bottlenecks are variable, therefore, and depend upon key input parameters that operate on several scales (Palma *et al.*, 1999). For example, in warmer-than-average years, the bottleneck could widen if a thermal threshold that limits the sounding depth of competent postlarvae deepens, exposing more potential nursery habitats to settlement (Sheehy & Bannister, 2002; Annis, 2004; Steneck, 2006). Year class strength is often set by chance encounter of postlarvae oceanographically-driven to coastal zones that happen to have nursery habitats. At the scale of embayments, a very high percent of American lobster postlarvae find, settle and survive in cobblestone habitats (Incze *et al.*, 1997, 2000), whereas a very high percentage of the same number of postlarvae entering an otherwise identical sandy bay would die. Thus, the large, bay-scale area of available nursery habitats may well be more important as a demographic bottleneck for this species than simply the availability of settlement space within any given square metre of cobblestone.

We stress the *demographic* consequences of ecological processes such as settlement, habitat selection, competition, and predation because only some of those processes result in death of the settlers (thereby having demographic effects). Intense competition at the time of settlement could cause postlarval lobsters to continue searching for available nursery habitat, which may affect their distribution but will not affect the year class strength unless this behaviour also increases their per capita mortality rates. This was determined for postlarvae entering small embayments in Maine in which most eventually found and settled into cobblestone nursery habitats without significant post-larval mortality (Incze & Wahle, 1991; Incze *et al.*, 1997).

Intraspecific competition at the time of settlement has modest demographic effects. Even in areas with the highest density of newly-settled lobsters, space within nursery habitats does not appear to be demographically limiting. When Wahle *et al.* (2001) artificially over-saturated cobblestone habitats with postlarval lobsters, the equilibrium densities were much greater than that ever found in the field, so cobble habitats are probably rarely limiting in nature. A similar cobble-stocking experiment was conducted for *H. gammarus* under predator-free conditions, with results similar to those of Wahle (2003). After a year, a high percentage of the experimentally introduced individuals remained (Linnane *et al.*, 2000a). Thus successful settlement may well drive the demography of lobsters but many ecological factors regulate it in complex and variable ways.

8.3.2 Post-recruitment patterns and processes

Distribution, abundance and body size

The American lobster undergoes an 'ecological niche shift' during its ontogeny; different ecological phases segregate into different habitats (Fig. 8.10). Over 80% of settlement occurs at depths less than 20 m (Wilson, 1999) and primarily in cobblestone habitats (Wahle & Steneck, 1991; Palma *et al.*, 1999). As lobsters grow toward harvestable size (83 mm CL), their annual migration range is on the order of 1–5 km (Krouse, 1980). By the time they reach large, reproductive-phase sizes (≧90 mm CL), they migrate 20–30 km annually, and a few tagged individuals have been observed to roam for hundreds of kilometres in less than a year (Campbell & Stasko, 1985; Campbell, 1986, 1989; Estrella & Morrissey, 1997).

Interestingly, 'No similar migrations of *H. gammarus* have been reported' (Cobb & Wahle, 1994). Bannister *et al.* (1994) found that most microwire-tagged hatchery-reared European lobsters remained near their points of release at least until reaching harvestable size. Electromagnetic telemetry studies revealed that relatively small-scale (∝10 km) migrations among adjacent reefs were common but few or no long-distance migrations were reported (Jensen *et al.*, 1994; Smith *et al.*, 1998). The longest reported *H. gammarus* migration is about 20 km (Bannister *et al.*, 1994), less than the average seasonal migration (>30 km/year, Campbell 1986) and an order of magnitude less than that of the longest-migrating *H. americanus*.

Recruitment cells of *H. gammarus* are so closed that little gene flow occurs among northern populations of this lobster (Jørstad *et al.*, 2004). Using allozyme, microsatellite, and mtDNA analyses, Jørstad *et al.*, (2004) found that genetically distinct subpopulations of *H. gammarus* persist, that are separated by only 142 km. Oceanographic conditions prevent larval exchange among coastal populations, but this genetic separation shows that migration of reproductive stocks must also be virtually nil (Jørstad *et al.*, 2004). In sharp contrast, the American lobster migrates long distances and shows no measurable stock differentiation within

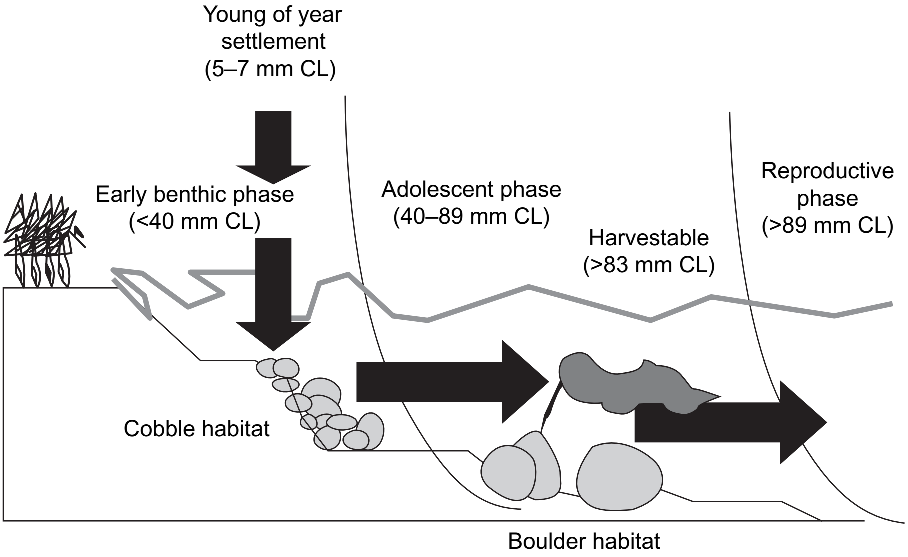

Fig. 8.10 Lobster population segregation among habitats and with distance from shore. Diagrammatic representation of shallow nearshore settlement into cobble habitat, diffusion to coastal boulder fields with increasing size and age, and eventual diffusion of larger reproductive-phase size classes to offshore habitats.

its range (including the Gulf of St Lawrence, southwest Nova Scotia, and Georges Bank; Harding *et al.*, 1997). Similarly, *N. norvegicus* does not migrate (Chapman, 1980). Since they settle and live in adult habitats, there is no segregation by size or sex resulting in rather discrete patches in abundance (Maynou *et al.*, 1998).

Because lobsters settle in shallow coastal zones (Wilson, 1999) and diffuse offshore at a large size (Fig. 8.10), their size frequency modes shift to progressively larger size with distance from the coast (which is also distance from their nursery habitats; Fig. 8.11). Small early benthic phase lobsters (<40 mm CL, Figs 8.8C, 8.11A, C) dominate rocky substrata in the shallowest coastal zones, and cobble nursery habitats harbour the smallest size classes (Fig. 8.11A). A few metres away, in sediment substrata, lobsters are significantly larger (Fig. 8.11B). Lobsters smaller than harvestable size (83 mm CL) dominate most shallow subtidal coastal zones. Distinctly larger lobsters (50–80 mm CL mode, Fig. 8.11E) are trawled from deeper inshore habitats within Maine state waters and have size-structure more similar to that of trap-caught lobsters (ASMFC, 2000). Trawl surveys conducted in adjacent offshore habitats in Maine yielded significantly larger lobsters (80–90 mm CL; Fig. 8.11G). These correspond to the size frequencies from the National Marine Fisheries Service (NMFS) semi-annual trawl surveys (Steneck, 2006). The ontogenetic segregation in some areas is so complete that almost no overlap exists between populations of seasonally migrating reproductive-phase lobsters (≧90 mm CL, Fig. 8.11F) and distinct but more stationary adjacent juvenile populations in the coastal zone (Fig. 8.11D; Campbell & Pezzack, 1986). Large reproductive-phase lobsters dominate all of the most distant offshore canyons of the Gulf of Maine's Georges Bank (Fig 8.11H; Skud & Perkins, 1969).

The ecological consequences of segregated reproductive populations may be profound. Connectivity studies between broodstock and settlement 'hotspots' (Fig. 8.8C) suggest the existence of a long-distance larval source–sink dynamic (Harding *et al.*, 1983; Incze & Naimie, 2000; Annis, 2004). This pattern has management consequences both for stock–recruitment relations (Wahle, 2003) and as a postlarval subsidy in coastal zones from reproductive lobsters living in offshore refugia where fishing pressure is low (Fogarty, 1998). This long-distance larval source–sink rela-

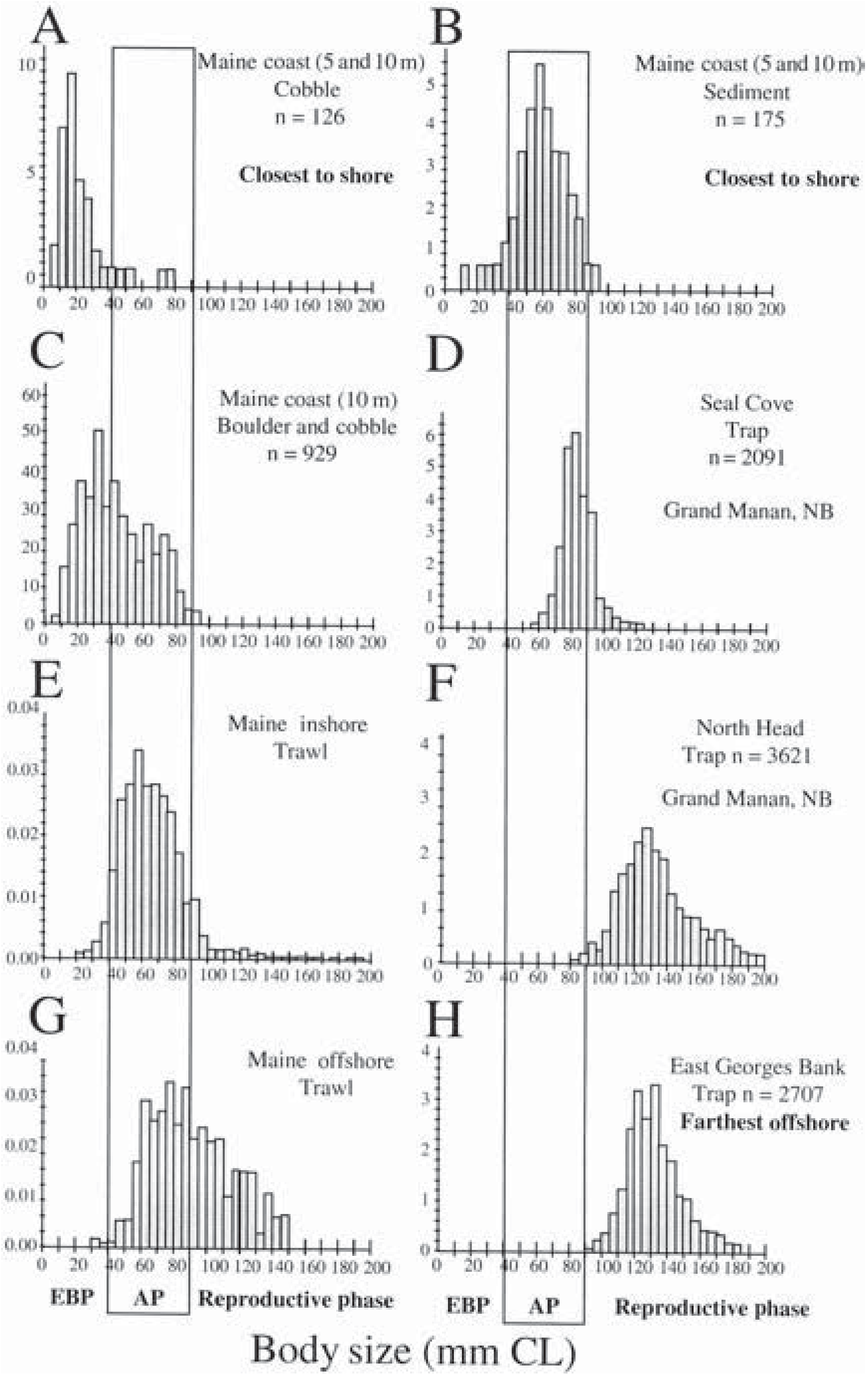

Fig. 8.11 Size structure of lobsters illustrating ontogenetic segregation illustrated in Fig. 8.10. The elongate vertical rectangle isolates adolescent phase (AP) lobsters 40–89 mm CL from smaller early benthic phase lobsters (5–39 mm CL) and larger reproductive phase lobsters (′ 90 mm CL). (A) and (B) illustrate shallow nearshore nursery habitat-related segregation of early benthic phase in cobblestone habitats (A) as distinct from adjacent sediment (B) (adapted from Wahle & Steneck, 1991). (C) Adjacent boulder habitat contains intermediate-sized individuals (Steneck, unpublished data). Segregation among size classes at larger spatial scales is evident around Grand Manan Island in New Brunswick, Canada where migratory reproductive-phase lobsters congregate seasonally in shallow northern coves (F, adapted from Campbell & Pezzack, 1986) whereas much smaller nonmigratory lobsters reside in southern coves at the same depths (D, adapted from Campbell & Pezzack, 1986). Maine State trawl surveys from inshore habitats (E, Maine DMR) show significantly fewer reproductive-phase lobsters than do the same surveys from adjacent sites somewhat farther offshore (<5.6 km) (G). Farthest offshore on Georges Bank (278 km) (H) virtually all lobsters are reproductive-phase.

tionship enables lobster stock to withstand higher levels of fishing mortality in coastal zones (Fogarty, 1998; Steneck, 2006).

Competition and predation

In a significant review paper, Wahle (2003) concluded for lobsters in general that, 'Post-settlement survival is strongly influenced by the three-way interaction of predation risk, habitat quality and body size. As a result, refuge habitat is more often a limiting factor than food, especially among small individuals still vulnerable to predators'. For this reason we will focus primarily on the ecological processes of competition and predation, which drive habitat selection, survival, and the demography of clawed lobsters.

Most clawed lobsters are solitary, shelter-preferring organisms by day and active foragers by night (Cobb & Wahle, 1994). Evidence exists of shelter competition for all three species. *Homarus gammarus* is known to compete for space during mating (Debuse *et al.*, 2003), but the demographic consequences are likely to be low because of the species' rarity so it is probably not shelter-limited. Population density and body size are inversely correlated for *N. norvegicus* (Tuck *et al.*, 1997), possibly because larger ones in competition for shelter space displace small lobsters. Although this pattern may affect local small-scale size structure, no evidence indicates that it influences overall population densities. In fact, throughout much of its deep-water range, population densities (maximum 0.006/m^2; Maynou *et al.*, 1998)(Fig. 8.7B) are three orders of magnitude lower than that of the American lobster. Higher population densities averaging 0.125/m^2 (one order of magnitude less than that of the American lobster) were studied at 30 m depths in Scotland (Chapman & Rice, 1971). At that density, active territorial fights over shelters were observed, consistent with the notion that intraspecific competition increases with population density. The competitive interactions were remarkably similar in detail to those observed in *H. americanus* (e.g. by Cobb, 1971), but the difficulties of scuba diving at 30 m leave many ecological questions about *N. norvegicus* unanswered. Conversely, because *H. americanus* is found both at high population densities and at depths amenable to protracted *in situ* study, considerably more has been published about its post-recruitment ecology.

Size-specific habitat space can be limiting and can drive intraspecific space competition among clawed lobsters living at relatively high population densities. In most cases, such competition has some effect on the size structure and/or the habitat in which they live. Size-specific habitat availability therefore controls local carrying capacity (e.g. Caddy, 1986), but depending largely on the predator environment, it may also control the demography of the species. That is, the consequences of competitive displacement in a predator-free environment merely redistribute individuals because competitively subordinate lobsters do not die. However, the per capita mortality rate increases significantly if competitive displacement occurs in a predator-rich environment (Wahle *et al.*, 2004). Size-mediated predator vulnerability therefore accounts for much of the variance in the post-settlement survival of lobsters.

Predation is a highly size-specific ecological process (Wahle, 1992), and even under pristine conditions (before human influence) the largest individuals (those over 20 kg) would probably have been immune to predation. The rate at which predation declines with body size relative to the availability of shelters is therefore likely to determine local and regional carrying capacity.

Today's fish predators are primarily small (<5 cm long), commercially unimportant species such as juvenile cunners (*Tautogolabrus adsperus*), sculpins (*Myoxocephalus* spp.), and shannies (*Ulvaria* spp). This guild of small predatory fishes is ubiquitous in shallow coastal zones, where average densities of nearly 1/m^2 have been recorded (Malpass, 1992). Attack rates on lobsters in coastal Maine decline precipitously with increasing body size (Fig. 8.12A). At settlement size (5–7 mm CL), tethered lobsters suffered up to 60 attacks per hour, but the rate decreased to 10 by the time they reached 8–9 mm and fell below detectable levels by the time they reached 20 mm CL (Wahle & Steneck, 1992; Fig. 8.12A). In parallel studies, lobsters up to 80 mm CL were tethered for as long as 45 days over a three year period, and not a single predator attack was recorded (Steneck, 1997; Steneck & Carlton,

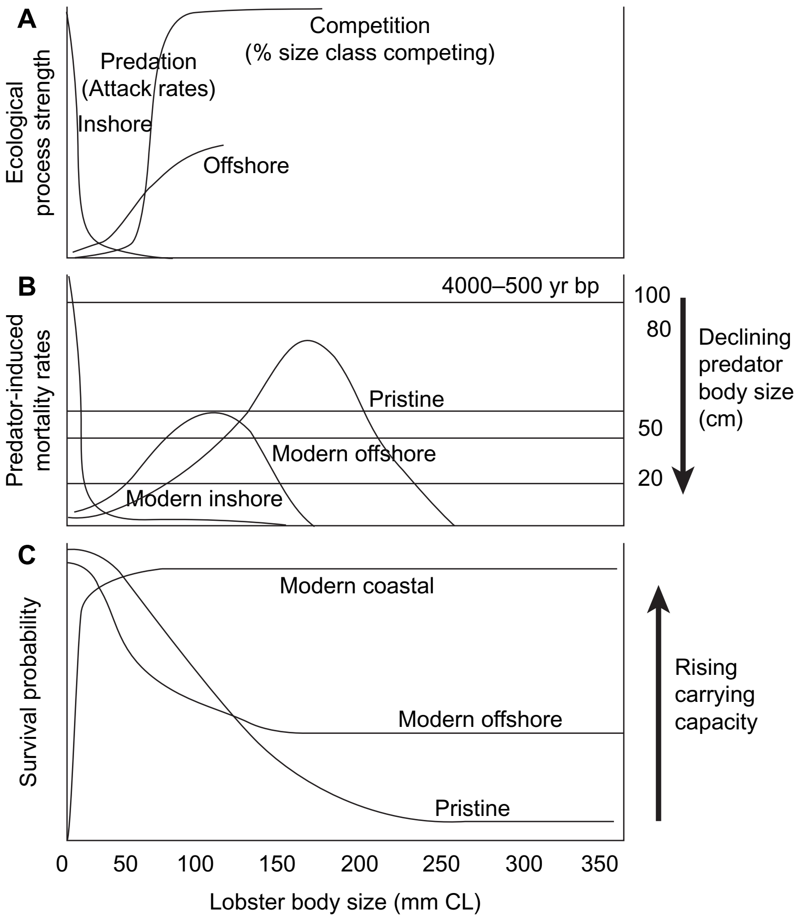

Fig. 8.12 Changes in ecological processes as a function of body size over space (e.g. inshore as opposed to offshore) and time. (A) The importance of predation and competition. Predator attack rates decline precipitously with size at 'inshore' shallow coastal sites (adapted from Wahle & Steneck, 1992) whereas they increase with size at 'offshore' sites where large predators persist (adapted from Steneck, 1997; Steneck & Carlton, 2001). The percentage of individuals competing for shelter space increased markedly above 60 mm CL (adapted from Steneck 1989). (B) Rates of predator-induced mortality in modern coastal and offshore regions based on tethering studies (Steneck & Carlton, 2001; see text). 'Pristine' conditions are those before measurable human effects. The size of large predators is estimated from archaeological studies (see text). Horizontal lines indicate the estimated predator size based on archaeological records (4000 to 500 years before present, Jackson *et al.*, 2001), modern offshore and coastal (Steneck, 1997). (C) Size-dependent survival probability in modern coastal and offshore habitats and under pristine conditions (all extrapolated from attack rates and reflected in B).

2001). This rapid decline in predation rates (Fig. 8.12A; Wahle & Steneck, 1992) with increasing size produces the low post-settlement predator-induced mortality rates (Fig. 8.12B) and high post-settlement survival (Fig. 8.12C) reported for *H. americanus* (Wahle & Incze, 1997; Palma *et al.*, 1998, 1999).

Competition for shelter space is conspicuous in *H. americanus* (Cobb, 1971). Arguably, intraspecific competition occurs among all size classes, but habitat limitations (e.g. shelter space; Caddy, 1986), aggression and range of detection all increase for lobsters larger than about 60 mm CL (Steneck, 1989; Fig. 8.11A). Early benthic phase lobsters settle into small shelter-providing habitats such as cobble (Fig. 8.11A) but with time, they outgrow cobble habitat and occupy adjacent sediment (Fig. 8.11B) and boulder (Fig. 8.11C) habitats. Shelter size and spacing regulates competition pressure. By experimentally reducing shelter separation, Steneck (1989) showed intraspecific competition among lobsters over 60 mm CL increased (Fig. 8.12A). Surprisingly, with increased population density and competition, large lobsters vacated the area diffusing to habitats with lower population densities. This 'demographic diffusion' (*sensu* Steneck, 1989) is evident in the decline of pre-harvestable sized lobsters (i.e. 60–83 mm CL) in shallow coastal zones (Figs 8.11B, C, E) and results in size-mediated habitat segregation (Figs. 8.10, 8.11). Since lobsters over 60 mm CL are virtually immune to predation (Steneck, 1997; Fig. 8.12A), this demographic diffusion only redistributes larger size classes from high-population-density, shelter-rich shallow coastal boulder habitats (see, e.g. Figs 8.9, 8.10C) with little consequence to overall lobster abundance. This demographic diffusion may contribute to the accumulation of larger, competitively aggressive lobsters in nearshore deep water (Fig 8.11 E, G) and on offshore banks (e.g. Fig. 8.11H).

Currently, the predation risk for American lobsters greater than 60 mm CL in size is too low to measure (Wahle & Steneck, 1992; Steneck, 1997), so reproductive-phase lobsters (usually >90 mm CL) can accumulate in offshore habitats (i.e. to the right of the vertical rectangle in Fig. 8.11). This size segregation occurs upon the onset of sexual maturity (Campbell & Stasko, 1985), allowing these lobsters to increase in abundance (Steneck, 2006) and to migrate seasonally into shallow coastal zones (e.g. North Head, Grand Manan Island in New Brunswick; Campbell & Pezzack, 1986; Fig. 8.11F) in the summer. The fishery-induced decline in coastal predators (Steneck, 1997; Jackson *et al.*, 2001) allows for the unprecedented accumulation of reproductive-phase lobsters (Steneck, 2006) that fuels the settlement-driven (Palma *et al.*, 1999) population explosion of American lobsters today (Fig. 8.7B).

On Cashes Ledge, a small, shallow kelp-forested ledge 80 km offshore in the Gulf of Maine, a relict population of large predatory finfishes persists (Steneck & Carlton, 2001). There the dominant predators are cod (*Gadus morhua*), wolfish (*Anarhichas lupus*), and large cunner. Interestingly, the guild of small predatory fishes such as sculpins, shannies, and rock gunnels are rare at offshore sites where large predators persist, consistent with the idea that they too were food for large apex predators such as cod (Fig. 8.12A–C; labelled 'offshore'). When early benthic phase lobsters were tethered at Cashes Ledge, they were not attacked (R. Wahle & R. Steneck unpublished data), but the attack rate increased with size of tethered lobsters at this offshore site (Steneck, 1997; Fig. 8.12A; labelled 'offshore'). This trend suggests that predatory fish forage optimally, seeking the greatest energy value per attack. They do not attack small lobsters because their food value is not worth the effort. Instead the moderately large predators (40–55 cm; Fig. 8.12B) eat larger size classes at increasing frequency, and the largest tethered size class (70–78 mm CL; Steneck, 1997) was attacked at the highest rate. Thus there exist entirely different size-dependent survivorship trajectories resulting from differences in the ecological importance of predation early in the life of lobsters (Fig. 8.12C). Inshore, where attacks by large predators are rare, high mortality rates are limited to the time of settlement. In contrast, where large predators persist today (e.g. 'offshore', Fig. 8.12A), early post-settlement mortality is low but it increases with size and thus remains an important agent of mortality (Fig. 8.12B) and survival (Fig. 8.12C) for a protracted period of time.

8.3.3 Ghosts of predators past: a top-down to bottom-up transition

> 'Next to man with his traps, the codfish is probably the most destructive enemy of the lobster, for it not only takes in the soft and hard shell animals alike up to 8 inches or more in length, but is very partial to the young from 2 to 4 inches long.' – Herrick, 1909.

Demographically important changes in natural mortality and ecosystem structure and function have occurred at an accelerating rate in recent years (Steneck *et al.*, 2004). Rapidly changing ecosystems can change the recruitment potential and the predation potential of the benthos (*sensu* Steneck & Dethier, 1994) such that the present is neither indicative of distant past or future ecosystem states.

The American lobster is endemic to the western North Atlantic where it evolved under intense predation from large predatory ground fish such as cod (Steneck, 1997; Steneck & Carlton, 2001; Steneck *et al.*, 2004). Evidence for this comes from archaeological midden deposits that indicate that cod and other large predatory ground fish dominated coastal zones for thousands of years to as recently as the last half century (Jackson *et al.*, 2001; Steneck *et al.*, 2002, 2004; Lotze & Milewski, 2004). Significantly, while cod bones comprise as much as 85% of the bone mass of some coastal Indian middens (Steneck, 1997), no lobster or crab exoskeletons have ever been found (Spiess & Lewis, 2001; Lotze & Milewski, 2004; Steneck *et al.*, 2004). Because lobsters produce massive exoskeletons when they are large, and large decapods including lobsters have an impressive fossil record (Feldman *et al.*, 1977; Bishop, 1986), had they been abundant and harvested, some should have been preserved in middens, as did happen with such chronically poorly-preserved invertebrates as sea urchins (Steneck *et al.*, 2004).

When cod were abundant in coastal zones, lobsters were often found in their stomachs (e.g. Herrick, 1909 quotation above). The cod that were abundant in coastal zones of Maine for thousands of years (4500–500 years before present, Steneck *et al.*, 2004) were large. Their reconstructed size averaged about one metre in length (Jackson *et al.*, 2001; Fig. 8.12B). At a unique offshore site in the Gulf of Maine where large ground fish persisted through the 1980s (Witman & Sebens, 1992), they were shown to attack the largest size class of tethered lobsters (70–78 mm CL) at the highest frequency, choosing to ignore the smallest lobsters (30–38 mm CL) (Steneck, 1997; Fig. 8.12A, see ascending curve labelled ‘offshore’). This result contrasted with the attack rate on tethered lobsters in coastal zones where only the smallest size class was attacked at high frequency (Wahle & Steneck, 1992; Steneck, 1997; Fig. 8.12A see descending curve labelled ‘inshore’).

The abundance of large coastal predatory finfish probably maintained high rates of natural mortality among larger pre-harvestable and harvest-sized lobsters (Fig 8.12B labelled ‘pristine’). The ‘bust’ period, when lobster stocks in Maine collapsed between 1920–1940 (Acheson & Steneck, 1997) may have resulted from the combined effects of the harvesting of large lobsters (i.e. those immune to even the largest predators) and consumption by predators of most smaller lobsters at or below harvestable size (Steneck, 1997; Fig 8.12B, C ‘pristine’). Large predatory ground fish were shown to have been abundant in Maine’s coastal zone through the 1920s (Rich, 1929), but they were rapidly extirpated from nearshore areas during the 1930s when cod and haddock spawning stocks were targeted (Ames, 2004). In 1939, Maine’s Department of Sea and Shore Fisheries declared that coastal ground fish stocks ‘have been depleted’ (Steneck, 1997). Immediately following the extirpation of coastal ground fish stocks, landings increased rapidly to a new high plateau (Steneck, 1997, 2006, Fig. 8.7), perhaps due to release from demographic control by predators. Thus predator-induced mortality has probably declined significantly over the past several decades due to the decline of predator abundance and size (Fig. 8.12B) and as a result only a narrow range of small lobsters remain vulnerable to predators today (Fig. 8.12 A–C).

As ‘top-down’ (*sensu* Power, 1992) forces such as predation lose control in regulating lobster populations in coastal habitats, ‘bottom-up’ forces such as settlement-driven demography (e.g. Palma *et al.*, 1999) probably have become more important (Steneck & Sala, 2005). This represents a fundamental change in how coastal ecosystems are structured, but more importantly, how they function. Predator loss may help explain why this species remains so resilient to fishing pressure. American and probably the other clawed lobsters of the North Atlantic, evolved in an environment of high predator-mediated adolescent and adult mortality. The persistence of *H. americanus* and its ability to thrive today, even under intense fishing pressure, may result from its highly efficient biology having a higher than average per egg survival (Wahle,

2003) and lower than average post-settlement mortality (Palma *et al.*, 1998).

The loss of large predatory finfish is not restricted to the Gulf of Maine. Apex predators have been extirpated globally (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Myers & Worm, 2003). Given the susceptibility of large, slow, clawed lobsters, their evolution of shelter-seeking behaviour is not surprising. Their reproductive efficiency and relatively short larval life may reflect traits that succeeded over evolutionary time under conditions of high adult predator-induced mortality rates. This pressure has been relaxed due to overfishing of predators (Steneck *et al.*, 2002; Steneck & Sala, 2005) perhaps resulting in a world with a significantly greater carrying capacity (Fig. 8.12C) than had existed in the past. This may help explain why these species have either persisted (*H. gammarus*, Fig. 8.7B) or even thrived (*H. americanus* and *N. norvegicus*, Fig. 8.7B) in recent years despite decades of intense fishing on them.

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Chapter 9
Homarus Species

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9.1 Introduction

Two very similar species are the only representatives in the genus *Homarus* (Family Nephropidae). They are intrinsically interesting as model systems in many biological fields, play important ecological roles, and are commercially important. *Homarus* may be among the most-studied invertebrate genera on the planet. Both species are large and long-lived, exhibit complex courtship and parental care behaviour and are quite aggressive. Much of the life history has been well studied but many ecological details are missing. Despite their commercial importance, much remains to be learned in order to manage the intensively fished stocks. In this chapter, we provide an overview of the life history characteristics of *H. gammarus* and *H. americanus*, review the ecology of predation and disease, and then examine population dynamics, fisheries, and management. There are two extensive monographs on *H. americanus*, one a century old but still useful (Herrick, 1895), the second is a very thorough treatment of all aspects of its biology (Factor, 1995). In many respects the two species we consider in this chapter are very similar. Our intention here is not an in-depth review, but an update on issues of current importance.

9.2 Overview of the species

Lobsters of the genus *Homarus* are found only in the North Atlantic Ocean, where they form the basis of important fisheries. *Homarus americanus*, found on the western side of the Atlantic, ranges from Labrador to North Carolina. *Homarus gammarus*, in the eastern Atlantic, ranges from north of the Arctic Circle in Norway to Morocco, including the Mediterranean and the United Kingdom. They are members of the family Nephropidae, which emerged in the mid-Jurassic (Williams, 1995), perhaps 150 million years ago. Williams (1995) speculated that the two species separated during the Pleistocene. *H. americanus* and *H. gammarus* are distinguished only by colour and a ventral tooth on the rostrum, present in *H. americanus* but absent in *H. gammarus*. They can be distinguished genetically but the differences between the species are slight (Williams, 1995; Tam & Kornfield, 1998; Ulrich *et al*., 2001). Tam & Kornfield's (1998) molecular data suggest that *Homarus* and *Nephrops* are closely related, and are distant from *Homarinus*. *Homarinus capensis*, a little-known and rare species found in South Africa was placed in the genus *Homarus* until Kornfield *et al.* (1995) erected the new genus on the basis of distinct morphology and molecular genetics.

Homarus are found primarily from the shallow sub-tidal region to water depths of 50 m or more. The American lobster, *Homarus americanus*, lives in a wide variety of habitats almost always characterised by the availability of shelter. Rocky substrate is the most common habitat, but clawed lobsters may burrow in cohesive mud or dig bowl-like depressions in sand. *Homarus americanus* is found to depths of 700 m at the continental slope where it inhabits burrows in the walls of submarine canyons. Thus habitat architecture is important to *Homarus*, and shelter choice changes over the life cycle.

Both species of *Homarus* support valuable commercial fisheries. Overall landings have shown a remarkable and as yet unexplained increase since the 1970s. *Homarus gammarus* supports a much smaller trap fishery. However, it too has seen an increase in catches since the late 1970s (see Section 9.7.2).

9.3 Life-history characteristics

9.3.1 Life cycle

The basic facts of the life cycle of both species of *Homarus* appear identical. Three larval instars and one postlarval instar are pelagic. Following settlement of the postlarva, the juvenile stage lasts in the order of 3–5 years and includes sizes from about 5 mm carapace length (CL) to size at maturity, which varies with location and temperature. Adult males are larger than adult females. Allometric growth of the claws (male claws are proportionately larger) and abdomen (female abdomens are proportionately wider) distinguish male from female. Adults are long-lived and iteroparous, capable of reproducing many times. For several years, considerable discussion swirled around the identification and naming of stages of the life cycle (Lavalli & Lawton, 1996; Waddy & Aiken, 2000). Stage- or age-based diagrams used to structure population models are straightforward and useful, as for example, used by Incze *et al.* (2003) and illustrated later in this chapter. Below we expand on this brief description of the life cycle beginning with courtship.

Courtship and mating are complex. As described by Atema and co-workers, (reviewed by Atema & Voigt, 1995) males compete for females by establishing a mating shelter. Larger, dominant males are more successful in obtaining mating burrows and in courting more females, thus this is a polygynous mating system. Females approaching moult assess the males, probably communicating chemically, and choose to cohabit with a male for one to several days prior to moulting. Mating usually takes place shortly after the female moults; the male deposits a spermatophore internally in the seminal receptacle of the female. Sperm may be stored for several years (Talbot & Helluy, 1995). There is a period of mate guarding after copulation. Females may mate between moults, while hard shelled (Dunham & Skinner-Jacobs, 1978; Waddy & Aiken, 1990), particularly if they are not inseminated. Females may occasionally mate with more than one male and multiple paternity in a brood has been identified genetically (Nelson & Hedgecock, 1977; Jones *et al.*, 2003).

Fertilisation is external. As eggs are extruded from the oviduct they pass over the seminal receptacle and stored sperm is released through paired grooves (Talbot & Helluy, 1995; Aiken *et al.*, 2004). Females carry fertilised eggs cemented to the pleopods of the abdominal segments for nine to eleven months. The eggs are large relative to those of many other crustaceans. Large eggs, combined with a relatively small clutch size and a significant level of parental care (the eggs being brooded by the female for 9–11 months) are uncharacteristic traits for marine crustaceans.

The eggs, which are generally extruded in the summer or fall, hatch in the spring, producing a prelarva which rapidly moults into the first larval stage (Talbot & Helluy, 1995). Three pelagic zoeal stages follow, lasting in total, two weeks to two months, depending upon temperature (MacKenzie, 1988; Ennis, 1995). Metamorphosis to a lobster-like body plan occurs at the moult from stage III to postlarva. As in other complex life cycles, the physical metamorphosis is accompanied by behavioural and habitat changes. The postlarva remains pelagic but swims forward using its pleopods; this is the only life stage in which the primary propulsion comes from these appendages. Two to four days after metamorphosis, bottom-seeking behaviour appears, and the postlarva, upon discovering appropriate nursery habitat, makes the transition from a pelagic to a benthic environment and becomes a permanent resident of the substratum (Cobb *et al.*, 1989). The newly-settled young of the year of *H. americanus* are quite habitat-specific and are relatively easy to capture (Wahle & Steneck, 1992) using airlift samplers. On the other hand, despite extensive efforts, *H. gammarus* young of the year have proved elusive. It is not clear whether they are simply uncommon, only infrequently settle in numbers large enough to detect, or if they are yet to be found in unexpected habitats (van der Meeren, 2003).

The juvenile phase of the life cycle is characterised by an early shelter-dependent period in which the lobster emerges infrequently from its burrow, followed by an increase in range of movement and habitat choice. While shelter-dependent, the nature of food consumed has been debated. Clearly the smallest benthic juveniles are capable of capturing, consuming, and existing on planktonic organisms (reviewed by Lawton & Lavalli, 1995). However, a study of the ontogeny of diet choice in *H. americanus* by Sainte-Marie & Chabot (2002) found no planktonic organisms in the stomach contents of even the smallest (7 mm CL) field-captured juveniles. Instead, soft tissue in the stomach contents suggested scavenging was a primary feeding choice. The transition from planktonic to benthic habitat thus requires a change in diet. A temporary slowing of growth rate accompanies this: postlarvae captured in the plankton had higher RNA : DNA ratios (a measure of recent growth) than did recently-settled young of the year captured on the bottom (James-Pirri & Cobb, 1997). The newly-settled lobsters may spend more time in shelter avoiding predators, than out and foraging, i.e. trading the risk of predation off against the risk of slower growth.

Smaller lobsters are more susceptible to predation and consequently spend more time in shelter when at risk (Wahle, 1992a). Larger juveniles and adult lobsters are increasingly more mobile, less at risk of predation and less dependent on shelter. The rate of growth, and thus the time spent in each of the life stages, is dependent on many factors, and the time from egg to maturity is highly variable.

9.3.2 Growth

The patterns of growth and the mechanisms controlling moult increment and intermoult interval have been studied intensively and reviewed in recent years (Fogarty, 1995; Waddy *et al.*, 1995; Chang *et al.*, 2001; Hartnoll, 2001). The effects of environmental factors such as temperature and food on growth rates are well known, and many of the endocrine mechanisms that control the moult cycle have been worked out. Age determination still remains elusive, however. Many early studies described growth using the von Bertalanffy function; however empirical models that incorporate the probability of moulting and the size increase at moulting are perhaps more realistic. This section provides a brief overview with emphasis on recent advances.

The endocrine mechanisms controlling the moult cycle are complex. In the simplest terms, during postmoult and intermoult, glands of the eyestalk produce the peptides, moult inhibiting hormone (MIH) and crustacean hyperglycemic hormone (CHH) that regulate growth by suppressing the production of moulting hormone by the Y-organs, located in the thorax. As the titre of MIH drops at the end of the intermoult period, the action of the eyestalk hormone rises, the titres of another hormone (methyl farnesoate, MF) rise, and the moult-promoting Y-organs produce ecdysteroids. These put in motion a complex and lengthy physiological process starting with premoult and concluding in ecdysis. Immediately after ecdysis, the haemolymph titres of ecdysteroids drop precipitously. The ecdysteroids and methyl farnesoate appear to work in tandem to influence moult interval, allometric growth, and vitellogenesis. Major changes over the period of the moult cycle in protein synthesis, structure of the integument, biochemistry, and behaviour are orchestrated by these hormonal changes (Chang, 1995; Waddy *et al.*, 1995; Chang *et al.*, 2001).

The stages of the moult cycle can be identified fairly crudely by rigidity of the carapace, or in more detail by changes in the morphology of the epidermis and setae of the pleopods. Waddy *et al.* (1995) provide a thorough review of moult stages and their detection in *Homarus.*

Growth rate is usually expressed as an increase in size over time. In arthropods, a size increase occurs only at the time of ecdysis. The increment and the interval between moults have been estimated from observations of lobsters reared in laboratory and tag–recapture studies or caging experiments in the field. Most studies find a close correlation between premoult and postmoult size regardless of location or environmental condition. Fogarty (1995) lists parameters of the Hiatt growth equation for *H. americanus* from many locations;

the slope of the regression is relatively invariant, ranging from 0.91 to 1.14. The growth increment, when expressed as a percentage of premoult CL, ranges between 10–20% (e.g. Wilder, 1963; Comeau & Savoie, 2001).

Injury such as limb loss or tagging may affect moult increment. Autotomy is frequent in crustaceans (Juanes & Smith, 1995) and *Homarus* is no exception. Autotomy is an energetic cost to the individual, and results in a slowing of growth. In *Homarus americanus*, Cheng and Chang (1993) found that autotomy decreased moult increment by 30–40%, and that moult interval was increased or decreased, according to when in the moult cycle the limb loss occurred. Even the injury associated with tagging can impact moult increment; *H. americanus* marked with streamer tags during premoult had smaller increments than those tagged in post- or intermoult (Comeau & Savoie, 2001).

More labile, and thus contributing more to the variability in growth rate, is the time interval between moults. It is often estimated from knowledge of the proportion of tagged individuals moulting in a year, using Hancock and Edwards' (1967) anniversary method. Frequency of moulting is influenced primarily by water temperature and season (Conan, 1985; Aiken & Waddy, 1995; Waddy *et al.*, 1995) but other factors also influence intermoult interval, such as nutrition, stress, and social conditions.

The time interval between moults increases with size, larger lobsters moult less frequently than do smaller ones. Combining a declining moult frequency and a relatively stable proportional increment produces the characteristic stepped growth function (Fig. 9.1) of crustaceans, here illustrated by data from individuals reared from the egg in captivity (Hughes & Matthiessen, 1962). Variability in both increment and interval is easily visible. Caddy (2003) suggests that moulting schedules might be modelled by incrementing the intermoult intervals by a constant proportion at each moult. Successive intermoult intervals would then follow a geometric progression represented as: r, ra^1, ra^2, ra^3, . . . , ra^m. Caddy found this progression to be a good fit with four growth data sets from *H. americanus*. The Hiatt equation also expands to a geometric progression and combining the two into a four-parameter growth function may provide a reasonable representation of growth in instances where data on moult frequency are of sufficient quality (Chapter 1).

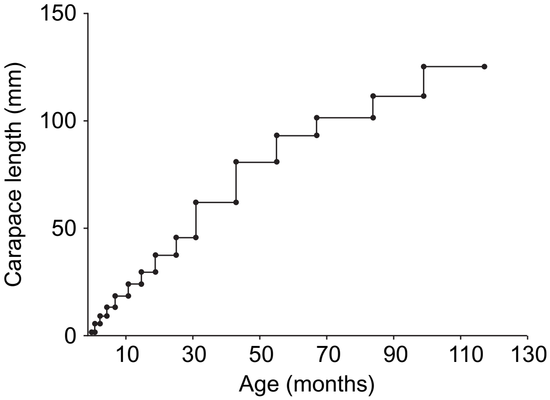

Fig. 9.1 Characteristic pattern of size increase combining moult interval and moult increment of *Homarus americanus*. Lobsters were grown in a hatchery from larval stages. Note the variability in both increment and interval. At greater age, N was very small. (Data from Hughes & Matthiessen, 1962.)

Many environmental factors influence the progression of the moult cycle, and thus growth rate. Of these, temperature is the most important. Between 8–25°C there is a proportional relationship between temperature and growth: metabolic rates are faster and growth rates higher at warmer temperatures (Waddy *et al.*, 1995). Growth rates measured in the field at about the same point in the range but where ambient temperatures differ provide a good example. *Homarus americanus* in the warmer waters of the southern Gulf of St Lawrence have higher growth rates than do those from the nearby but colder Bay of Fundy (Campbell, 1983; Comeau & Savoie, 2001). Wahle *et al.* (2001) grew young of the year (YoY) *H. americanus* in field cages at two sites in the Gulf of Maine separated by 10 km. Mean temperature differed by 2°C, and the YoY at the warmer site were, on average, 6 mm CL larger at the end of three months. In southern New England, YoY lobsters that settle earlier in the season are larger at each instar and have a higher growth rate than those that settle at the end of the season (James-Pirri *et al.*, 1998). This must be due, at least in part, to the accumulation of more growing degree-days by the earlier settlers. These authors surmised that the early settlers, which are 30–50% larger by the end of the first growing season, are likely to have a lower risk of predation and perhaps overwinter more successfully. Simulated seasonal changes in temperature are associated with changes in metabolic rate and electron transport system activity in *H. gammarus* (Tully *et al.*, 2000). There appeared to be no metabolic compensation for temperature change.

9.3.3 Age

Determining the age of a lobster seems a hopeless task since all hard parts are shed at each moult, making impossible the use of techniques used in vertebrates. In *Homarus*, age may be estimated by cohort analysis for the first year or two after settlement (e.g. Wahle *et al.*, 2004), but after that, variation in growth rate obscures cohort patterns. Size-at-age relationships can be generated from culture operations, or from tag and recapture growth data, but for various reasons these are quite variable and less than fully satisfactory. An alternative to deriving age from size is needed, although size- or stage-based population models are now used frequently. The ‘age pigment’, lipofuscin, has long been known to be the result of cellular processes combating free radicals. It accumulates in all cells at a rate determined by metabolic rate of the individual and is very stable after formation. Cells in the nervous system are long-lived and accumulation of lipofuscin in them gives an estimate of chronological age. The potential for age determination using this compound in crustaceans has only recently been given much attention.

Sheehy (1989, 1990) noted the occurrence of lipofuscin in a wide variety of crustaceans. Studies on *H. americanus* and *H. gammarus* both confirm its potential and suggest caution in its use. *Homarus gammarus* tagged and released into the wild at 3 months of age were recaptured 5–9 years later. Body size bore no significant relationship to the known age at capture, but the amount of lipofuscin in the medulla terminalis was significantly correlated ($r = 0.64$) with chronological age. In this study (Sheehy *et al.*, 1996) 43% of the lobsters in a relatively narrow age window were correctly classified to age within one year. A later study with wild (untagged) *H. gammarus* indicated that larger lobsters might attain considerable age (maximum 42 years in males and 74 years in females). Age at size was far from constant; the minimum legal size contained at least seven year classes (Sheehy *et al.*, 1999). In *H. americanus* reared for 4–27 months at a constant warm temperature in the laboratory, carapace length-corrected lipofuscin accumulation was strongly correlated with chronological age (Wahle *et al.*, 1996).

The variability in age estimates, while considerably less than age-at-length estimates, is large. This may be explained in part by the physiological nature of lipofuscin accumulation as a metabolic by-product. Lobsters raised for 22 months at three seasonally varying temperature regimes showed seasonal oscillations in accumulation of lipofuscin (Tully *et al.*, 2000). The accumulation of lipofuscin was related to the number of degree-days to which the lobsters were exposed. The direct relationship between temperature and metabolic rate measured by Tully *et al.* (2000) in *H. gammarus* suggests that the thermal history of an individual must be accounted for in order to resolve age classes with the best accuracy possible. Correcting for mean annual temperature variation experienced by individuals did allow better identification of year classes (Sheehy & Bannister, 2002). Lipofuscin accumulation was highly sensitive to small differences in temperature. A fundamental assumption then is, that in order to know an individual’s thermal history, it must be resident in one location, and not migratory. Age determination by measurement of lipofuscin accumulation may work better in *H. gammarus* than in *H. americanus*, as the latter species appears to be more likely to move long distances, particularly after maturity. Short-lived and warm-water species (the spiny lobster, *Panulirus cygnus* (Sheehy *et al.*, 1998) and the blue crab *Callinectes sapidus* (Ju *et al.*, 2003) have shown some success in the use of lipofuscin for age estimation. Lobsters released from a hatchery in Norway showed a linear and close ($r^2 = 0.88$) relationship between lipofuscin accumulation and age (Uglem *et al.*, 2005). However, age and size were also closely linked ($r^2 = 0.78$) suggesting in this case that lipofuscin data would add little to accurate age estimation. Environmental variables other than temperature may also play a role. Antioxidants in the diet of the Norway lobster (*Nephrops norvegicus*) significantly reduced the accumulation of lipofuscin, thus influencing age estimates (Castro *et al.*, 2002). It probably is safe to say that this apparently promising technique for age determination in crustaceans must be further refined and standardised before it becomes a routine member of the fisheries biologist's tool kit.

9.3.4 Maturation

The simplest measures of maturity are the presence of eggs on the abdomen of a female and sperm in the vas deferens of a male. Allometric changes in abdomen width and claw dimensions have also been used to determine size at maturity. However, the gradual nature of the allometric change makes it difficult to be precise in assigning age and size at maturity for individuals (Conan *et al.*, 2001). Size and age at maturity are dependent on summer water temperature and vary across the geographic range of the lobster. In *Homarus americanus* females, 50% of the population matures at 70 mm CL or less in southern New England waters, but at over 100 mm CL in the colder Bay of Fundy (Waddy *et al.*, 1995). The effect of temperature on size at maturity is made clear where warmer summer temperatures prevail near areas of cooler water. For example, Estrella and McKiernan (1989, in Waddy *et al.*, 1995) found that size at female maturity varied by 21 mm CL within one-half a degree of latitude. Lobsters in warm Buzzards Bay waters were much smaller when mature than those in the colder temperatures off Cape Cod. The range of size at maturity of female *H. gammarus* is less well-documented, but the size at which 50% of the females bear eggs ranges from 80–140 mm CL, depending on site (Fig. 9.2) (Free *et al.*, 1992; Tully *et al.*, 2001; Lizárraga-Cubedo *et al.*, 2003). Mortality imposed by fishing may be a selective pressure causing maturity at a smaller size (Landers, 2001) in *H. americanus* in Long Island Sound, but there is little other evidence to support this. The same is probably true for *H. gammarus.*

Maturity in male lobsters is less obvious, and it is important to distinguish between gonadal maturity and functional maturity. Male *H. americanus* have sperm present in the vas deferens when they are as small as 45–50 mm CL apparently with little effect of location (Krouse, 1973; Briggs & Mushacke, 1980; Conan *et al.*, 2001). Similar studies are not available for *H. gammarus*. Gonadal maturity and functional maturity are not equivalent, and it is not likely that small lobsters are capable of mating with large females (Templeman, 1934) because of the lobster's courtship behaviour. Gosselin *et al.* (2003) showed that the amount of sperm deposited in a female *H. americanus* varies according to the size of the female (suggesting that males gauge the amount of sperm transferred) and that larger males transfer more sperm than do smaller ones. In those areas where the fishery removes nearly all the larger males while protecting large females (through maximum size restrictions and v-notching), there may be reason for concern about the potential for sperm limitation.

Once female *Homarus* are mature, they generally produce a clutch of eggs every second year. The reproductive schedule has best been worked out for *H. americanus*; considerably less is known about the reproductive cycles of *H. gammarus* (van der Meeren, 2003). In general, moulting and spawning occur in alternate years for females less than 120 mm CL (Waddy *et al.*, 1995). Temperature and age may alter the cycle. Small females inhabiting the warmest waters may moult and spawn the same summer (Waddy *et al.*, 1995; Comeau & Savoie, 2002) and larger, older females (>120 mm CL) exhibit a three year cycle, spawning in two consecutive years then moulting in the third (Fig. 9.3) The complexity and variability in the cycles of female reproduction may make it difficult to properly construct life cycle diagrams for *Homarus*; matrix modellers, beware.

9.3.5 Clutch size and fecundity

The number of eggs carried by a female at any one time (clutch size) varies with size of the individual, and lifetime egg production (fecundity) is the sum of eggs produced over all clutches. Clutch size varies with female size; most reports indicate a power relationship between the two. Tully *et al.* (2001) described the carapace length–clutch size

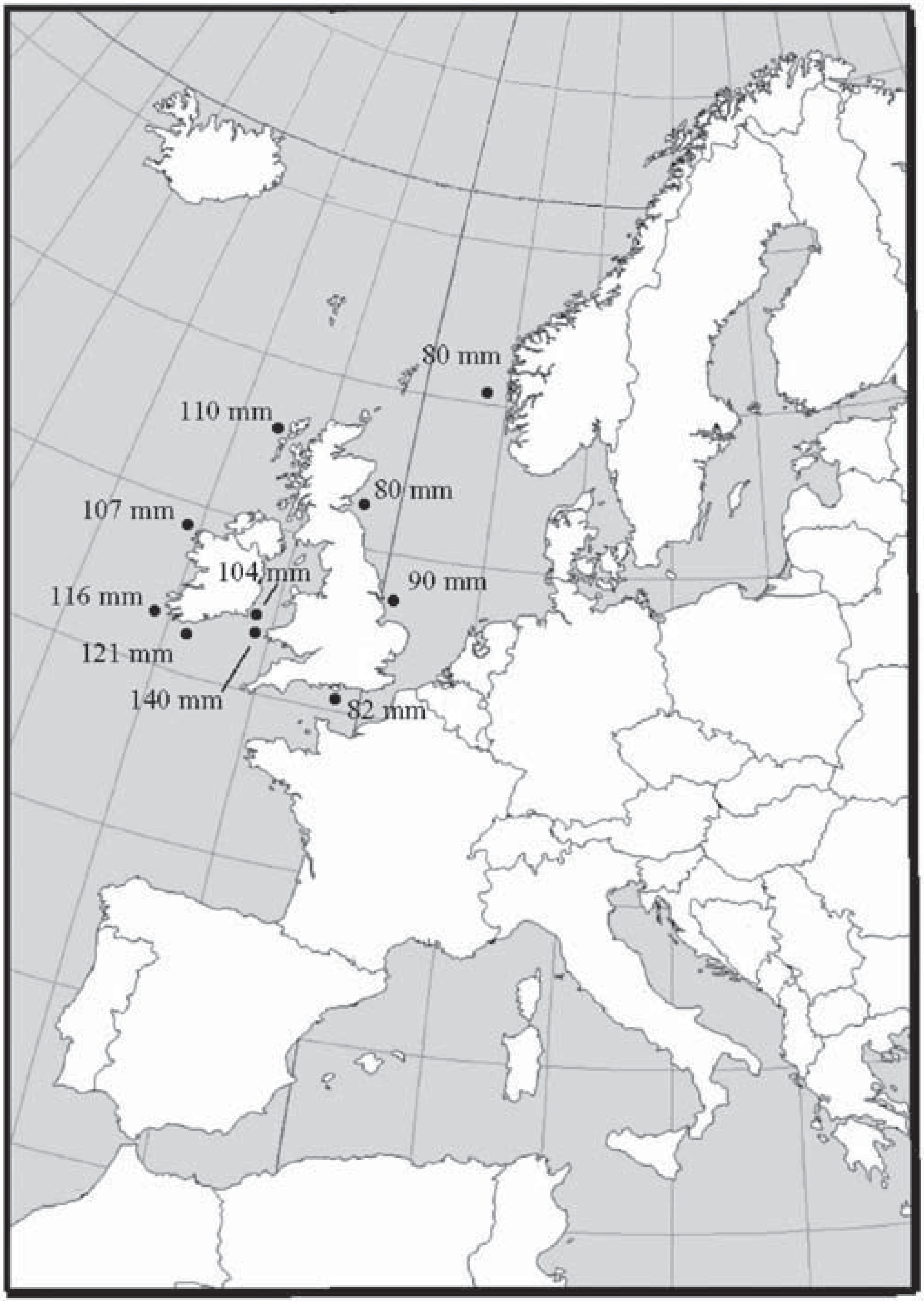

Fig. 9.2 Geographic variation in size (mm carapace length) at maturity for *Homarus gammarus*. (Data from Free *et al.*, 1992; Lizárraga-Cubedo *et al.*, 2003; and Tully *et al.*, 2001.)

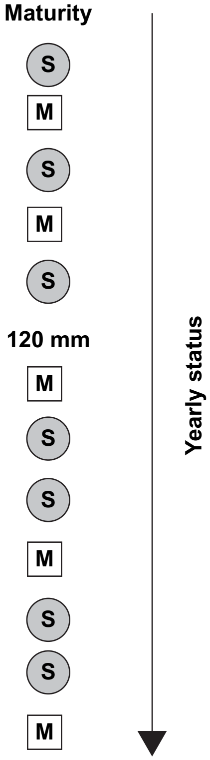

Fig. 9.3 Reproductive cycle of female American lobster, *Homarus americanus*. The annual status alternates between spawning (S) and moulting (M) until a size of 120 mm CL. Females larger than 120 mm CL moult every third year and spawn in the two intervening years. This is the basic theme, variations abound. (For greater detail see Waddy *et al.*, 1995, from which data for this figure were taken.)

relationship of *H. gammarus* in Ireland as CS = $0.0044 \cdot \mathrm{CL}^{3.16}$. They compared clutch size measurements for *H. americanus* with those of *H. gammarus*, finding that *H. americanus* clutches were larger at all size classes of females.

The relationship between clutch size and carapace length may not vary greatly over the range of *H. gammarus* (Tully *et al.*, 2001; Lizáraga-Cubedo *et al.*, 2003). However, regional differences are recognised in *H. americanus* (Estrella & Cadrin, 1995; Fogarty, 1995). Regional differences in allometric growth of the abdomen of *H. americanus* suggest that clutch size is constrained by brooding capacity, and that fecundity estimates for management purposes should be calculated on a regional basis (MacCormack & DeMont, 2003).

Lifetime fecundity in an iteroparous species is the sum of all the eggs produced. If a female carries 15 clutches in a lifetime (Cobb *et al.*, 1997), then a female *H. americanus* that lives out her full reproductive life expectancy might produce 750 000 eggs. However, since the fishery removes so many individuals shortly after maturity, *H. americanus* may in fact be a relatively short-lived and functionally semelparous species (Fogarty & Gendron, 2004). The potential lifetime fecundity is not likely to be reached by any individual.

Egg loss during incubation can impose significant loss (mortality) for many decapods. Reported decreases in clutch size from the time of spawning to hatching are varied. *Nephrops norvegicus* from the Bay of Biscay suffer a 40–50% loss during the incubation period (Morizur, 1981). The swimming crab, *Necora puber*, loses 14–19% of the clutch (Norman & Jones, 1993). Nemertean egg predators and fungal infections are the cause of loss in some species. In *Homarus americanus*, losses of 15–50% of the egg mass during incubation have been reported (Perkins, 1971; Campbell & Brattey, 1986; Savoie & Maynard, 1991). Handling (e.g. capture and release from a trap) may also cause loss (Talbot & Helluy, 1995). Egg diameter increases with development (Tully *et al.*, 2001) thus the loss of eggs may be less visible due to an increase in volume of the clutch. If egg counts for clutch-size estimates are to be made, the magnitude of egg loss in *Homarus* suggests that the counts be done at one stage of egg development only, probably only shortly before hatching.

9.4 Larval dynamics

Lobster populations in equilibrium gain individuals through larval recruitment and immigration while losing them to emigration and mortality. Larval supply is a critical component for understanding the dynamics of lobster populations. We are beginning to understand some of the complex relationships among advection, larval abundance, larval behaviour, and the early benthic stages. A considerable amount of work addresses abundance, distribution and transport of *Homarus americanus* larvae. However, similar work on larvae of *H. gammarus* is scarce, perhaps due to the low abundance of planktonic larvae (Nichols & Lawton, 1978). In both species, the larvae generally are found near the surface, but sampling only the top half-metre of the water column does not adequately represent the whole population (Harding *et al.*, 1987; Nichols & Lovewell, 1987). In both species, diel vertical migration has been described, which will complicate abundance estimates. In the following section we focus on *H. americanus* since so little is known of the dynamics of larval abundance and delivery for *H. gammarus*.

In an early speculation on advection of larval *H. americanus*, Rogers *et al.* (1968) suggested, from drift bottle data, that surface residual drift would not be sufficient to carry passive larvae from offshore to inshore lobster grounds, in southern New England. Later, a physical model coupled with behavioural data on swimming suggested that larval subsidy to inshore populations was possible (Katz *et al.*, 1994).

When the entire Gulf of Maine was considered in a coupled physical–biological model (Incze & Naimie, 2000), it became clear that location and timing of larval release is of great importance to the trajectory taken and consequently to arrival locations. Timing (early, mid- or late season) affected both water temperature (and thus larval development time) and the residual current velocities. The net alongshore advection is greatest in the north and east of the Gulf suggesting that many of the larvae hatching there are exported. This may explain the near-absence of settling-stage lobsters and lower abundance of juveniles and adult lobsters along the farthest north and east part of the coast of Maine (Palma *et al.*, 1999). The model suggested transport distances (from hatch location to settlement site) may exceed 200 km and that larvae in this coastal transport are unlikely, in most circumstances, to be repopulating the region from which they originated. The sea breeze blowing shoreward on an almost daily basis may be important in transporting final stage larvae and postlarvae into shallow cobble nurseries. In particular, advection due to unpredictable winds, coupled with the complexity of flow around headlands and within bays (Hudon & Fradette, 1993; Incze & Naimie, 2000) may play a role in retention in very local areas. These results have importance for understanding the relationship between stock and recruitment and metapopulations in the Gulf of Maine. Molecular genetics might cast some light on the connections between source and sink in the Gulf of Maine. It might also be interesting to speculate on what the topography of the Gulf of Maine was like as few as 10 000 years ago, when sea levels stood as much as 130 m lower (Emery *et al.*, 1988). Behavioural strategies selected then for larval retention or dispersal may not be adaptive now.

A 20-year data set on pelagic abundance of *H. americanus* larvae and postlarvae taken by Scarratt (1964) fifty years ago in the southern Gulf of St Lawrence was pivotal in provoking research into the mechanisms linking larval settlement and recruitment to the fishable stock. At the time, Scarratt (1973a) concluded that there was no relationship between postlarval abundance and stock size. Fogarty and Idoine (1986) revisited the data set, pointing out that it makes biological sense to force the curve through the origin: where no postlarvae exist, there would be no adults, assuming a closed population. Forcing the curve through the origin results in an asymptotic curve (Fig. 9.4) with a very steep rising limb. The assumption of a closed population has never been rigorously tested (Wahle, 2003), although there is evidence of reduced advection to the area.

A similar relationship was described between egg production and recruitment to the fishery in Arnold's Cove, Newfoundland (Ennis & Fogarty, 1997). An asymptotic curve suggests that somewhere in the life history between the pelagic postlarval stage and the fishable stock there is a strong density-dependent effect (Fogarty & Idoine, 1986). These compensatory stock–recruit relationships prompted much-needed research into the processes controlling abundance of early life-history stages.

There clearly is a relationship between the production of postlarvae (PL) and the abundance of newly-settled young of the year (Incze *et al.*, 1997). When postlarval production was calculated using moult stage and temperature-dependent growth rates, it accounted for up to 90% of the variation in YoY abundance. In a later study, Incze *et al.*

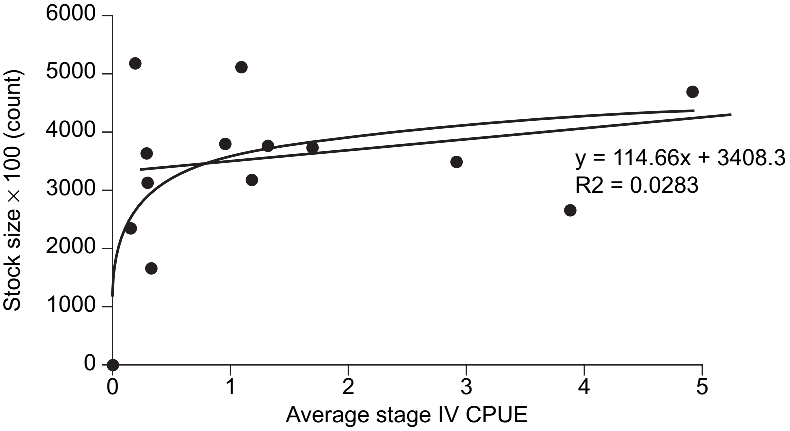

Fig. 9.4 Stock–recruitment relationship for *Homarus americanus* showing Scarratt's (1964, 1973a) data with a non-significant linear regression fitted to them. Using the same data, an asymptotic curve forced through the origin (Fogarty & Idoine, 1986) is superimposed.

(2000) again showed that postlarval supply was correlated with YoY recruitment. These authors discovered that advection shoreward accounts for the frequently observed higher density of YoY on the bottom than postlarvae at the surface. Only a very small proportion of postlarvae get off the advective conveyor belt (settle) at any given location, and that proportion is similar in high and low recruitment years (Incze *et al.*, 2000).

A clear understanding of the mechanisms affecting mortality rates from egg to maturity are of great importance to providing clear and appropriate management advice. This is difficult when variability in the system is great. Miller (1997) examined abundance of spawners, postlarvae, and recruits to the fishery in seven locations along the Nova Scotia coast, finding consistent spatial differences in productivity among the locations. Postlarval abundance, but not egg abundance, was correlated with recruits. More recent reports have emphasised the importance of settlement strength to recruitment.

Using thermally-corrected lipofuscin concentration to determine age and assign lobsters of a wide size range to age cohorts, Sheehy and Bannister (2002) showed that large differences in year-class strength could be demonstrated for *H. gammarus* in Bridlington Bay (UK). They also demonstrated that geographically-separated populations have different thermal histories, so must be treated separately. By examining wind field data for each year, Sheehy and Bannister (2002) concluded that years with greater onshore winds were positively correlated with year-class strength.

Year-class strength clearly varies in *H. americanus* as well. Wahle *et al.* (2004) used airlift sampling to develop a time series of density of newly-settled young of the year in Rhode Island and the Gulf of Maine (Fig. 9.5). Annual fluctuations in the settlement index were significantly correlated with the abundance of older juveniles present in the same area. Projections from the settlement index to fisheries landings were made, using a logistic growth model with a range of ages at recruitment to account for growth variability. It is not yet clear whether those projections will be borne out. The Bridlington Bay data (Sheehy & Bannister, 2002) suggests settlement year-class strength can be seen in the abundance of older year classes, but as yet the processes operating after juveniles leave nurseries are not well known, and decoupling may occur (Wahle *et al.*, 2004).

The stock–recruit relationship for *H. americanus* found by Fogarty and Idoine (1986) and Ennis and Fogarty (1997) provides a 'black box' implication of density-dependent population regulation, and the shape of the curve suggests strong resilience to exploitation. However, given the extent of larval drift described above, the necessary assumption of a closed system may not be tenable in other locations. It is possible that *H. americanus* consists of a number of spatially discrete populations, linked by dispersal processes, that is, a metapopulation. Katz *et al.* (1994) used a hydrodynamic

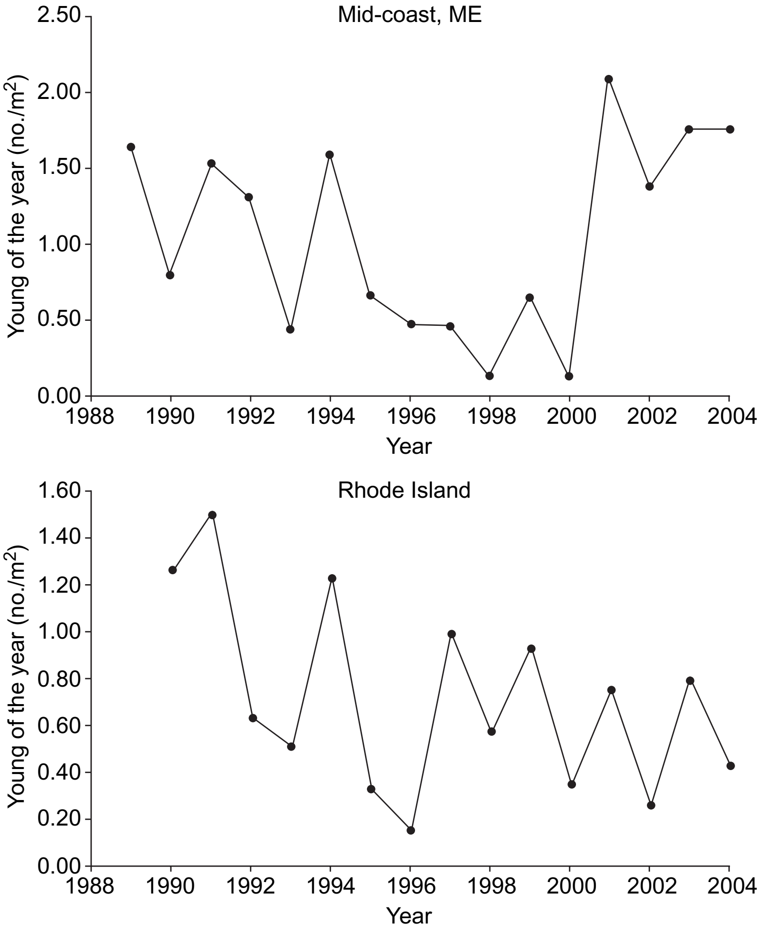

Fig. 9.5 Annual variation of abundance of young of the year *Homarus americanus* sampled in two areas: the Boothbay Harbor region, Maine (upper panel) and Rhode Island (lower panel), USA. (Data kindly provided by R.A. Wahle.)

model of surface drift combined with postlarval directional swimming to suggest the possibility that inshore stocks in southern New England may receive a larval subsidy from offshore populations. Adult migrations (Cooper & Uzmann, 1973; Fogarty, 1998) may also contribute significantly to the source–sink dynamics. Export from one subpopulation that subsidises another may contribute significant resilience to the sink population. If the source population is subject to lower fishing mortality while the sink population is heavily exploited, then higher fishing mortality rates can be supported in the sink population (Botsford & Fogarty, submitted). Fogarty (1998) modelled the situation in southern New England and concluded that as little as a 10% larval subsidy from offshore to inshore would suffice to maintain the inshore population at what would be otherwise unsustainable levels of F (fishing mortality rate).

The transition from planktonic to benthic environments after metamorphosis may be difficult. Norden (2003) tethered planktonic postlarvae of *H. americanus* at several depth intervals between the surface and a rocky bottom earlier demonstrated to be an appropriate nursery habitat. Mortality of swimming postlarvae near the bottom – and corresponding density of predatory fish – was much higher than near the surface. There does seem to be a gauntlet of predators to be run during the process of settlement, and that gauntlet seems to be concentrated in the metre or two above the bottom. This may explain the colouration of the postlarva, which is cryptic for bottom habitat but conspicuous at the surface. Switching diets may also present a challenge. Estimated nutritional status using RNA : DNA ratios showed newly-settled *Homarus americanus* to be significantly less well-nourished than those sampled in the plankton (James-Pirri & Cobb, 1997). Avoiding predators in the new environment may take precedence over feeding, or simply the transition to a new diet may take time. Settlement by a postlarva early in the season yields quite different growth results than settlement late in the season (James-Pirri *et al.*, 1998). Early settlers are 30–50% larger and two to three moults further developed by the end of the growing season than are the last postlarvae to settle. This may have profound consequences on subsequent growth and mortality rates.

Palma *et al.* (1999) pointed out the importance of spatial and temporal scales in studying settlement patterns. Newly-settled American lobsters were found in artificial collectors at shallow depths, but not at depths of 20 m or more. At the hundreds of km scale, settlement in the collectors was much lower to the east along the Maine coast, coinciding with lower larval densities there. Once settled, mortality of early juvenile *H. americanus* appears to be low compared to that of the rock crab, *Cancer irroratus* (Palma *et al.*, 1998). The processes controlling growth and survival in the early benthic phase have only recently begun to be investigated.

A goal of research on juvenile life stages is to determine if a functional relationship can be described between settlement and recruitment to the fishery. Incze *et al.* (2003) attempted this for one location in the Gulf of Maine. In the framework of a life-history model (Fig. 9.6) they asked whether the number of young of the year, coupled with knowledge of habitat requirements, the amount of habitat, and the estimated rate of settlement, can be scaled up to a much larger segment of the population. Current settlement rates, known habitat area, and estimated egg production were more than sufficient to explain fishery landings in Lincoln County, Maine. They estimated that larval mortality was <0.07 per day. Using a life-history approach may allow models to be built that will forecast future fishery landings. However, vital rates used in the model doubtless vary across the range of the lobster so results are likely to differ from location to location.

9.5 Population dynamics

Understanding the mechanisms underlying changes in population abundance, demographics, or structure are the essence of the discipline of ecology, and are equally important to resource managers and fishermen. Population dynamics of exploited

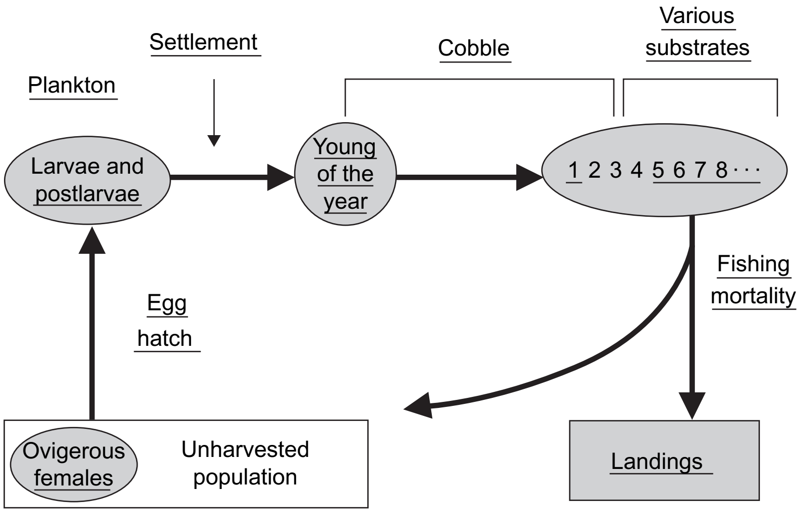

Fig. 9.6 Life-history model of *Homarus americanus* used to search for links between the early stages and subsequent landings. Numbers are the benthic stage, age in years. Underlined elements are associated with field data. (Slightly modified from Incze *et al.*, 2003.)

species are well studied because of the need to project yield and to regulate the activity of fishermen to ensure the resource is sustainable. The dynamics of *H. americanus* populations were the subject of a comprehensive review by Fogarty (1995). Many of the general conclusions and many of the types of models reviewed therein are surely applicable with only slight modification to *H. gammarus*. We intend to report primarily on some of the themes investigated in the last decade or so: advances in stock identification, larval supply, making links between early life history stages and recruitment, and metapopulation dynamics.

A candidate mechanism for population regulation in *H. americanus* is a demographic bottleneck. Caddy (1986) suggested the crevice-dwelling nature of lobsters is a critical issue in understanding mortality and recruitment. He pointed out that the fractal nature of the rocky habitat suggests that an obligate crevice-dweller will be faced with a decline in the number of crevices available to it as it grows. Using a combination of behavioural observations and modelling, Wahle (1992b) confirmed the constraints placed by shelter size on habitat choice in *H. americanus*. Caddy (1986) suggested that recruitment to the fishery is a function not only of the usual suspects (parental stock size, climate, predators, and competitors) but is also a function of the amount of habitat available at some stage (size class) prior to recruitment. If habitat is in short supply, a 'bottleneck' exists at a particular size class through which only a subset of the population can pass, thus controlling population density, size structure and perhaps other life-history characteristics. Stone crabs (*Menippe mercinaria*) appear to exhibit a demographic bottleneck (Beck, 1995, 1997).

The possibility of a demographic bottleneck at some point in the early benthic phase (5–40 mm CL) of *H. americanus* has been suggested from field data as well. Cobble habitat, preferred by juveniles, appeared to be in short supply at their study area on the coast of Maine (11% of all substrate types; Wahle & Steneck, 1991). Population densities of juvenile lobsters in cobble are variable but may be as high as nearly 7/m^2, suggesting habitat availability may be a limiting factor at this stage. Shelter use by smaller lobsters is reinforced by size-dependent risk of predation. Lobsters tethered in the field experienced much higher mortality if they were small or without shelter (Wahle & Steneck, 1992). In the laboratory, small lobsters responded to the presence or odour of a predatory fish by increasing time spent in shelter, while larger juvenile lobsters displayed aggression (Wahle, 1992b).

A combination of variations in postlarval supply, density-dependent mortality and emigration is responsible, at least in part, for differences in juvenile population density. Measurements of pelagic postlarval density on the upwind and downwind side of an island showed a 'supply shadow' of lower postlarval density on the downwind side of the island. Sampling newly-settled *H. americanus* using standardised cobble plots sited on either side of the island convinced Wahle and Incze (1997) that differences in delivery resulted in different densities of newly-settled lobsters. Experimentally increasing newly-settled lobster densities and following density changes in replicate cobble plots suggested that as the animals grew, crowding at the initial settlement site eventually results in larger animals moving to lower density areas. Thus the initial difference in population density set by postlarval supply may be smoothed by an effective bottleneck for the upper end of the size class of smaller juvenile lobsters. Mortality was not measured in these experiments, but it is likely to play a role as well.

As little as 20 years ago, population structure was inferred from morphometrics and enzyme assays. Morphometry continues to be important and increasingly sophisticated (Cadrin, 2000), while the tools of molecular genetics have revolutionised population analyses. Chela size of adult male *H. americanus* from inshore southern New England could be differentiated from those originating in an offshore canyon (Cadrin, 1995). MacCormack and DeMont (2003) used 'nominal length' (body mass$^{1/3}$) as a scalar in an examination of regional differences in allometric growth of *H. americanus* at three locations within 100 km of each other in Nova Scotia. They found that carapace length did not exhibit isometric growth when related to nominal length. More significantly, regional differences were found in female abdomen area (related to carapace length) between two sites on opposite sides of Nova Scotia and thus in different hydrographic regimes. A morphometric study of *H. gammarus* at nine widely-separated locations in England found no differences in male characters, while females were discriminated between some locations by the number of spines on the claws and on the rostrum. However, there was no correlation of morphological differences and geographic distance, suggesting that the difference in female spines is the product of local adaptation. Tshudy and Parsons (1998) found no regional or substrate-linked morphological variation in a relatively small sample of *H. americanus* from the Gulf of Maine.

The mitochondrial genome was used by Tam and Kornfield (1998) to infer a strong clade consisting of the two species of *Homarus* and *Nephrops*, but excluding *Homarinus*, which until recently, had been classified in the genus *Homarus*. Harding *et al*. (1997) used RAPD (random amplification of polymorphic DNA) profiles to examine the structure of the *H. americanus* populations from a canyon near Georges Bank, a bay in Nova Scotia, and in the Gulf of Maine and found very little genetic divergence. Slightly more differentiation was seen between these locations and the Gulf of St Lawrence. Earlier studies employing allozyme analyses (Tracey *et al*., 1975), suggested some differentiation in the malic enzyme locus among lobsters from inshore southern New England, offshore canyons and the southern Gulf of St Lawrence. On a smaller scale, *H. americanus* from the western end of Long Island Sound (LIS), a long, narrow and poorly flushed embayment, were recently found to be genetically distinct from lobsters in the central and eastern parts of the sound, using nine microsatellite loci (Crivello *et al*., 2005). The difference, which was much greater that that predicted by geographic separation, may have been due to a recent massive mortality in the western LIS area (Crivello *et al*., 2005).

The genetics of population structure of *Homarus gammarus* has only recently been examined. Along the Norwegian coast, microsatellite and mitochondrial DNA studies (Jørstad *et al*., 2004) confirmed the genetic differentiation of lobsters from north of the Arctic Circle (Tysfjord region) and other parts of Norway. They also were able to distinguish lobsters from Tysfjord and a location 142 km away along the highly-convoluted coast. They suggested that locally-discrete populations might be maintained by hydrographic conditions allowing little larval dispersal between the two regions. Triantafyllidis *et al*. (2005) used mtDNA to look for genetic differentiation across the entire range of *H. gammarus*. Their analyses indicate the existence of genetically differentiated subpopulations, broadly defined as northern Norway, Mediterranean, Netherlands and Atlantic groups. Although the differences are not great, the population of *H. gammarus* cannot be considered panmictic.

It is clear that with today's knowledge we are unable to find strong evidence for much stock distinction across the range of the American lobster. Recent evidence for the European lobster suggests significant genetic structure to the population is possible. Subpopulations may exist within the apparently panmictic *H. americanus* population but they are not easily identified genetically. Morphometry provides some evidence of divergence, yet morphological features are often affected by environmental factors. The apparent homogeneity within the population may be the result of many releases of lobsters from one part of the range into another (Harding *et al*., 1997). Management strategies for *Homarus americanus* will continue to rely on life history characteristics until, or if, more progress is made in stock definition via genetics or morphometrics.

9.6 Sources of mortality

9.6.1 Ecological role of predation

Considered in an ecosystem complex, clawed lobsters play a critical role as predator, prey and host. Lobsters are omnivorous, feeding on a great range of benthic organisms. The range of prey species and amount consumed changes as a function of lobster size, temperature, prey availability, and moult cycle. Stomach content analysis of four size categories of Canadian *H. americanus* showed an ontogenetic shift in prey preferences (Sainte Marie & Chabot, 2002). There was a decrease in proportion of diet comprised of soft animal tissue and an increase in the consumption of rock crabs (*Cancer irroratus*) as lobsters grew. Gendron *et al.* (2001) found that a diet lacking in rock crab resulted in reduced growth and ovary development in *H. americanus*. The effect of bait on prey preferences could to be a potential major contributor to lobster biomass production (Saila *et al.*, 2002).

Predation can have a significant effect on marine populations (Chapter 8). Predation losses can sometimes exceed losses due to fisheries mortality (Bax, 1998). Change is direct when a predator kills a prey. Indirect effects occur where predation occurs on shared prey resources, affects intermediate predators, or influences prey behaviour and resource availability (Bax, 1998). Under threat of predation, individuals are known to change foraging tactics, shelter use and social behaviour (Krebs & McKenzie, 1989; Wahle, 1992a; Davies, 1993). Predation has long been recognised to have an impact on lobster abundance (Herrick, 1895), especially at the smaller sizes (Wahle, 1992a). In tethered field trials, the smallest of early benthic phase lobsters suffered the highest predation rates (Wahle & Steneck, 1992). Mortality due to predation decreases as the lobster grows (Wahle, 1992a). Adequate shelter reduces predation on *H. gammarus* by gobies (*Pomatoschistus minumus*), rockling (*Ciliata mustela*) and green crabs (*Carcinus maenas*) (Ball *et al.*, 2001).

Groundfish have been suspected as being major predators of American lobster. With recent reductions in groundfish fishing mortality, several previously overfished fish populations have increased, bringing into question their impact on the ecosystem and specifically their impact on larger lobsters. Nelson *et al.* (2003) found that benthic crustaceans including *Homarus americanus*, were the primary diet of striped bass (*Morone saxatilis*) in Massachusetts. Worm and Myers (2003) showed a strong relationship between the increase of invertebrates (northern shrimp, *Pandalus borealis*; snow crab; and American lobster) with the decrease in Atlantic cod (*Gadus morhua*). On the other hand, Steimle *et al.* (2000) found little evidence of predation by Atlantic cod, winter flounder (*Pleuronectes americanus*), yellowtail flounder (*P. ferruginea*), thorny skate (*Raja radiate*), Greenland cod (*Gadus ogac*) or spiny dogfish (*Squalus acanthias*) in the southern Gulf of St Lawrence. They did find lobster consumption by shortfin sculpin (*Myoxocephalus scorpius*), cunner (*Tautogolabrus adspersus*) and white hake (*Urophycis tenuis*). Watts and MacPherson (2002) found no evidence of lobster predation by white hake. New predators may be emerging with the changing environments. For example, the abundance of ctenophores has increased in Narragansett Bay, RI (Sullivan *et al.*, 2001) and they may be significant predators on lobster larvae, or competitors for food during the summer months (Cobb, unpublished observation).

9.6.2 Disease

Parasites have important roles in ecological communities (Chapter 5). They can limit species distributions and abundance by altering survival, reproductive output, behaviour, and inter- and intraspecific interactions (Curtis, 1987; Keymer & Read, 1991). In theory, parasites can regulate populations (Anderson & May, 1978). Some commensal organisms are beneficial such as the epibiotic bacterium that protects the embryos of *Homarus americanus* against a common fungal pathogen (*Lagenidium callinectes*) (Gil-Turnes & Fenical, 1992). Some perform an as yet unknown function such as the acoelomate metazoan, *Symbion pandora*, found in the mouthparts of the Norwegian lobster, *Nephrops* (Funch & Kristensen, 1995) and the European lobster (Nedved, 2004).

More is known about the negative or pathogenic effects of parasites. In 1978, a nemertean, *Pseudocarcinonemertes homari*, was identified as causing heavy mortality of eggs in the Bay of Fundy (Aiken *et al.*, 1985). The bacterium *Aerococcus viridans* was identified in 1947 (Snieszko & Taylor, 1947) as the pathogen producing gaffkaemia, a fatal disease infecting both species of *Homarus* (Wilk *et al.*, 1987).

Recently, new diseases or syndromes have appeared in *Homarus americanus*. Tall *et al.* (2003) described limp lobster syndrome as causing lobsters to be weak, lethargic, and slow or ineffectual in their responses to stimuli. The causal agent was related to the bacterial strain *Vibrio fluvialis*. In 1999, lobsters in western Long Island Sound, USA experienced an acute mortality event. Preliminary analysis revealed lobsters were infected with a previously unknown paramoeba, but researchers have been unable to determine if these were responsible for the deaths. Shortly after the acute mortality, moribund lobsters with a change in colouration were being reported. These lobsters were found to have high levels of calcium particles in their gills (Dove *et al.*, 2004). This 'calcinosis' is attributed to extreme metabolic and respiratory failure caused by prolonged exposure to unusually high temperatures. As ectothermic organisms, lobsters are especially sensitive to fluctuations in their thermal environment (Spees *et al.*, 2002).

The appearance of a widespread disease phenomenon was observed in 1997 (Castro & Angell, 2000). This disease, now referred to as epizootic shell disease, has become a major problem in southern New England with an incidence of 30–35% of the nearshore population. Although three bacteria have been isolated from the lesions (Becker *et al.*, 2004), researchers have been unable to definitively link the bacteria to causing shell disease (Smolowitz, personal communication). Theories of the causes of shell disease currently range from lobsters being immune-suppressed, possibilities of a change in bacterial ecosystems (O'Kelly, personal communication), to possibly being connected to endocrine-disrupting chemical compounds (Biggers & Laufer, 2004).

The effects of disease on lobsters are poorly understood. This is a field in which little research has been conducted, yet potentially disease may play a major role in individual survivability by direct mortality or indirectly by behavioural changes, and ultimately affect population characteristics. Extreme behavioural changes have been noted in lobsters infected with gaffkaemia, *Aerococcus viridans homari*, beginning with the cessation of feeding activity leading to death in a classic spread-eagle position (Getchell, 1989). Recently, Stentiford *et al.* (2000) reported on behavioural and locomotor changes that occurred in the Norway lobster, *Nephrops norvegicus*, infected with the parasitic dinoflagellate, *Hematodinium* spp. They found that lobsters showed a progressive decline in overall swimming performance and decreased ability to recover from strenuous activity as the infection severity increased. It was also found that infected lobsters made longer and more numerous burrow departures than uninfected animals, leading to significantly more time spent on the sediment surface altering their catchability rates. These altered catchability coefficients have been incorporated into stock assessments.

Parasites and disease can be significant factors in population dynamics. The physiological reaction to the disease, as well as the immune response, can affect an individual's behaviour and survival, and ultimately influence population structure and evolution. There is evidence suggesting that disease presents a major force shaping behaviour that is as profound as the forces of predation or resource utilisation (Anderson & May, 1979; Hart, 1990). In theory, any parasite control behaviour by the host will represent some cost to the host, such as reduced feeding time, or distraction from predator avoidance. The greater the cost of the behaviour, the more beneficial it is expected to be (Hart, 1990). Some behaviour may serve to avoid or enhance the possibility of infection (Brown & Brown, 1986). Aggression might be reduced to avoid potential wounds due to an aggressive encounter. Therefore, combat with an infected individual may be avoided. If combat occurs and the infected individual is harmed, bacteria could be released into the immediate areas. If the healthy individual is harmed, infection could prove to be fatal.

9.7 Harvest of wild populations

9.7.1 Gear type and methods

There are both inshore and offshore fisheries for *H. americanus*. The inshore fishery is carried out by smaller vessels (ranging from skiffs to vessels about 15 m in length) usually carrying one or two crew. The offshore vessels typically average 39 m in length, with living accommodation and carry three or four people.

The offshore (canyons and continental shelf) fishery originally started as a trawl fishery in the late 1950s. This peaked in the 1970s and was gradually replaced by a trap fishery by the 1980s. The offshore trawl fishery was important for the development of markets for larger lobsters and the refrigerated holding systems still used today on the offshore trap boats. Today, the regulations limit the catch of trawlers to 100 per day or 500 per trip. In some states trawl landings are prohibited. In some states there are small trawl fisheries primarily targeting lobsters during or after the moult when they are found in deep muddy pockets.

The primary method of fishing for both species is with the pot or lobster trap. There are various designs, shapes and sizes, although there is a maximum size allowed overall in some fisheries. Traps can be fished as singles (one trap, one buoy) or as a trawl (multiple traps placed on one ground line with two or three buoys). Trawls can range from 10–50 traps in length. Individual traps are used in areas where tidal currents may be high, the lobsterman is fishing solo, or where specific grounds are spotty and fishermen want to maximise the area of influence of the one trap. Trawls are used to prevent loss of gear especially in high traffic areas, for increased ease of setting and hauling, and for covering larger areas.

Rectangular lobster traps are constructed of wood lath or plastic-covered wire mesh. They contain a 'kitchen' where the bait is hung and at least one 'parlour' area with at least two escape vents (either rectangular or circular). Lobsters enter through the entrance funnels, and then move through the no return funnel into the parlour section(s). Lobsters smaller than the legal size can escape through the escape vents. If wooden, traps have a lathe-spacing equivalent to the escape vents to allow for escape. Some round traps have a single opening on the top.

Traps are usually retrieved using a hydraulic hauler that allows for rapid redeployment after they are emptied and re-baited. Bait may vary between regions or ports, usually reflecting local availability and price. Herring and skate are sought after for the attractive smell and endurance properties, but other species are used. In the *H. americanus* fishery in Long Island Sound, fish racks of any species from local fish retail stores are frequently used. Artificial bait is currently being evaluated. The first product used cowhide, for durability, but after 'mad cow disease' was discovered, this has been discouraged.

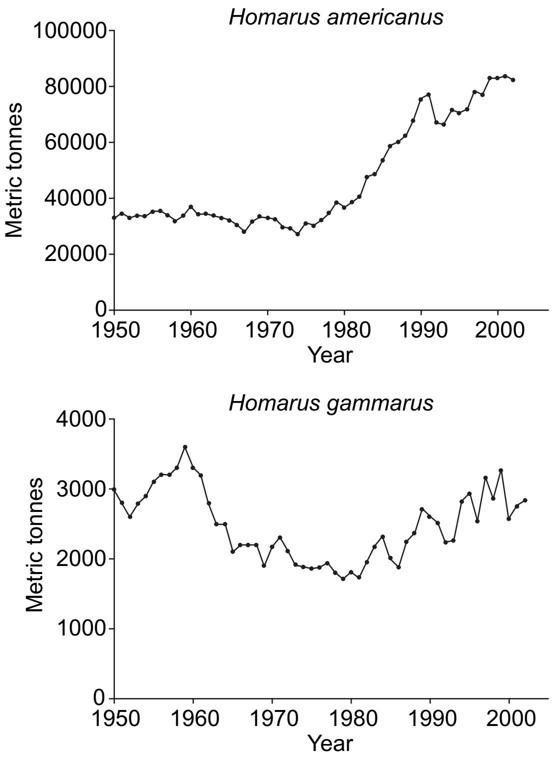

Fig. 9.7 Commercial catch of *Homarus* 1950–2002. Top panel: European landings; bottom panel: US and Canada landings. (Data from FAO website accessed May 2005: http://faostat.fao.org/faostat/collections?version=ext&hasbulk=0&subset=fisheries)

9.7.2 Landings and effort

The lobster resource in Canada and the United States is considered one of the most valuable of fisheries. Reported lobster landings (Fig. 9.7) are currently at or near historically high levels in both countries (Fogarty & Gendron, 2004). There were dramatic increases in the 1980s and 1990s, which may be related to shifts in environmental and ecological conditions affecting production levels. However, there have been recent severe declines in the stocks in southern New England and in some Canadian lobster fishing areas that may reflect continued ecological or environmental change and effects of near coastal habitat disruption.

The principal landings of *H. gammarus* now occur in the United Kingdom, Ireland, the Channel Islands and France. Landings have historically averaged 2500 tonnes per year and are important to the fishing communities throughout their range (Mercer *et al.*, 2001). There was a major collapse in the *H. gammarus* population in Norway beginning in the 1960s. Other northern European countries and countries in the Mediterranean have experienced declines in reported landings as well. For example, Sweden's landings peaked in 1933 at 299 tonnes, and in 2002 were reported at 19 tonnes. Landings in Denmark peaked at 511 tonnes in 1944 and are now reported at 11 tonnes (FAO website, http://faostat.fao.org/). Landings in Italy, Yugoslavia and Algeria have been reduced to zero. The most dramatic decrease was in Turkey where peak landings exceeded 2000 tonnes in 1964 and dropped to zero in 1970. They are currently reporting 10 tonnes annual landings (FAO website, http://faostat.fao.org/).

Landings and effort are sometimes used as equivalents; however, effort is a complex parameter that involves fisherman, equipment, and lobster behaviour. Since traps are passive devices, lobsters must have a motivation to enter them. Many factors affect the catch rate including location, bait, trap design, soak time, temperature and the presence of other animals (Cobb, 1995). Laboratory studies of the behaviour of *Homarus americanus* indicate that only a small portion of lobsters that encounter the traps actually enter it and are subsequently captured (Karnofsky & Price, 1989). This complicates the relationship between catches or catch per unit effort (CPUE) and abundance or density, as well as between effort and mortality (Addison & Bell, 1997; Addison & Bannister, 1998). Encounter probability depends upon the lobster having the external or internal motivation to leave its shelter (i.e. state of hunger, gender, reproductive status, time of day, water temperature, light level, odour cues). In general, *Homarus* leave their shelters when light intensity falls below $2 \cdot 10^{-2}$ W/cm^2 (Weiss, 1970). Some individuals are day-active, but overall, *Homarus* can be considered nocturnal and possesses a biological clock that runs on an approximately 24-hour period. (Jury *et al.*, 2005). In deeper or murkier water with lower light levels, it is possible that lobsters are more active or active for longer periods. Catch rates may be more complex than previously believed; data obtained from *in situ* video indicates that entry rates in traps for *H. americanus* do not increase at night (Jury *et al.*, 2001).

Temperature affects the trap encounter rate; walking rates increase linearly between 2–10°C, are constant between 10–20°C and increase again above 20°C (McLeese & Wilder, 1958). Catchability is lowest at time of ecdysis (Miller, 1990). Changes in serum protein have been noted over the moult cycle suggesting that a high level of feeding may be required to recover from moulting (Ennis & Fogarty, 1997). Many fishermen plan their maximum effort to correspond to the moult cycle.

Miller (1990) estimated effective area fished by comparing trap catches and diver surveys and found that trap catches do not adequately describe male : female ratios, sizes or reproductive status of the lobsters in the area adjacent to the traps. Tremblay and Smith (2001) used comparisons between direct estimates of density and trap catches of American lobster to demonstrate seasonal differences in effective areas fished. European lobsters (*H. gammarus*) exist at lower densities that the American lobster (*H. americanus*) and may affect the effective area fished, trap saturation and density estimates.

Trap saturation (decreasing catch rates with increasing catch) occurs as a result of the interaction between the animal and the gear (Fogarty & Addison, 1992). Addison and Bell (1997) modelled the capture process involved in catch rates of clawed lobster. Noting that the variance to mean ratio for lobster catch in individual traps was less than or close to unity, implying a random or even distribution of lobsters among traps, they hypothesised that behavioural interactions reduced the incidence of high numbers of lobsters per trap. Lobster *in situ* video analysis confirmed these models (Jury *et al.*, 2001).

Intense gear saturation in stationary baited traps has been reported for a variety of crustaceans including American lobster (Waltz, 1989); European lobster (Addison & Bannister, 1998), blue crab (*Callinectes sapidus*) and crayfish (*Oronectes virilis*) (Momot, 1998). This means that traps are competing with each other for the lobsters available for capture. The lack of proportionality between trends in fishing mortality rate (F) and fishing effort (f) suggests that the catchability (q) has not remained constant but has steadily fallen off as effort has risen during the 1990s. Crecco (2000) demonstrated that widespread and persistent evidence of intense gear saturation has existed since 1982 in the USA. Groeneveld *et al.* (2003) tested for the effects of saturation on CPUE in the spiny lobster *Palinurus gilchristi*. They were unable to distinguish the effects of saturation from seasonal or aerial fluctuations.

Management of lobster stocks using effort controls can be as complex as the catch rate. Gendron and Brethes (2002) used a spatially-explicit model to assess the impact on fishing mortality by modifying effort patterns. There was a greater impact on exploitation rates if effort was reduced early in the season and restricted to offshore sites. Acheson (2001) also examined the behaviour of lobstermen under an effort-control system and found that the total number of traps increased under a trap limit, reflecting diverse responses based on social and economic factors.

9.8 Mariculture and population enhancement

Scientists, fishermen and fishery managers have long prophesised the commercial demise of *Homarus* fisheries. Over a century ago, Herrick (1895) citing a 25% decline in New England landings of *H. americanus* between 1889 and 1892 was motivated to write, ‘These figures illustrate very forcibly the decline which, unless speedily checked, threatens to destroy this valuable fishery.’ Similarly, J.N. Cobb (1899) noted alarming declines in the lobster catch (and catch per trap) in Maine. Clearly the fishery did not collapse, but expanded. Presently however, some fishing areas in the USA and Canada appear to be truly overfished and the catch has declined significantly, leading to calls for ‘rebuilding’ the population to a level at which managers and fishermen can agree that the landings are stable. Solutions proposed run the gamut from restocking hatchery-reared young, to installation of artificial reefs, to meeting biological reference points in the fishery, to high-tech mariculture. We addressed management via fishery regulations earlier in this chapter, here we note the lack of progress towards true intensive mariculture and give a brief overview of stock and habitat enhancement efforts.

9.8.1 Mariculture

Intensive lobster mariculture, the culturing of marine organisms in high-density, technically sophisticated facilities, has been examined and touted since the mid-1880s (Aiken & Waddy, 1995; Nicosia & Lavalli, 1999). Research in the 1970s and 1980s, primarily on *H. americanus*, demonstrated the feasibility of lobster mariculture. This has been reviewed by Aiken and Waddy (1995) in considerable detail. Little progress has been made since that review. The chief constraint to developing the culture of *Homarus* to a commercial scale is the economics of the situation. Despite consumer appetite for lobsters, the remarkable increase in landings by the natural fishery has been able to meet demand at reasonable prices. The demand is for lobsters that weigh about 500 g, the weight of lobsters near the minimum legal size in many areas. Consumer preference and legal constraints on holding or selling lobsters smaller than minimum size discourages the development of a market for smaller lobsters that would be more economical to produce. Because of this, Aiken and Waddy (1995) advocate the development of a market for small lobsters although, as they point out, commercial constraints, particularly of providing warm water and effective feed, are formidable. Research attention has refocused on population enhancement or restocking programmes in which lobsters are cultured to a young age but a size at which predation is less likely (Wahle, 1992b). Extensive aquaculture (‘sea ranching’) also has been suggested, but economic analysis for *H. gammarus* ranching in Norway where the fishery is nearly completely collapsed, still is negative (Moksness *et al.*, 1998).

9.8.2 Stock enhancement

Common sense suggests to many that contributing young to a population should increase the number of adults available to the fishery. This reasoning led, for many years, to the proliferation of lobster hatcheries whose primary goal was to rear and release larvae. Despite the continuing lack of evidence that the release of hatchery-produced young can economically make an impact on the population, there were 20 or more lobster hatcheries in the USA, Canada and Europe between 1880 and 1900 (Nicosia & Lavalli, 1999). Early efforts at stock enhancement for clawed lobsters in Norway and the United States involved lobster 'parks' in which ovigerous females, captured in the fishery, were held until their eggs hatched. When this was seen as ineffective, rearing eggs separated from the female in jars was tried with great success – up to 93% of the eggs hatched into first stage larvae and were released into the environment. The release of millions of stage I larvae probably made little difference to the population. Later efforts reared lobsters to the fourth (postlarval) stage before release (Nicosia & Lavalli, 1999) but still without demonstrable enhancement of the population. However, rearing lobsters to 5–12 months of age in a hatchery before release holds more promise. As yet, such a programme does not seem economically viable (Bannister & Addison, 1998; Agnalt *et al.*, 1999). Still unresolved is the issue of quality of the hatchery-reared juveniles.

9.8.3 Habitat enhancement

The enhancement of population size by providing additional appropriate habitat is often suggested under the assumption that habitat is limiting the growth of the target species. Artificial reefs are primarily targeted at finfish production, and while lobsters are certainly found at artificial reefs intended for finfish (Briggs & Zawacki, 1974), reef building is not frequently targeted at crustaceans. An exception is shell reefs constructed to mitigate habitat-loss for juvenile Dungeness crab, *Cancer magister* (Dumbauld *et al.*, 2000).

Artificial reefs designed specifically for *Homarus* have been built on both sides of the Atlantic. In 1965, a 3000 m^2 reef of large sandstone boulders was placed 2.5 km from the nearest known good lobster habitat in Northumberland Strait, Canada (Scarratt, 1973a). Colonisation was slow, after two years biomass was low, although the size of individual lobsters was larger than that in nearby natural lobster ground. After seven years, the reef communities were similar to natural areas and lobster populations had similar characteristics as well (Scarratt, 1973a, b).

There is a positive relationship between lobster size and shelter size (Cobb, 1971). Larger lobsters will choose, or construct, larger shelters. They may also maintain a minimum distance between occupied shelters through aggression (Lawton & Lavalli, 1995). These observations were used to fabricate shelters for a reef in Rhode Island, USA (Sheehy, 1976). The shelter units had either three small crevices or a single large crevice and were sited in arrays on a featureless sand substrate about 0.6 km from a rocky habitat. Vagrant lobsters arrived within a week. A year later, lobsters ranging from postlarvae to egg-bearing females resided on the reef and the biomass of lobsters was higher than in the nearby rocky area. Occupancy rate of small and medium lobsters was higher in the more closely-spaced arrays. Planning for appropriate inter-neighbour distance may be a critical design feature for clawed lobster reefs (Sheehy, 1976).

The utility of combining the disposal of solid waste and artificial reefs was explored in the UK. Pulverised fuel ash, waste from burning coal, was compacted into bricks stacked underwater into 4 m · 1 m conical units in array on sandy substrate at 10 m depth in Poole Bay on the south coast of England (Jensen *et al.*, 1994, 2000a, b). Although the nearest known natural lobster habitat was over 2 km distant, the reef was occupied within weeks by vagrant lobsters. Settlement later by postlarvae was inferred from the presence of very small lobsters. The size distribution of lobsters on the reef and in the fishery was similar initially, but later the reef saw larger lobsters than are found in the fishery (Jensen *et al.*, 2000a, b). This may have been a result of lower fishing effort on the reef or perhaps because the crevices in the reef units were larger than in the natural habitat.

The impact of new habitat in the form of a specially designed reef for lobsters in Rhode Island, was examined by Castro *et al.* (2001). Rock rubble was placed on featureless shell-mud substrate forming six replicate reefs, each 10 m · 20 m. The development and dynamics of the lobster population of the reef was monitored by trapping, tagging

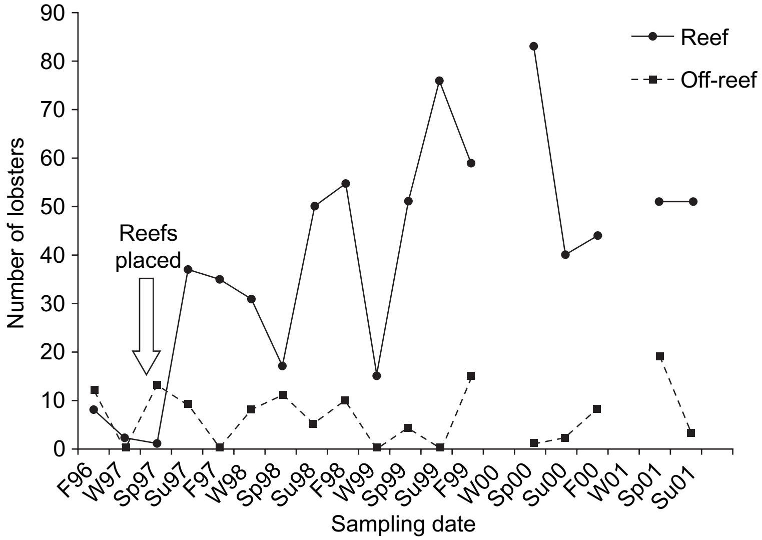

Fig. 9.8 Number of lobsters sampled by divers on an artificial reef and in a nearby natural area in Narragansett Bay, RI, USA from Autumn 1996 until Summer 2001. Arrow: installation of reef. (From Castro, 2003.)

and diver surveys for five years (Castro, 2003). Before the reef was built, few lobsters were found on the soft sediment of the site; within three months vagrant lobsters had moved in. After the first year, lobster density on the reef was equal to or greater than nearby natural areas (Fig. 9.8). Lobsters on the reef were larger in each year after the first than in nearby (2 km) rocky areas. A few tagged lobsters were recaptured numerous times on the reef suggesting a long residence time. Postlarval settlement corresponded to the density in natural areas.

The relationship between crevice size and lobster body size (Cobb, 1971) was incorporated into models of the creation of interstitial spaces by different sizes of stone (Barry & Wickins, 1992; Wahle, 1992b). In planning for an artificial reef for lobsters of all sizes it would be useful to estimate the numbers and sizes of habitable crevices in reefs made of different size rock. If a reef were planned with enough shelters for all sizes, it might reduce the chances of a local demographic bottleneck. Immigrants and newly-settled recruits to the reef would have to be accommodated and if juveniles were seeded, would compete for shelter with the seeded population. Such models of crevice size are important to an initial understanding of the constraints on habitat use as well as the practical question of what rock sizes to use in constructing a reef for *Homarus*, or for any lobster (Spanier, 1994).

9.9 Management and conservation

The New England Fishery Management Council manage the offshore fishery in the USA while fisheries within 5.5 km of the shore are managed by the various states under the interstate fishery management plan by the Atlantic States Marine Fisheries Commission (ASMFC). The Department of Fisheries and Oceans manage Canadian fisheries.

Canada and the USA (and even some individual states) have divided up the ocean into more uniform management zones. The ASMFC currently uses six areas; Maine has further divided their coast up into seven lobster zones co-managed with the fishermen. There are 41 Canadian lobster fishing areas or LFAs each with its own season, varying in length from eight weeks to eight months. Other management strategies in each LFA include restrictions on licenses, and number and type of traps. Area management has the advantage of allowing for customisation of harvesting rules to reflect local tradition and stock abundance. The major disadvantage is that enforcement is complicated when management strategies are not uniform throughout the lobster's range. In some cases, stock areas do not match up with management areas making assessment almost impossible.

The American lobster has traditionally been managed through input controls. The most common include v-notching (a v shape is cut on the tail fan of the female telsons on the second uropod on the right, returned to the sea, and thenceforth illegal to take), minimum and maximum carapace length, prohibition on possession of ovigerous females, trap numbers and size. The rationale for these measures has been based on the yield-per-recruit considerations, preserving the breeding populations and marketing factors. These analyses have been used as qualitative guides to regulation rather than hard targets. An egg-per-recruit (EPR) reference point was formally adopted in both the USA and Canada. In the USA, an EPR of 10% of the predicted EPR of an unexploited population has been implemented as a management limit (threshold) yet no target has been developed. In Canada, a goal of doubling EPR relative to 1995 levels has been adopted as a management target (Fogarty & Gendron, 2004). Until 2005, a two-phase approach was used: the modified Collie-Sissenwine DeLury model was used to estimate current F levels and an EPR model was used to estimate F10%. A recent review of the assessment process in the USA has concluded that that none of the assessment methods reviewed were able to adequately estimate absolute EPR or the F10% threshold. They recommended the use of trends in F and EPR or quantities based on relative quantities (ASMFC, 2004).

Output controls such as quotas have not been used except for one fishing area off southern Nova Scotia. There are two examples of closed areas in Canada, one in Bonavista Bay and one in LFA 40 for fixed lobster gear on Brown's Bank, Nova Scotia. The latter example was established in 1979 to protect a large concentration of reproductive females on Brown's Bank. Impacts from this marine protected area on lobster stocks were unclear (Petruny-Parker *et al.*, 2005). Rowe (2001) conducted extensive studies in Bonavista Bay. There were differences detected in some lobster population parameters inside and outside the reserve, but the data suggested no change in densities or proportion of ovigerous females.

European lobster fisheries have been either unregulated or minimally regulated by minimum size or prohibitions on landing berried females (Browne, 1999). Until 1992, the only management of Irish lobster stocks was a minimum size and a ban on their capture using scuba diving. A lobster v-notching programme, set up by the South Wexford Lobster Fisheries Cooperative in 1994, now operates nationwide. The positive effects on reproductive potential in *H. gammarus* of a v-notching programme in Ireland were demonstrated by Tully (2001). In 2002, a new minimum size of 87 mm CL (a size smaller than the mean size at first maturity recorded for *H. gammarus* (Tully *et al.*, 2001)) was put in place under the EU regulations which apply to landings of crustaceans in all European waters. Another change in minimum size occured in Norway in May 2005 with an increase to 88 mm CL or 25 cm total length. Additional measures in Norway include a closed season from 1 January–30 September and trap limitations of 20 for recreational fishermen.

9.10 Conclusions

Despite the amount of knowledge accumulated about the genus *Homarus*, much that is critical to wise management is unknown. Stocks of *H. gammarus* have nearly disappeared in some parts of the range and attempts at stock enhancement are being made. An as yet unexplained increase in landings of *H. americanus* over the past 20 years continues to bring record landings to the Gulf of Maine but not to southern New England. Fishing down predators, range expansion and supplemental feeding with bait may explain part of the increase, while disease and overfishing may explain the losses. But we are just beginning to understand the early life history of *Homarus* as exemplified by the continuing puzzle as to the whereabouts of the newly-settled young of the year of *H. gammarus*. We are only just beginning to recognise the importance of source–sink dynamics, and the tools to examine them, hydrodynamic models, microsatellite DNA analysis and satellite imagery are becoming more sophisticated. The development of stage-structured models was a great advance in population modelling. If the promise of temperature-corrected lipofuscin age-determination is borne out, we may be able to employ age-structured models with confidence. It may be important to recognise and incorporate into population dynamics work the observation of Fogarty and Gendron (2004) that we have, through our fishing practices, turned a long-lived, iteroparous genus into a considerably shorter-lived, functionally semelparous one. Such a significant 'man-made' change in evolved natural life-history characteristics could have unpredictable consequences.

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Chapter 10
Jasus Species

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10.1 Species and distribution

No other palinurid genus is so widely distributed in southern waters as *Jasus*. Occurring in mid-south latitudes of the Southern Ocean and in the South Atlantic, Indian, and South Pacific Oceans, *Jasus* lobsters (Plate 10.1) are found not only near coasts but also on offshore ridges, banks and seamounts. Several species live, seemingly precariously, around small island groups that are among the most remote places on earth – Tristan da Cunha, St Paul and Amsterdam Islands, and Desventuradas Island – and at least one species is confined to isolated non-emergent seamounts. The only large landmasses inhabited by *Jasus* are southern Africa, Australia, and New Zealand.

Until quite recently, *Jasus* lobsters were separated into the 'verreauxi' group, containing only *J. verreauxi*, and the 'lalandii' group containing all other species. The 'lalandii' group comprised *J. lalandii* living throughout much of the Southern Ocean until Holthuis (1963) recognised that, based on adult morphology and colour, there were separate species. Holthuis and Sivertsen (1967) accordingly subdivided the 'lalandii' group into the 'lalandii' subgroup (*J. lalandii* off southern Africa, *J. edwardsii* in New Zealand, and *J. novaehollandiae* in Australia) and the 'frontalis' subgroup (*J. frontalis* off Chile, *J. tristani* in the South Atlantic Ocean, and *J. paulensis* in the south Indian Ocean). George and Kensler (1970) extended the list of external characters used by Holthuis and Sivertsen (1967) to distinguish species in the 'lalandii' group and provided additional support for the existence of the subgroups. The morphology of *J. caveorum*, a species discovered in the east South Pacific Ocean in 1995, suggested its inclusion in the 'frontalis' subgroup (Webber & Booth, 1995).

DNA analysis has supported the distinctions within the 'lalandii' group between *Jasus edwardsii*, *J. lalandii*, *J. tristani*, *J. frontalis*, *J. paulensis* and *J. caveorum*, but not between *J. edwardsii* and *J. novaehollandiae* (Brasher *et al.*, 1992a; Ovenden *et al.*, 1992, 1997). *J. edwardsii* and *J. novaehollandiae* have since been synonymised (Ovenden *et al.*, 1997). However, DNA studies have not supported subdivision of the 'lalandii' group into the 'lalandii' and 'frontalis' subgroups (Ovenden *et al.*, 1997), so the morphological and colour distinctions between adults of these groups may be of less evolutionary significance than previously thought. Table 10.1 lists key biological features of *Jasus* lobsters and demonstrates how similar the species are biologically.

Because *J. verreauxi* is morphologically so different from the other *Jasus* species, Holthuis (1991) recognised the need for two subgenera: *Jasus* (*Sagmariasus*) for *J. verreauxi*, and *Jasus* (*Jasus*) for all other species. More recently, *Sagmariasus* has been elevated to full generic status because *S. verreauxi* differs from *Jasus* lobsters in numerous significant ways other than only adult morphology (Table 10.1), the 'packhorse', 'green', or 'eastern' Australasian rock lobster becoming *Sagmariasus verreauxi* (H. Milne Edwards, 1851) (Booth & Webber, 2001). The name *Sagmariasus* comes from a combination of the Greek 'sagmarion', meaning packhorse, and '*Jasus*' (Holthuis, 1991); this acknowledges the distinctive protruding branchial regions resembling a laden horse in large individuals, and that this genus is closer to *Jasus* than to any other. The largest of all palinurids, the apparently primitive *S. verreauxi* is morphologically very close to its likely ancestral form, *S.* (previously *Jasus*) *flemingi* (Glaessner, 1960). There are no known significant biological differences

Table 10.1 Life history and other parameters of *Jasus* spp., and the main features that distinguish *Sagmariasus verreauxi* from *Jasus* spp.* 1, NIWA unpublished data; 2, Booth (1984); 3, Montgomery (1995); 4, Montgomery (1992); 5, Holthuis (1991); 6, Pollock (1991); 7, Roscoe (1979); 8, Webber & Booth (1995); 9, Annala *et al.* (1980); 10, Annala (1991); 11, Grua (1960) (referred to as *J. lalandii*); 12, Pollock & Goosen (1991); 13, Arana *et al.* (1985); 14, J. Kittaka (unpublished laboratory results); 15, Pollock (1986); 16, Booth (1986); 17, Montgomery (1999); 18, Annala & Bycroft (1987); 19, Heydorn (1969); 20, Dupre (2000); 21, Kittaka *et al.* (1997); 22, Montgomery & Kittaka (1994); 23, McWilliam & Phillips (1987); 24, Booth & Phillips (1994); 25, Kittaka *et al.* (1988); 26, Kittaka (1988); 27, Lazarus (1967); 28, Baez (1973); 29, Lesser (1978); 30, C. Grobler (pers comm); 31, Crear (2000) (projected); 32, Pollock (1973); 33, MacDiarmid & Kittaka (2000); 34, Booth (1997); 35, Montgomery & Craig (1997); 36, Phillips & Booth (1994); 37, Dupre (2003); 38, Kittaka *et al.* (2005); 39, Ritar & Smith (2005); NZ, New Zealand; Aust, Australia; max, maximum; min, minimum; ?, unknown; spr, spring; sum, summer; aut, autumn; win, winter; Sw, seaweed; Crev, crevice; sur, surface; bot, bottom; exop, exopod; M, male; F, female; Presum, presumably.

Character	*S. verreauxi* (NZ)	*S. verreauxi* (Aust)	*J. edwardsii*	*J. lalandii*	*J. paulensis*	*J. tristani*	*J. frontalis*	*J. caveorum*
Max male (female) size (mm CL)	284 (264)[1,2]	264[3] (242)[4]	235 (180)[5]	190 (140)[6]	115 (95)[6]	175 (115)[6,7]	220 (190)[5,6]	>129 (?)[8]
Squamal sculpturing on abdomen	Absent[5]	Absent[5]	Present[5]	Present[5]	Present[5]	Present[5]	Present[5]	Present[8]
Large rostral spine	Present[5]	Present[5]	Absent[5]	Absent[5]	Absent[5]	Absent[5]	Absent[5]	Absent[8]
Antennules	Stout[5]	Stout[5]	Slender[5]	Slender[5]	Slender[5]	Slender[5]	Slender[5]	Slender[5]
Female size at maturity based on setae (eggs) (mm CL)	150 (160)[2]	170 (same)[4]	60–120 (same)[9]	65 (same)[6,10]	65–75 (same)[11]	56–60 (same)[6,12]	75–77 (same)[13,37]	? (?)
Female age at maturity (y)	~7[1,14]	?	3–7[1,9]	5[15]	?	?	7[37]	?
Colour change at maturity	Yes[16]	Yes[4]	No	No	No	No	No	?
Separate breeding areas?	Yes[16]	Yes[4,17]	No	No	No	No	No	?
Egg-bearing (hatching) season	Spr/sum (sum)[2]	Spr/sum (sum)[17]	Win/spr (spr)[9]	Win/spr (spr)[15]	Win (spr)[11]	Win (spr/sum)[7,19]	Win/spr (spr/sum)[13,20]	Win (?)[8]
Min (max) clutch size · 10^3	387 (2040)[10]	?	38 (540)[10,18]	33 (490)[10]	?	7 (137)[12]	61 (524)[10]	? (?)
Brood period (mo)	2–3[2]	2–3[17]	3.5[9]	~4[15]	4–6[11]	4–6[7,19]	4–6[13,20]	?
Egg diameter (mm)	0.6[10]	?	0.8[10]	0.7–0.8[10,12]	?	0.8[12]	0.6–0.8[13,37]	?
Duration of phyllosoma stage (mo) – wild (in culture)	8–12[16] (6–12)[21]	8–12[17,22] (?)	12–24[24] (7–12)[25,38,39]	14–18[15] (10)[26]	? (?)	? (?)	? (?)	? (?)

Cont.

Table 10.1 *Continued*

Character	*S. verreauxi* (NZ)	*S. verreauxi* (Aust)	*J. edwardsii*	*J. lalandii*	*J. paulensis*	*J. tristani*	*J. frontalis*	*J. caveorum*
Exop on 3rd maxilliped (5th pereopod)	Yes (yes)[21]	Yes (yes)[23]	No (no)[29]	No (no)[27]	No (no)[1]	?	No (no)[28]	?
Puerulus collector type (capture depth)	?	Sw (sur)[22,35]	Crev (bot)[1,36]	Crev (bot)[30]	? (?)	? (?)	? (?)	? (?)
Weight after 1st year (g)	?	100–260[31]	40[1]	~20[32]	?	?	?	?
Main moult season for mature M (F)	Win (win)[21,33]	? (?)	Spr (aut)[1]	Spr/sum (aut)[15]	? (aut)[11]	Spr (aut)[7]	Aut (aut)[20]	?
Propensity to migrate large distances	High[34]	High[3,4,17]	Some[34]	Low[15,34]	Low[34]	Low[34]	Low[34]	Presum low

*Additional to those differences listed above are the following:

1. *Sagmariasus verreauxi* is a warm-water species (typical surface winter to summer water temperatures of 16–22°C for breeding populations) compared with the temperate-water *Jasus* spp. (typically in waters 8–16°C). *S. verreauxi* lives mainly between the latitudes of 30° and 40° S; *Jasus* spp. 30–48° S. Mature *Jasus* spp. are much more commonly taken on rocky reefs than are *S. verreauxi*, which are fished mainly on light foul, sand, and mud substrates (Lie, 1969; Booth, 1986).
2. The mitochondrial genome of *S. verreauxi* is highly distinct from that of all *Jasus* spp. In all maximum parsimony trees, *S. verreauxi* formed a sister lineage to *Jasus* (Ovenden *et al.*, 1997). There was large (18–24%) genetic divergence between *S. verreauxi* and *Jasus* spp. in a cladistic analysis of nucleotide substitutions in the 16S ribosomal RNA and cytochrome oxidase subunit I genes of mtDNA (Brasher *et al.*, 1992b; Ovenden *et al.*, 1992, 1997; Ovenden & Brasher, 2000). These authors considered 18–24% to be outside the range normally expected for metazoan species whereas the mean divergences between pairs of *Jasus* spp. were 0.7–10%, well within this range.
3. Holthuis (1991) noted that his new subgenus *Sagmariasus* differed from the nominotypical subgenus by: (1) the absence of any sculpturing on the abdomen; (2) the presence of a much stronger, more prominent rostrum which, with the frontal horns, forms a tridentate plate; and (3) 'much less slender' antennules. Furthermore, *Sagmariasus* differs from *Jasus* in being distinctly green as juveniles rather than distinctly red. At maturity, *S. verreauxi* change from dark green to olive/brown green to orange-yellow (Booth, 1986), whereas *Jasus* spp. remain a similar shade of red throughout their lives.
4. Phyllosomas of *S. verreauxi* differ from *Jasus* spp. in having a rudimentary palp on the first maxilla, lacking subexopodal spines on the pereiopods, having no spines on the second and third segments of the antennae, and having the cephalic shield overlapping the coxae of the second rather than first pereiopods (Baisre, 1994).
5. The puerulus stage of *S. verreauxi* is readily distinguishable from *Jasus* spp. through its characteristically large rostral horn (Archey, 1916; Lie, 1969). Although of similar size to that of *Jasus* spp., the puerulus of *S. verreauxi* has longer antennae (Kittaka *et al.*, 1997), and the large adult size leads to a very much larger ratio of postlarva:adult size than in *Jasus* spp.
6. In New Zealand, and probably Australia, there is a strong contranatant migration by juveniles as they approach maturity (Booth, 1986; Phillips *et al.*, 2000), much more striking than in *Jasus* species. The greatest minimum distance covered by one tagged individual was 1070 km.

between the New Zealand and Australian stocks of *S. verreauxi*, except for a provisional result (Brasher *et al.*, 1992b) suggesting similar haplotypes on the same side of the Tasman Sea, in either Australia or New Zealand, and the possession in some of the samples of unique restriction sites (Ovenden & Brasher, 2000). This may mean that the New Zealand and Australian stocks should be considered separate species (George, 1997), but more sampling is needed.

Projasus lobsters, together with *Jasus* and *Sagmariasus*, make up the Silentes – palinurids that lack a stridulating organ at the base of the antennae (George & Main, 1967). All other palinurids belong to the Stridentes.

Jasus tristani is found at the Tristan da Cunha Archipelago and Gough Island, and on the Vema Seamount (Heydorn, 1969) (Plate 10.2). *J. lalandii* lives on the west and south coasts of southern Africa between 23° S and 28° E (Namibia and South Africa) (Pollock, 1986). *J. paulensis* lives in the Indian Ocean around St Paul and Amsterdam Islands (Holthuis, 1991), on seamounts over a wide area to the north-east of these islands (exploratory fishing referred to by Webber & Booth, 1988), and may be occasionally taken at Kerguelen Island (e. g. de la Rue, 1954, in Holthuis, 1991). A *Jasus* lobster has also been reported, in places in commercial quantities, from seamounts and banks on the Southwest Indian Ridge south and south-east of Madagascar between 36° S and 38° S. Although this lobster has been recorded as *J. lalandii* (Romanov, 2003), G. Duhamel, Museum national d'histoire naturelle, Paris (personal communication) has confirmed that *J. paulensis* is found there (Registration MNHN-Pa1801). Any *Jasus* lobsters on the nearby Walters Shoals (33° 12∞S, 43° 52∞E) (Collette & Parin, 1991), part of the Madagascar Ridge, are likely to be the same species.

J. edwardsii is widespread in Australasia. In Australia, it is found south from Geraldton in the west, along the south coast and around Tasmania, and as far north as Coffs Harbour on the east coast (Phillips *et al.*, 2000). It is also on seamounts and rises in the Tasman Sea. In New Zealand coastal waters *J. edwardsii* occurs from the Three Kings Islands in the north to the Auckland Islands in the south, and east to the Chatham Islands (Booth, 2000). *J. caveorum* is found on the non-emergent Foundation Seamount Chain in the east South Pacific Ocean, where it has been taken between 140 m (the shallowest depth fished) and 180 m (Webber & Booth, 1995). *J. frontalis* is known from the Juan Fernandez Archipelago and Islas Desventuradas off Chile in the east South Pacific Ocean (Arana, 1987; Holthuis, 1991).

A rock lobster best fitting the description of *Jasus* was taken in quantity (tonnes) in the early 1960s on South Pacific Ocean seamounts south-east of the Foundation Seamount Chain, near 40° S 100° W (author's unpublished data). No specimens are available and recent fishing in this general area has failed to relocate the source of these lobsters. Further, a *Jasus* larva, which could not be allocated to any known species, was taken in the South Atlantic Ocean (Booth & Ovenden, 2000), suggesting at least one more species yet to be discovered.

Sagmariasus verreauxi forms small commercial fisheries in south-east Australia (about 100 t per year) and northern New Zealand (about 20 t) (Montgomery, 1999; Booth, 2000; Phillips *et al.*, 2000). There are two species of *Projasus*, *P. bahamondei* off Chile, which is fished commercially (Retemal & Arana, 2000), and *P. parkeri* in the west South Pacific Ocean and Tasman Sea, south Indian Ocean, off southern South Africa, and in the east South Atlantic Ocean (Webber & Booth, 1988). *P. parkeri* is the deepest-known palinurid, being found between 300 m and at least 800 m.

10.2 Reproduction, life history and growth

Jasus edwardsii and *J. lalandii* are the most studied species, but the following – which also draws on the somewhat more scattered reports concerning the other *Jasus* spp. – shows that the species are reproductively very similar (Table 10.1).

Sexual maturity in female *Jasus* is reached at 56–120 mm carapace length (CL), 3–7 years after settlement, depending on species and, for particular species, the locality. Size and age of males at maturity are much more difficult to gauge, size anyway usually being similar to or smaller than that of the females in the same area (Pollock, 1986; MacDiarmid, 1989; Turner *et al*., 2002).

Breeding of *Jasus* is mainly over the winter months. Females spawn once each year, in autumn (April to May), and the eggs hatch in spring to summer (September to January). Fertilisation is external, the male depositing a packet of sperm on the sternum of the female. The packet starts to disintegrate immediately and so the female must rapidly extrude her eggs, egg laying and attachment taking about 50 minutes. In *J. edwardsii*, mating takes place soon after the female moults, large females moulting and mating earlier than smaller females (MacDiarmid & Booth, 2003). Large males prefer to mate with large females and if no males are available, females can resorb eggs, sometimes resulting in ovarian scars and reduced clutch sizes the following year. Indeed, sperm limitation may be a limiting factor in the reproduction of fished populations (e.g. MacDiarmid & Butler, 1999). The eggs are small (just under 1 mm diameter) and fecundity is high (tens of thousands to hundreds of thousands), incubation in *J. edwardsii* lasting 100–150 days depending on water temperatures (MacDiarmid & Booth, 2003).

Jasus are typical shallow-water palinurids in that they spend months as phyllosoma larvae in waters tens to hundreds of kilometres from shore (Lazarus, 1967; Lesser, 1978; Pollock, 1986, 1990a, 1991; Booth, 1994; Booth & Ovenden, 2000; Bruce *et al*., 2000). Early development comprises naupliosoma and phyllosoma larval phases and a post-larval puerulus phase. Hatching to the short-lived (hours) and small (1–2 mm long) naupliosoma takes place near sunrise over several days (MacDiarmid, 1985). The phyllosoma is a long-lived (months), leaf-like, transparent, planktonic zoeal larva that reaches 35–50 mm in length. Phyllosomal instars are grouped into stages, based on development. Early phyllosomas are rapidly transported offshore and most of the phyllosoma development takes place in oceanic waters.

The larval development period of *J. edwardsii* and *J. lalandii* in nature is estimated to be at least 12–22 months, even though larvae can be cultured to metamorphosis in 7–12 months (Kittaka, 1988; Kittaka *et al*., 1988, 2005; Ritar & Smith, 2005). The mid- and late-stage *Jasus* phyllosomas (Fig. 10.1) are distinguishable from other palinurids mainly by the shape of the cephalic shield; also, unlike most other palinurids, *Jasus* larvae

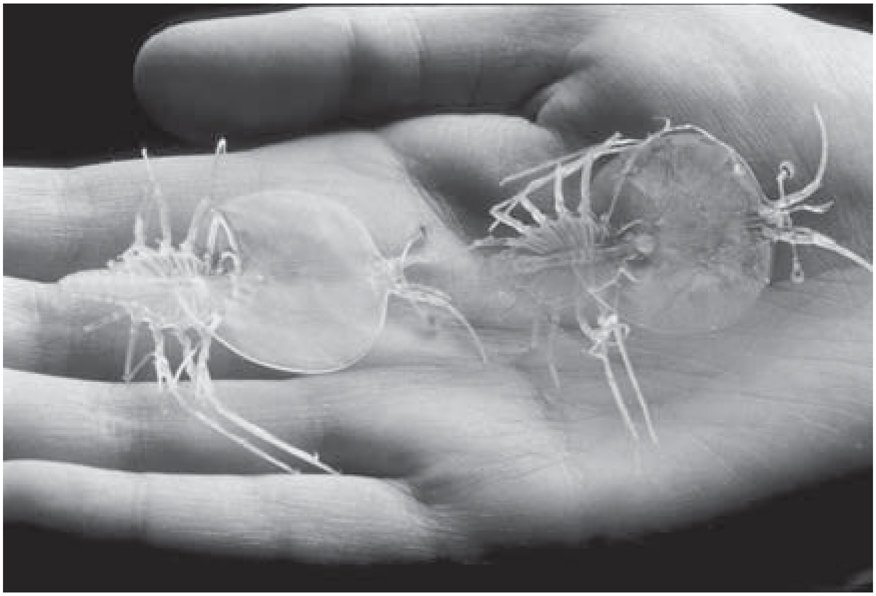

Fig. 10.1 Final-stage phyllosoma larvae of *Jasus edwardsii*.

do not have an exopod on the third maxilliped. This may also be true of the *Projasus* phyllosoma, which is yet to be described. (*S. verreauxi* has this exopod, at least in the later stages.) However, *Jasus* spp. larvae cannot be separated morphologically, mtDNA being the only way to determine the species. They return shoreward as pueruli after metamorphosing near the shelf break. Settlement is often highest during winter (Holthuis & Sivertsen, 1967; Pollock, 1986; Booth, 1994; Kennedy *et al.*, 1994), which, given hatching is mainly in spring, points to a larval life of about 18 months. But settlement is often also high in summer, and indeed can occur at any time of the year, so a larval life longer than 18 months is also likely.

Phyllosomas in culture swim horizontally only weakly (Kittaka, 1994) and this, together with their shape, suggest that these larvae are suited to passive drift. This means that currents are likely to be important in the transport and dispersal of larvae during their months offshore. Indeed, the strength of the east-directed flow in the Southern Ocean (e.g. Shannon *et al.*, 1973), together with the duration of the larval stage, mean that theoretically *Jasus* larvae could disperse over large tracts of the Southern Hemisphere. However, in general, *Jasus* larvae appear to remain near (within a few hundred kilometres) the adults (Booth & Ovenden, 2000), suggesting that larvae make use of either or both behavioural strategies and physical mechanisms to avoid being carried too far from parent ground. Eddies in particular may be crucial in this and in providing a means of shoreward transport for the late-stage larvae (Chiswell & Booth 1999; Bruce *et al.*, 2000). It is therefore unlikely that larval recruitment mechanisms on the scale of ocean basins exist for *Jasus* spp. (see Pollock, 1990b). *Jasus* larvae that do appear to be transported great distances from their point of hatching are *J. edwardsii*, carried the 2000 km from Australia to New Zealand (Chiswell *et al.*, 2003), and possibly *J. tristani* larvae from near Tristan da Cunha to the Vema Seamount (Lutjeharms & Heydorn, 1981), although there may be a local recruitment mechanism in effect at Vema, as there must be for the other island and seamount populations of *Jasus* such as *J. frontalis*.

Fig. 10.2 Pueruli of *Jasus edwardsii*, the white digestive gland indicating that settlement has taken place.

The puerulus stage (Fig. 10.2), a stronger horizontal swimmer than the phyllosoma, completes the oceanic phase by returning to shallow waters (mainly <20 m) and settling in small holes and crevices. The puerulus resembles the juvenile in shape and is 25 mm long, but is almost completely transparent. Any feeding by pueruli is probably confined to small, soft materials (Nishida *et al.*, 1990; Jeffs *et al.*, 1999). Settlement is mainly at night and at any part of the lunar phase, is usually seasonal, and levels of settlement at particular sites can vary ten fold or more from year to year (Booth, 1994). There is growing evidence that the ocean climate – the large-scale response of the ocean to the atmospheric climate – influences levels of puerulus recruitment. For example, in the south-east of the North Island of New Zealand, high *J. edwardsii* settlement rates are correlated with southerly storminess, this in turn being a significant component of El Niño conditions (Booth *et al.*, 2000).

The higher settlement with southerlies may be a consequence of enhanced westward (Ekman) surface drift in the upper layers of the ocean. This could act on the late-stage phyllosomas, helping transport them towards the shelf break where metamorphosis takes place, and/or it could assist the shoreward swim of pueruli. But the pattern and mechanism may vary with location: for example, there was not a higher *J. edwardsii* settlement in El Niño years off eastern Tasmania, Australia (Frusher *et al.*, 1999; Gardner *et al.*, 2001).

The pueruli of *J. edwardsii* moult into juveniles 1–3 weeks after settlement, according to water temperature (Booth & Stewart, 1993; Frusher *et al.*, 1999). Duration of the first juvenile instar varies seasonally between 30–70 days. Because they are so cryptic and difficult to tag and recapture, little is known of growth and its variability until the lobsters reach about three years of age. However, field and laboratory studies show that *J. edwardsii* moult many times in the first year, reaching about 38 mm CL; they are about 58 mm CL by the end of the second year, and about 75 mm CL after three years.

Males and females have similar growth rates until they mature, after which the moult increment of females falls off dramatically as more resources go into egg production. Mature lobsters usually moult only once a year, although moulting may be less frequent among the larger lobsters. Females usually moult in late summer to early winter – before breeding so that the pleopodal setae are fresh for egg attachment – and males in late spring/early summer. Growth rates can vary a lot from place to place, even over quite short distances and in relation to the quality of diet, and they can also vary a lot from year to year (e.g. Melville-Smith *et al.*, 1995; Mayfield *et al.*, 2000a, b).

10.3 Ecology and behaviour

Again, most is known of *J. edwardsii* and *J. lalandii*, but it is expected that all *Jasus* spp. will be similar. *Jasus* lobsters live mainly on rocky reefs, but can also be found on light foul ground, from the intertidal to 200 m (and occasionally to 400 m) (Pollock, 1986; Frusher *et al.*, 1999; Pollock *et al.*, 2000; MacDiarmid & Booth, 2003). Although several species are found on seamounts, ridges or banks well away from major landmasses, so far only *J. caveorum* is known to be confined to them.

Pueruli and young juveniles are asocial, normally occupying small holes and crevices, but as they grow they become increasingly communal, often aggregating in dens (Butler *et al.*, 1999; Frusher *et al.*, 1999) that provide shelter from predators and storms, and shade from the sun. Once mature, however, propensity to shelter together varies seasonally, especially among the males (MacDiarmid & Booth, 2003). During mating, males tend to be aggressive and both males and females are more solitary. Once mating is over, both sexes increasingly share dens, and at the moult certainly do.

Jasus lobsters forage between dusk and dawn, eating a wide variety of mainly sessile or slow-moving species including other crustacea, molluscs, echinoids, and a variety of algae (Fielder, 1965; Barkai *et al.*, 1996; Frusher *et al.*, 1999; MacDiarmid & Booth, 2003). *J. lalandii* appears to be a particularly selective forager (Mayfield *et al.*, 2000a); its ability to digest plant tissue may be limited, but interestingly, this species actively selects and can digest sponges (Barkai *et al.*, 1996). Cannibalism can be a significant cause of mortality, particularly among moulting lobsters (e.g. Mayfield *et al.*, 2000b).

In a few places, *Jasus* rock lobsters undertake long-distance migrations (Booth, 1997). These large-scale, directed migrations of juveniles in certain areas are probably important to the larval recruitment process because they can counter the effects of larval drift and so help maintain populations. For example, during spring and early summer, variable but generally small proportions of small male and immature female *J. edwardsii* move various distances against the general direction of flow of the coastal current along the east and south coasts of the South Island of New Zealand towards Fiordland and south Westland (Street, 1995). Migrations of at least 100 km have been observed from many tagging sites, with no evidence of any return migration; the greatest minimum distance covered by an individual tagged lobster was 460 km and the highest minimum rate of movement was 6.8 km d^{-1} (Street, 1971).

But such migrations do not appear to be common. More widespread among *Jasus* lobsters are inshore–offshore movements associated with moulting and breeding (Booth, 1997; Atkinson & Branch, 2003; Gardner *et al.*, 2003). For example, female *J. edwardsii* move inshore during autumn to moult, with mating and egg laying taking place up to a month later (Frusher *et al.*, 1999; MacDiarmid & Booth, 2003); males move inshore in spring to moult. In spring, towards the end of the egg-bearing period, females may migrate to the deep, seaward edges of reefs or beyond onto sand where, during the day they may form pods, their antennae facing outwards for protection. Larval dispersal at hatching here, as well as near headlands with high water movement, is probably enhanced.

The nearshore shelf waters along the coast of southern Africa south from central Namibia to Namaqualand, South Africa are characterised by regular periods of oxygen depletion brought about by biological decay. These have far-reaching effects on the behaviour and productivity of *J. lalandii* (Pollock *et al.*, 1997; Cockcroft, 2001), the seasonal variation in the depth of the oxygen-depleted waters bringing about seasonal changes in depth distribution of the lobsters (Pollock, 1986; Grobler & Noli-Peard, 1996). Indeed, large numbers of lobsters may come ashore to escape oxygen-depleted waters. For example, recent estimated lobster strandings, associated with decomposing phytoplankton blooms, have included 60 t in 1994, nearly 2000 t in 1997, and 200 t in 1999 (Cockcroft, 2001).

10.4 Predators and diseases

The smaller coastal and offshore midwater fishes presumably eat early-stage phyllosomas. Larger phyllosomas have been significant components of the stomach contents of larger pelagic fishes such as tunas and bramids, recent reports mirroring the specific examples given by Phillips and Sastry (1980). Pueruli are found in the gut of fishes, both pelagic and benthic, and are also taken by invertebrates such as octopuses. Young lobsters are eaten by a wide range of fish and invertebrates, including various cods, sea breams, wrasses, scorpion fish, conger eels, small sharks, and octopuses (Frusher *et al.*, 2000; MacDiarmid & Booth, 2003). As they grow, the lobsters are prone only to being preyed on by larger fishes and octopuses, eventually only large predators such as groupers and sharks being a threat.

The literature and field reports suggest that *Jasus* lobsters have low rates of debilitating disease and parasite infestation. In the Australian and New Zealand fisheries, the most obvious problem has been chitin and tissue erosion along the margins of the telson and uropods, which is possibly accentuated by multiple handling in the fishery.

10.5 Population dynamics

The typical pattern in the main commercial *Jasus* fisheries – as in virtually all fisheries – has been heavy exploitation of new areas, usually with phenomenally high initial catch rates followed by their dramatic decline and then, where managers have been able to exert control, some stability. New areas maintained many national landings in their early years, being fished further and further from port for the first time. But all the main fisheries are now fully exploited. Although offshore seamounts and banks continue to reveal new lobster grounds – and it is to be expected that many more will be found, some possibly even containing new species of *Jasus* (see Section 10.1) – these populations can be expected to be small and quickly extinguished, as for example the population on the Vema Seamount. The large area of seamounts near St Paul and Amsterdam Islands discussed earlier that apparently contain *J. paulensis* may still be only lightly fished but it is not expected to contain large resources of lobster capable of sustaining significant and enduring fisheries.

The greatly-extended larval life, which means that larvae invariably recruit towards the shore some distance from their point of hatching, and the likely role of ocean processes in determining levels of puerulus recruitment and therefore fishery production, mean that – beyond no breeding stock leading to no recruitment – there is unlikely to be a stock–recruitment relationship for any particular area fishery. Most *Jasus* fisheries are probably largely recruitment-driven rather than being directly and proportionally dependent on the number of breeders. Increasingly, the size and status of *Jasus* populations are being seen as a balance between the effects of the ocean climate, larval recruitment levels, environmental change, and fishing pressure.

Stock assessments have moved away from surplus production models of sustainable catch to more sophisticated length-based models based particularly on Bergh and Johnson (1992) and Punt and Kennedy (1997) to estimate productivity and stock status. These assessments lead to estimates of vulnerable stock size against such reference points as B_0 (virgin biomass) and B_{MSY} (biomass that will support the maximum sustainable yield). In several fisheries, stock rebuild trajectories, triggered by decision rules, initiate rebuild where necessary. These models can be very sensitive to the estimated growth rates, which can vary enormously between areas and over time. Problems with high interannual variability in growth are best illustrated by *J. lalandii* off the west coast of South Africa. Here the poor condition of lobsters – probably through decreases in ocean productivity, in turn linked to changes in the ocean climate – have led to greatly-reduced somatic growth rates and fishery production (Pollock *et al.*, 1997). Apparently stable fisheries can also undergo radical change in productivity over short periods through such things as shifts in levels of puerulus recruitment, which again may be related to environmental fluctuations (e.g. Booth *et al.*, 2000).

Only in fisheries with puerulus settlement monitoring programmes (*J. edwardsii*) and standardised potting surveys (*J. lalandii*) in place are long-term, fishery-independent estimates of the relative levels of recruitment possible; otherwise, recruitment is usually estimated within assessment models. Dive pre-recruit surveys have generally been found to be too labour-intensive, and catch sampling and logbook records of pre-recruit abundance from the commercial fishery unreliable, in predicting recruitment to *Jasus* fisheries. Growth rates have been reasonably well estimated through large tagging programmes, particularly in South Africa, South Australia, Tasmania, and New Zealand – but only for lobsters from about three years of age (about 70 mm CL). Natural mortality, *M* is unknown in *Jasus* and is often estimated within the assessment model. The most widely-used instantaneous rates are around 0.1–0.2.

It is only for the *J. lalandii* and *J. edwardsii* fisheries that there are frequent and regular, formal stock assessments. For the other species, they have been sporadic; recent assessments of *J. paulensis* and *J. frontalis* include those of Vranckx and Hureau (1977) and Yanez *et al.* (2000) respectively.

10.6 Harvests of wild populations and their regulation

All main fisheries are considered fully exploited, the occasional new areas generally being small offshore pockets quickly fished down. For all *Jasus* fisheries except those in international waters, output controls (quotas) generally prevail, but with input controls in common including a minimum legal size (MLS) and the prohibition on harvesting berried females. Many fisheries also have closed seasons and pot limits. The size limits first imposed were typically based on the smallest lobster the markets would accept, but in some instances these have later been modified to maximise egg per recruit. In most areas the size limit presently in place allows most females to breed before recruiting to the fishery.

The main commercial *Jasus* fisheries are for *J. lalandii* (South Africa and Namibia) and *J. edwardsii* (Australia and New Zealand). Smaller fisheries exist for *J. tristani* (Tristan da Cunha and Gough Island), *J. paulensis* (St Paul and Amsterdam Islands), and *J. frontalis* (Juan Fernandez and Islas Desventuradas). *J. caveorum* on the Foundation Seamount Chain are only occasionally fished. Regulations that apply in each fishery are given in Table 10.2 and the landings reported to the Food and Agriculture Organization (FAO) for the five years 1997–2001 are in Table 10.3. *Jasus* rock lobsters are also important recreational species in southern Africa, Australia, and New Zealand, and

Table 10.2 Management measures in effect in *Jasus* fisheries in 2004. Tristan, *J. tristani* at the Tristan da Cunha Archipelago and Gough Island; Namib, *J. lalandii* in Namibia; S Afr, *J. lalandii* in South Africa; St Paul, *J. paulensis* at St Paul and Amsterdam Islands; Austr, *J. edwardsii* in Australia; NZ, *J. edwardsii* in New Zealand; J Fernan., *J. frontalis* at Juan Fernandez Archipelago and Islas Desventuradas. (The Vema Seamount, Southwest Indian Ridge, and the Foundation Seamount Chain are in international waters.) ′ , measure applies; —, measure does not apply.

	Tristan	Namib.	S Afr.	St Paul	Austr.	NZ	J Fernan
Minimum legal size	′	′	′	′	′	′	′
Berried females protected	′	′	′	′	′	′	′
Number of boats	′	′	′	′	′	—	′
Type of gear	?	′	′	′	′	′	′
Number of pots	?	′	—	—	′	—	—
Characteristics of pots	?	′	′	′	′	—	—
Escape gaps	′	—	—	′	′	′	′
Sanctuaries	?	′	′	—	′	′	—
Closed season	′	′	′	′	′	A few	′
TACC	′	′	′	′	′	′	′
Recreational fishing prohibited	?	—	—	′	—	—	?

Table 10.3 Landings (t) of *Jasus* spp. for 1997–2001, from FAO (2001) for *J. frontalis*, A. Cockcroft (pers comm) for *J. tristani* (TACs given, which were thought to be fully caught) and *J. lalandii* (South Africa), K. Grobler (pers. comm.) for *J. lalandii* (Namibia), G. Duhamel (pers. comm.) for *J. paulensis*; S. Frusher for *J. edwardsii* (Australia), and Sullivan (2003) for *J. edwardsii* (New Zealand).

	1997	1998	1999	2000	2001
J. tristani	342	323	323	331	331
J. lalandii (Namibia)	257	260	307	342	327
J. lalandii (S Africa)	1679	1917	1793	1716	1610
J. paulensis	343	343	345	346	340
J. edwardsii (Australia)	4778	4887	4763	4638	4455
J. edwardsii (New Zealand)	2585	2726	2748	2796	2593
J. frontalis	32	21	22	17	21

of customary significance particularly in New Zealand.

10.6.1 South Africa and Namibia

The main fishery for *J. lalandii* lies between 25° S in Namibia and 34° S, to the east of Cape Peninsula in South Africa, a distance of about 1055 km, and in depths between 5 and 100 m (Pollock, 1986; Pollock *et al*., 2000).

The stability experienced by the South African commercial fishery during the 1980s ended in 1989 when instead of the usual 3500–4000 t being landed annually, only 3491 t of the 3900 t total allowable catch (TAC) were caught (Pollock *et al*., 2000). Landings were even lower the next year. These poor catches are believed to have been caused by a decrease in recruitment to the harvestable biomass in direct response to a dramatic reduction in somatic growth rates. This reduction has taken place for unknown reasons, but may be related to a large-scale environmental perturbation, possibly the 1990–1993 El Niño event influencing change in the productivity of the southern Benguela Current, and has affected both juveniles and adults (Pollock *et al.*, 1997; Hazell *et al.*, 2002). Changes were made to the minimum legal size soon after and the annual total allowable commercial catch (TACC) was rapidly reduced from 3790 t in 1990–1991 to 1500 t in 1995–1996. There has been a modest improvement in growth rate since, and a gradual increase in TACC to just over 1900 t in 1998–1999 (Pollock *et al.*, 2000).

A size-based model (Bergh & Johnston, 1992) has allowed investigation of the predicted temporal trends in various parameters thought to influence population dynamics. Such assessments suggest that the resource is heavily depleted, with the harvestable biomass at about 5% of its virgin level and spawning biomass at about 20% of that level. The operational management procedure in place is a standardised method for incorporating and analysing data to be used when setting annual TACCs, requiring as inputs the previous year's TACC and indices of commercial CPUE, the fishery-independent monitoring survey CPUE, and somatic growth rate estimates (Pollock *et al.*, 2000). The TACC is allocated proportionally over six zones (Groeneveld, 2004).

The Namibian fishery for *J. lalandii* is managed largely independently from that in South Africa (Grobler & Noli-Peard, 1997; Pollock *et al.*, 2000), recent TACCs being about 300 t. This fishery has undergone much change: catches in the 1960s were up to 9000 t, falling to a TACC and landing of 100 t in 1991–1992. Environmental change, including the extent of the oxygen depletions, appears to have a strong bearing on catch rates in this fishery.

10.6.2 Australia

Known locally as the 'southern' rock lobster, *J. edwardsii* has the widest distribution of any palinurid in Australia, supporting significant commercial fisheries in the states of South Australia, Tasmania, Victoria, and southern Western Australia (Phillips *et al.*, 2000). Most lobsters are taken at depths of 1–200 m, fishers using baited traps that they usually pull daily. There is currently no evidence that the breeding stock has reduced to a level that is affecting recruitment to the fishery, even though egg production levels have fallen to low levels in most areas of the fishery – well below 20% of the levels before exploitation.

All states control fisheries through limited entry, which restricts the numbers of boats and the numbers of traps that can be used (Phillips *et al.*, 2000). Most states have defined the size and design of the traps that can be used, including the need for escape gaps or large mesh to reduce capture and handling of undersized lobsters. There are seasonal closures and minimum legal sizes – according to varying size at maturity and non-biological historic decisions. Most of the fishery (Tasmania and southern South Australia) is now under TACC management with individual transferable quotas (ITQs) and consideration is being given to this form of management in Victoria.

In South Australia, about 65% of the approximately 2500 t commercial catch is taken in the Southern Zone, management of which is based on a TACC with ITQs (Phillips *et al.*, 2000). The Northern Zone still has an effort-controlled management system, but has a system of voluntary time closures to compensate for increases in effective fishing effort resulting from improved fishing efficiency. There are about 180 boats and 12 000 traps in the Southern Zone and 70 boats and 4000 traps in the Northern Zone. In Tasmania, there are over 300 boats using about 10 000 traps to take the TACC of about 1500 t. Victoria is divided into two zones, an eastern one with about 70 boats and 2600 traps and a western one with about 90 boats and 5400 traps; about 80% of the 400–500 t annual catch comes from the western zone. The limited-entry Western Australian commercial fishery is small – 100 t or less each year.

10.6.3 New Zealand

The main commercial fishery for the 'red' rock lobster *J. edwardsii* is along the east, south, and south-west coasts, including around Stewart Island. The once enormous Chatham Islands fishery – up to 6000 t per year – now has an annual landing of about 300 t. There are about 500 boats in the commercial fishery, the main depth range fished being 5–100 m. Vessels fish up to 400 traps, but more commonly 50–150. Traps are not restricted in number or type, except that they must have gaps to allow escape of small lobsters. There are seasonal restrictions on fishing in only three areas.

Fisheries in New Zealand must be managed so that stocks are maintained near B_{MSY}, the biomass that will support the maximum sustainable yield. Hence there are TACCs, and fishers fish under ITQs. The fishery is managed as two stocks, the North and South Island (including Stewart Island) stock (NSI) and the Chatham Islands stock (CHI). Within the NSI stock are three substocks: northern (NSN, composed of two Quota Management Areas (QMAs), each with separate TACCs), central eastern (NSC – three QMAs), and southern (NSS – two QMAs). The sum of the TACCs for the NSI stock for the 2003/04 fishing year was 2325 t of which 2159 t was landed; for the Chatham Islands these values were 360 and 286 t.

All stocks are fully exploited; the status of each relative to B_{MSY} is not entirely clear but in general, TACCs are being achieved (Sullivan, 2003). Stocks are assessed using a length-based model based on Punt and Kennedy (1997). A transition matrix that has no reference to age except at the recruitment phase is used, the heart of the model being a stochastic growth transition matrix that calculates the probabilities that animals of a certain length will grow into a vector of possible future lengths (Starr *et al.*, 2003). The model is fitted to standardised catch per pot lift, proportions at size from catch sampling, historical growth rates, and growth increments from ongoing tag–recapture programmes.

10.6.4 Other Jasus *fisheries*

Commercial exploitation of *J. tristani* at the Tristan da Cunha Archipelago (Tristan da Cunha, Inaccessible, and Nightingale Islands) and Gough Island is by the islanders and by a South African-based company (Pollock *et al.*, 2000). Recent annual landings have been about 320 t. There are individual TACCs for each of the four islands, along with size limits and gear restrictions. It is generally believed that this fishery is sustainable at current levels of fishing (Pollock, 1994; Pollock *et al.*, 2000). The Vema Seamount fishery was short-lived owing to severe over-exploitation of a very small, isolated fishing ground during the 1960s (Heydorn, 1969).

The *J. paulensis* fishery at St Paul and Amsterdam Islands is affected by a Reunion-based trawler with associated dories. Annual catches are 300–400 t (G. Duhamel, personal communication). Since the discovery of *J. caveorum* on the Foundation Seamount Chain in 1995, at least 20 t have been taken, using traps. Annual landings of *J. frontalis* from the Juan Fernandez Archipelago and Islas Desventuradas in the east South Pacific Ocean are about 20 t (FAO, 2001). Lobsters are fished at depths of 2–200 m with two-chambered pots (Arana, 1987).

10.7 Aquaculture and enhancement

Both *Jasus* and *Sagmariasus* lobsters are at the forefront of spiny lobster aquaculture initiatives. The first rock lobster species to be cultured from egg to settlement was *J. lalandii*, taking 10 months (Kittaka, 1988). *J. edwardsii* has also been grown to metamorphosis, taking 7–12 months (Kittaka *et al.*, 1988, 2005; Ritar & Smith, 2005). *Sagmariasus verreauxi* remains, however, the first and only species to be cultured from egg to settlement, then to be ongrown to breeding age (Kittaka *et al.*, 1997; J. Kittaka, personal communication).

Hatchery production of pueruli might be aimed at ongrowing onshore or in sea cages, or for release into the wild – but successful achievement of these is still some time off. Considerable research is presently being directed towards establishing commercial-scale larval culture and juvenile ongrowing of *J. edwardsii* in Australia (see http://www.frdc.com.au/research/programs/rleas); description of this work is beyond the scope of this chapter, but details can be found in Chapter 6.

Aquaculture can also involve ongrowing larvae or pueruli collected from the wild. In New Zealand, fishers can elect not to fish their quota and every year for each tonne of quota not fished, take 40 000 (or 30 kg) pueruli and young juveniles for ongrowing. A similar scheme exists in Tasmania, Australia but in order to maintain or better ‘biological neutrality’, 50% of the lobsters must be returned to the sea after being grown for one year. The aim in both countries is to produce lobsters of optimal market size, a size that may or may not be over the MLS enforced in the wild fishery. But the economics of this approach remain far from clear: collection costs have been high, there have been problems with lobster mortalities in recirculating water systems, and production so far has been very low.

Interest in the enhancement of marine resources – manipulating the physical or biotic environment in order to increase harvests, and/or supplementing natural recruitment by introducing new stock – is growing internationally. The most successful enhancement technique practised (and still only experimentally) for palinurids anywhere is the provision of artificial shelter for settling pueruli and young juveniles of *Panulirus argus* in the Caribbean, simple shelters being shown to significantly increase juvenile survival, abundance, and catches (e.g. Butler & Herrnkind, 1997; Briones-Fourzán & Lozano-Álvarez, 2001). Although trials are underway in New Zealand using a similar approach for *J. edwardsii* (NIWA, unpublished), there is no known enhancement of *Jasus* species.

10.8 Management and conservation

Universal among *Jasus* fisheries (apart from those in international waters) are an MLS and protection of breeding females. Also there are output controls, which limit commercial harvests, and caps on daily amateur catches. Specifics of these were discussed above and also appear in Table 10.2. In most, but not in all instances, does the MLS ensure breeding throughout the range of the lobster. For example, in New Zealand most female *J. edwardsii* in the south and south-east of the South Island do not breed before recruiting to the fishery, but any fisheries implications of this are not clear. No maximum legal sizes are in place for any *Jasus* sp.

Worldwide there is growing pressure to secure more areas as protected areas. The stated purposes of these are many, the main ones concerning restoring sections of the shore to a pristine state and increasing larval productivity. If widespread enough, protected areas can provide significantly more breeding lobsters, and may help to negate any possible genetic consequences from fisheries selection in the harvested stock. In New Zealand, for example, there are 15 widely-distributed, mainly small (<1000 ha) marine protected areas where no marine life, including lobsters, may be taken. Sanctuaries also exist in southern Africa and Australia. *Jasus* rock lobsters are often the conspicuous species used to demonstrate recovery in size and number after the establishment of marine sanctuaries. The greatest immediate commercial benefit of these areas for lobster fisheries may be cross-boundary movements of lobsters into surrounding fished areas (e.g. Kelly *et al.*, 2002).

Trap fisheries are generally viewed as being relatively selective for the species harvested and to bring about little damage. Perhaps the greatest impact is to benthic epifauna such as corals, particularly where a trap is dragged along reef edges and ledges during hauling. By-catches in *Jasus* trap fisheries are generally not viewed as significant. Traps in Tasmania set for rock lobsters catch over 30 fish species, 10 crustaceans and 10 other invertebrates (Frusher & Gibson, 1999), but the use of escape gaps reduces this by-catch significantly. Furthermore, most by-catch reaches the surface alive and can be returned alive.

10.9 Conclusions

Jasus species and fisheries are widespread in southern waters, several being associated with remote island groups and one, *J. caveorum*, only on seamounts. There is a great deal of similarity in the biology of these *Jasus* species, which in turn differ in numerous ways from *Sagmariasus* (formerly *Jasus*) *verreauxi*, a species confined to Australasia. *Jasus* breed over winter and have a long-lived and widely-dispersed phyllosoma larval phase. Both larval behaviour and the oceanography are thought to play important roles in the retention of larvae and in the recruitment of the postlarval puerulus to the coastal reefs. All known *Jasus* stocks are fully exploited; although further stocks may be located, it is expected that they will be localised to seamounts and ridges and unable to sustain significant and enduring fisheries. *Jasus* fisheries are managed mainly by quotas, together with size and season restrictions and prohibition on the harvesting of egg-bearing females. The largest fisheries are for *J. edwardsii* in Australia and New

Zealand, and *J. lalandii* in South Africa. Stock assessments mainly use length-based models to determine productivity and stock status, often leading to estimates of vulnerable stock size against such reference points as B_0 and B_{MSY}. All main commercial fisheries are trap fisheries, which are relatively selective for the species being harvested and cause relatively little collateral damage. The use of escape gaps reduces by-catch significantly, much of which can be returned alive. There is not yet any significant aquaculture or enhancement production of *Jasus* spp. *Jasus* rock lobsters are often a conspicuous species used to demonstrate recovery in individual size and population numbers after the establishment of marine sanctuaries, more and more of which are being set up worldwide.

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Chapter 11
Panulirus Species

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11.1 Species and distribution

Lipcius and Eggleston (2000) have succinctly summarised the systematics, evolution and morphology of more than 20 species of *Panulirus* found in the tropical and subtropical waters of the world's oceans. Variously known as 'rock' or 'spiny' lobsters (and even rocklobsters in Australia), depending on local traditions and trade requirements, they provide a valuable source of seafood and exports for a large number of countries.

The worldwide distribution of *Panulirus* lobsters is shown in Plate 11.1. In some areas there is a wide range of species. For example, some 10 species are recorded from India but the fisheries are confined to *P. polyphagus*, *P. versicolor*, *P. ornatus* and *P. homarus*. Fisheries are based on almost all *Panulirus* species but not all have been successfully managed. For example, fisheries for commercial *Panulirus marginatus* in the Hawaiian Islands, *Panulirus pascuensis* at the Easter Islands, and *Panulirus japonicus* in Taiwan have essentially disappeared, although the same species may be fished in other areas. This review concentrates on the larger fisheries, or those showing interesting developments in recent years, as part of their quest for sustainable management.

11.2 Life history, growth and reproduction

The life cycle of all *Panulirus* species is complex and includes a long oceanic larval phase, which varies in length between species (see diagrammatic life history for *P. cygnus*, Fig. 11.1). In the western rock lobster, *Panulirus cygnus*, it is estimated to be 9–11 months (Phillips *et al.*, 1979). Tropical species in contrast, may have shorter oceanic cycles, and in *Panulirus ornatus* for example, the larval phase is estimated to be only 4–7 months (Dennis *et al.*, 2001).

Spiny lobsters hatch as planktonic phyllosoma larvae (about 1–2 mm long) and develop through a series of moults, increasing in size. After developing in offshore waters, phyllosoma return towards the continental shelf where the final stage larvae metamorphose into the puerulus, a non-feeding stage (about 30 mm in total), which then swims towards the coast.

When the puerulus settles, it moults after a few days to weeks into a benthic juvenile stage. Small juveniles (often called post-pueruli) are usually found in shallow coastal reefs and larger juveniles and adults in deeper water offshore. It is in these depths that they reach maturity, that mating takes place, and that the life cycle is completed.

For many spiny lobster species there are data on female fecundity, growth rates of juveniles and age at maturity in the wild, natural diets of the juveniles and adults, natural densities in the wild, as well as some information on cannibalism and health. By contrast, there are few data on the ecology of the larvae and puerulus stages of *Panulirus*, except for *P. cygnus* in Western Australia (Booth & Phillips, 1994); *P. argus* off the Cuban and Florida coasts (Butler & Herrnkind, 2000; Yeung & Lee, 2002); and *P. japonicus* off Japan (Yoshimura *et al.*, 1999; Sekiguchi & Inoue, 2002).

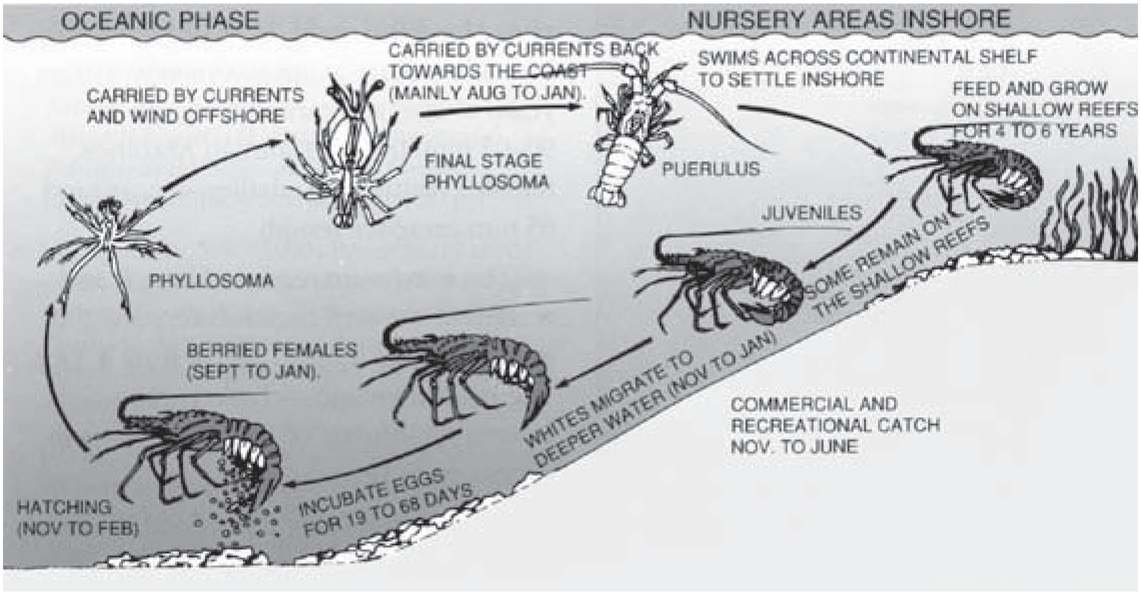

Fig. 11.1 Schematic life history of the western rock lobster, *Panulirus cygnus* (from Kailola *et al.*, 1993).

Growth rates are a key component of stock assessment models for any species. In the case of *Panulirus* lobsters, the need to have reliable information on this important parameter has encouraged considerable research on the subject in most of the commercially important species (e.g. Smale, 1978; Phillips *et al.*, 1992; Skewes *et al.*, 1997). As with all decapods, lobsters of this genus grow rapidly to maturity, but slow down thereafter. Growth rates are highly variable across the genus, with tropical species tending to grow very much faster than their temperate relatives. For example, maturity is reached approximately six to seven years after settlement in *P. cygnus* (Chittleborough, 1976), a temperate species, whereas it is reached after only two years in the tropical species *P. homarus* (Smale, 1978).

As with growth, the necessity to have a good understanding of reproduction in a managed fishery has encouraged much research on this subject in the commercially-fished species within the genus. Obviously size at maturity of females and males varies for different species in the genus, but research has shown that this parameter can vary substantially both spatially (e.g. in *P. cygnus*, Chittleborough, 1976; *P. homarus*, Mohan, 1997; *P. argus*, Arango & Marquez (1995) and *P. guttatus* Robertson & Butler, 2003) and temporally (e.g. *P. marginatus*, Polovina, 1989; DeMartini *et al.*, 2003) for the various species.

The temperate species in this genus tend to have a well-defined breeding season during which they carry one or more broods of eggs (*P. cygnus*, Chittleborough, 1976). By comparison, the tropical species tend to spawn throughout the year (e.g. *P. inflatus* and *P. gracilis*, Briones-Fourzán & Lozano-Álvarez, 1992). Overall therefore, the tropical species produce more eggs per year on average than the temperate species, but are likely to have a shorter life expectancy than their temperate relatives due to higher mortality rates that are generally considered to be a feature of the warm tropical water environments.

11.3 Predators and diseases

The phyllosoma larvae, puerulus, juvenile and adult stages are all subject to predation (Chapter 8). Phyllosoma and pueruli are often part of the stomach contents of pelagic fish (Phillips & Sastry, 1980) and nearshore fish prey on pueruli and small juveniles (Howard, 1988). Larger juveniles and adults fall prey to sharks and fish, as evidenced in Cuba (Cruz & Phillips, 2000).

Rock lobsters are more susceptible to developing health problems including infectious diseases when they have been stressed, injured, have just moulted or are about to moult, have had unsuitable feed or been held at a high stocking density (Chapter 5). Stress often occurs when lobsters are held in water of less than optimal water quality and during capture and transport, especially if they have been held in air during this process. The majority of diseases identified in rock lobsters to date have been the result of opportunistic infections rather than primary pathogens. Opportunistic pathogens commonly include bacteria, fungi and protozoa that are present in the lobster's environment but do not cause disease unless lobsters are stressed or damaged by some of the factors outlined above.

Some of the more common disease problems seen in rock lobster include 'white tail', caused by an intracellular protozoan parasite, tail fan necrosis or shell disease, weak lobsters (often the result of a generalised bacterial infection) and fouling of the gills and carapace. 'Turgid lobster syndrome' in which the soft areas of the lobster bulge from the harder shell, and pink-fleshed lobsters are conditions that are sometimes seen and may have a number of causes. Further investigation is needed to identify the range of environmental, physiological and disease conditions that can result in the two latter syndromes.

11.4 Ecology and behaviour

A very thorough review of juvenile and adult ecology is undertaken in Chapter 8 and of behaviour in Chapter 3. *Panulirus* lobsters are widespread and numerous, particularly on rocky and coral substrates, though some members of the genus, such as *P. polyphagus*, are found on the soft muddy bottom. Without exception, they remain hidden by day and emerge to forage nocturnally so as to avoid their many predators. All members of the genus are non-specialist feeders, foraging on a wide range of food items.

In the relatively few *Panulirus* species for which this information is recorded, there is a general trend for the juveniles to be found in shallow inshore areas (e.g. *P. japonicus*, Yoshimura & Yamakawa, 1988; *P. argus*, Butler & Herrnkind, 2000; *P. cygnus*, Phillips *et al.*, 2001), shallower than those depths at which the bulk of the adult population is to be found.

Early juvenile spiny lobsters tend to be solitary in the small holes or dens that they choose, but as they grow they become gregarious. For example, Fitzpatrick *et al.* (1990), showed that in *P. cygnus*, over 95% of newly-settled pueruli and postpueruli (6–10 mm) CL were solitary, but less than 20% of animals that had been settled for about a year (i.e. 20–25 mm CL) were solitary. Their gregarious behaviour is considered an effective anti-predator strategy (Butler *et al.*, 1999). Natural mortality rates of lobsters, but particularly juvenile animals, are extremely high. Herrnkind and Butler (1994) estimated mortality of *P. argus* to be 96–99% in the first year after settlement and Phillips *et al.* (2003) had similarly high estimates of 80–96% for *P. cygnus* juveniles at the end of their first year after settlement. In the case of *P. cygnus*, as few as 3% of settling pueruli are estimated to survive to recruit into the fishery 3.5 years after they first settled as pueruli (Phillips *et al.*, 2003).

Several species of *Panulirus* undertake substantial migrations as they approach or reach sexual maturity (e.g. *P. argus*, Kanciruk & Herrnkind, 1978; *P. cygnus*, Phillips, 1983; *P. ornatus*, Bell *et al.*, 1987). Once settled in their dens, spiny lobsters can stay for long periods of time, often occupying the same holes, or at least holes within the same home range, for months or even years (Chittleborough, 1974).

11.5 Population dynamics and regulation

Exploitation rates on commercially fished populations of spiny lobsters, where they have been measured, are frequently high (e.g. 0.71–0.83 for *P. argus* in Chinchorro, Mexico (Sosa-Cordero *et al.*, 1996), 1.43 for male and 0.8 for female *P. polyphagus* trawled off Bombay, India (Kagwade, 1995), and 0.92–2.30 for *P. cygnus* caught by pots in different regions of the fishery in Western Australia (Wright *et al.*, 2006). However, they are highly fecund species and provided a reasonable level of the breeding stock is maintained, they are able to sustain high catch levels under most circumstances.

Long time-series of pueruli, early postpueruli and pre-recruit abundances and their relationship to subsequent commercial and recreational landings, have provided managers with the ability to predict catches in the *P. cygnus* fishery and the Cuban catch component of the *P. argus* fishery (Caputi & Brown, 1986; Cruz *et al.*, 1995; Caputi *et al.*, 1995; Melville-Smith *et al.*, 2004).

11.6 Harvest of wild populations and their regulations

All *Panulirus* fisheries are now considered fully exploited. This is an important point, because the nature of fishing is an aggressive activity, with participants seeking to achieve higher or more valuable catches. With the lack of ability for fishers to increase their catch size we have seen a strong trend towards value-adding to the catch, usually by marketing live lobsters to the highest paying customers who are often on the other side of the world to where the catch is made.

Most of the large fisheries for this genus have management measures such as input or output controls, legal minimum sizes and others (Table 11.1). Controls are variable in their scope and enforcement, but as a generalisation it could be said that management controls in the African and Asian sub-regions are few and weak – though there are exceptions – Japan and South Africa being cases in point.

As with the lack of management controls on the African and Asian continents, there is also a lack of information in the Food and Agriculture Organization's (FAO) statistics on the landings of spiny lobsters throughout these regions. We have endeavoured to present information on the landings of those species that contribute amongst the largest spiny lobster tonnages on world markets. We acknowledge that in many cases (in particular *P. longipes* and *P. ornatus*), the landings in Table 11.2 are gross underestimates of actual catches.

In some commercial lobster fishing situations, regulations on the fishery have been extreme. For example the US National Marine Fisheries Service (NMFS) and a Federal District Court ruling halted lobster (*Panulirus marginatus*) fishing in the Hawaiian Islands in mid-2000, because of pressure from several environmental lobby groups who considered that the lobster fishery was contributing to the starvation of the monk seals by harvesting one of the seals' food sources (Environment News Service, 2000; Tighe, 2000).

In the following section, we have selected a few *Panulirus* fisheries for more detailed discussion. These fisheries have been chosen because they are widespread in terms of global coverage and in most cases are very productive.

11.6.1 Australia and Papua New Guinea

Panulirus cygnus

The western rock lobster, *Panulirus cygnus*, is found only in temperate waters on the west coast of Australia. The juveniles populate the shallow inshore limestone reefs and the breeding stock is found offshore (35–90 m) and at the Abrolhos Islands, which are situated on the continental shelf edge (Phillips *et al.*, 2000a).

The Western Rock Lobster Fishery currently has 545 boats operating about 57 000 pots. Their average annual catch over the last decade of 11 400 tonnes (Fig. 11.2) is valued at around US$300 million, making this Australia's most valuable single-species fishery. In addition to the commercial catch, recreational fishers take about 600 tonnes a year (Melville-Smith *et al.*, 2004). The ability of this fishery to survive is maintained by analysis of a comprehensive fisheries database, some of which dates back to the 1960s (e.g. catch, effort, length-frequencies, fishery-independent breeding-stock surveys, puerulus settlement monitoring, recreational catch monitoring); an extensive set of management controls (including a limited fishing season and legal minimum and maximum sizes); and an effective compliance programme.

Table 11.1 Management measures in effect in selected *Panulirus* fisheries in 2005.

	P. argus	*P. argus*	*P. argus*	*P. argus*	*P. argus/ P. laevicauda*	*P. cygnus*	*P. gracilis*	*P. inflatus*
	Bahamas	British Virgin Is	Mexico	USA	Brazil	Australia	Mexico	Mexico
* Notes	7	7	6		11		6	6
Minimum legal size	∞	∞	∞	∞	∞	∞	∞	∞
Berried females protected	∞	∞	∞	∞	no	∞	∞	∞
Number of boats	no	no	no	no	∞	∞	no	no
Type of gear specified	∞	∞	∞	∞	∞	∞	∞	∞
Number of pots	no	no		∞	no	∞	no	no
Characteristics of pots	no	no		∞	no	∞		
Escape gaps	no	no		no	no	no		
Sanctuaries	∞	no	∞	∞	∞	∞		
Closed season	∞	no	no	no	no	no	no	no
TACC	no	no	no				no	no
Recreational fishing allowed	no	no	no	∞	no	no	no	no

Table 11.1 *continued*

	P. interruptus	*P. interruptus*	*P. ornatus*	*P. ornatus*	*P. ornatus*	*P. ornatus/ P.polyphagus/ P. homarus*	*P. ornatus/ P. homarus/ P. longipes*	*P. ornatus/ P. homarus/ P. longipes*
	Mexico	USA	Australia (Queensland)	Papua New Guinea	Torres Strait	India (indicative)	Kenya	Somalia
*Notes	6	9, 10	4, 5	1, 3, 5	2, 3, 5		12	12
Minimum legal size	∞	∞	∞	∞	∞	∞ for export	no	no
Berried females protected	∞	∞	∞	no	no	no	legislated, not enforced	no
Number of boats		∞	no			no	no	no
Type of gear	∞	∞			∞	no	no scuba	no
Number of pots		no	N/A	N/A	N/A	no	N/A	no
Characteristics of pots		no	N/A	N/A	N/A	no	N/A	no
Escape gaps	no	no	N/A	N/A	N/A	no	N/A	no
Sanctuaries	no	no	∞ Green zones	no	no	no	∞	No
Closed season	no	no	no	no	no	no	no	no
TACC	Voluntary		no	no	no	no	no	no
Recreational fishing allowed	no	no	no		no	no	none exists	none exists

*Notes

1. Only 7 freezer boats, unlimited dinghies.
2. Licence cap in place for fully transferable licences (24 primary boats), however Traditional Inhabitant licences are not capped.
3. Berried females rarely encountered in area of fishery.
4. Queensland waters south of 14° S latitude are closed to commercial fishing for lobster.
5. J. Prescott, pers. comm.
6. P. Briones-Fourzán, pers. comm.
7. R. Power, pers. comm.
8. A.A. Fonteles-Filho (2000).
9. Fish and Game Commission, California (2001). Sport fishing, California regulations. Office of State Publishing, California, USA.
10. Fish and Game Commission, California (2001). Digest of California, commercial fish laws and licensing requirements. Office of State Publishing, California, USA.
11. Fonteles-Filho (2000); C. Chaffee pers. comm.; R. Schärer, pers. comm.
12. A. Kulmiye, pers. comm.

Table 11.2 Landings (tonnes) of *Panulirus* spp. for 1997–2003 (*from FAO, 2005 and **from other sources). The FAO data are best considered indicative of the scale of landings of each species from each area, rather than being accurate representations. NA indicates data unavailable.

		1997	1998	1999	2000	2001	2002	2003
Australian spiny lobster	*Panulirus cygnus*	9 902	10 478	13 009	14 433	11 273	8 983	11 387
Caribbean spiny lobster*	*Panulirus argus*	36 756	34 165	38 098	37 631	31 863	38 344	33 327
Longlegged spiny lobster*	*Panulirus longipes*	1 082	1 098	1 166	1 716	1 924	1 782	2 082
California Spiny Lobster**	*Panulirus interruptus*	1 879	1 663	1 634	2 148	1 978	1 795	NA
Tropical spiny lobsters, various*	*Panulirus* spp.	11 282	10 047	10 286	11 203	12 687	13 257	14 287
Ornate lobster** (Torres Strait and the east coast of Queensland, Australia)	*Panulirus ornatus*	566	573	390	393	109	201	508

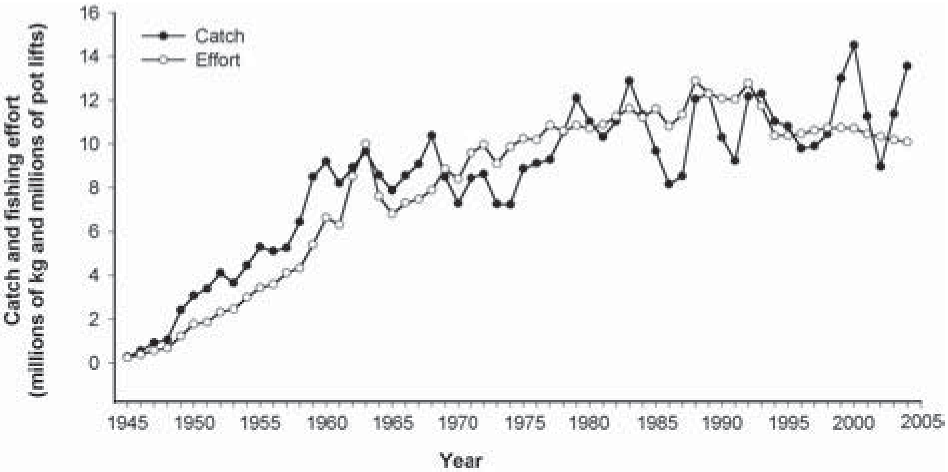

Fig. 11.2 Annual western rock lobster, *Panulirus cygnus*, catch and nominal fishing effort.

Effort in the fishery is controlled by input restrictions on the number of pots allowed and number of days fishing, which are implemented after considerable consultation with industry.

The principal method of ensuring the sustainability of the fishery is by monitoring the size of the breeding stock, using data from both a commercial at-sea monitoring programme and an annual fishery-independent breeding-stock survey (Chubb, 2000). When the breeding stock fell to low levels in the early 1990s, management initiatives succeeded in returning it to what are considered to be safe levels (Phillips & Melville-Smith, 2005). In recent years, breeding stock levels have once again shown declines caused by effective effort increases as a result of technology changes improving fishing efficiency (e.g. improved GPS positioning, bottom discrimination and seabed mapping tools etc). Efforts are underway to address this by introducing management changes that will reverse egg production declines.

Catches in the fishery are very variable from year to year (Fig. 11.2), but fishers have acquired sufficient scientific knowledge to understand that they fluctuate for environmental reasons and to take this into account in their fishing operations. Environmental effects have been shown to drive the level of settlement in a particular season (reviewed by Caputi *et al.*, 2003). These settlement levels are in turn highly correlated with catches three to four years later (Caputi *et al.*, 1995; 2003), which provides a means of predicting future catches and managing the fishery accordingly.

In 2004, the State Government embarked on a policy under which each fishery in Western Australia will be required to have a sustainability report. This report will include a clear statement on the harvest level of the fishery to be allocated among the various user groups identified for that particular fishery. The western rock lobster fishery is the first to have had a fishery status report prepared (Anon., 2005) and this report will form the first stage in a process of allocating catch shares to recreational, commercial and customary (indigenous) fishers. Catch data for these three user groups for seasons 1997/98 to 2001/02 are presented in Table 11.3.

The fishery was awarded Marine Stewardship Council certification as a well-managed fishery in March 2000, the first in the world to receive this imprimatur (MSC). It is currently in the process of re-certification after the initial five-year period.

Panulirus ornatus

There has been an artisanal fishery on *P. ornatus* in the Torres Strait and the east coast of Papua New Guinea for hundreds of years. Commercial fishing began in the area in the late 1960s and is restricted to the indigenous Torres Strait Islander people, who derive from it a significant portion of their income (Phillips *et al.*, 2000a). The fishery (Fig. 11.3) is managed as a joint authority fishery between the Australian and Queensland governments and under an agreed treaty between Australia and Papua New Guinea (PNG). Under the treaty, the catch is shared between PNG and Australia. This is achieved by Australia endorsing PNG boats to fish in Australian waters (Williams, 2004).

Diving is the method of fishing, with fishers free-diving to about 4 m, or using hookah to around 20 m, from small outboard-powered dinghies and returning their catches to land-based processors or processing vessels. There are currently upwards of 500 dinghies and about 25 small freezer boats being used in the Australian and PNG fishery (Williams, 2004). It is possible to catch these lobsters by trawling and during the 1970s and 1980s, prawn trawlers targeted migrating animals, but this fishing method was banned in 1984 because of the danger to the breeding stock (Williams, 2004). Young lobsters grow quickly and first start recruiting to the commercial fishery about a year after settlement (Dennis *et al.*, 1997). In spring each year, most of

Table 11.3 Estimated catches (in tonnes) made by the three western rock lobster user groups, over the period 1997/98 to 2001/02 (from Anon., 2005).

Fishing year	Total commercial	Total recreational	Estimated total indigenous	Total catch*
1997/98	10 478	486	8.3	10 964
1998/99	13 009	626	10.6	13 635
1999/00	14 433	747	12.6	15 180
2000/01	11 273	564	9.6	11 837
2001/02	8 983	545	9.3	9 528

*The indigenous catch is included in the total recreational catch figure.

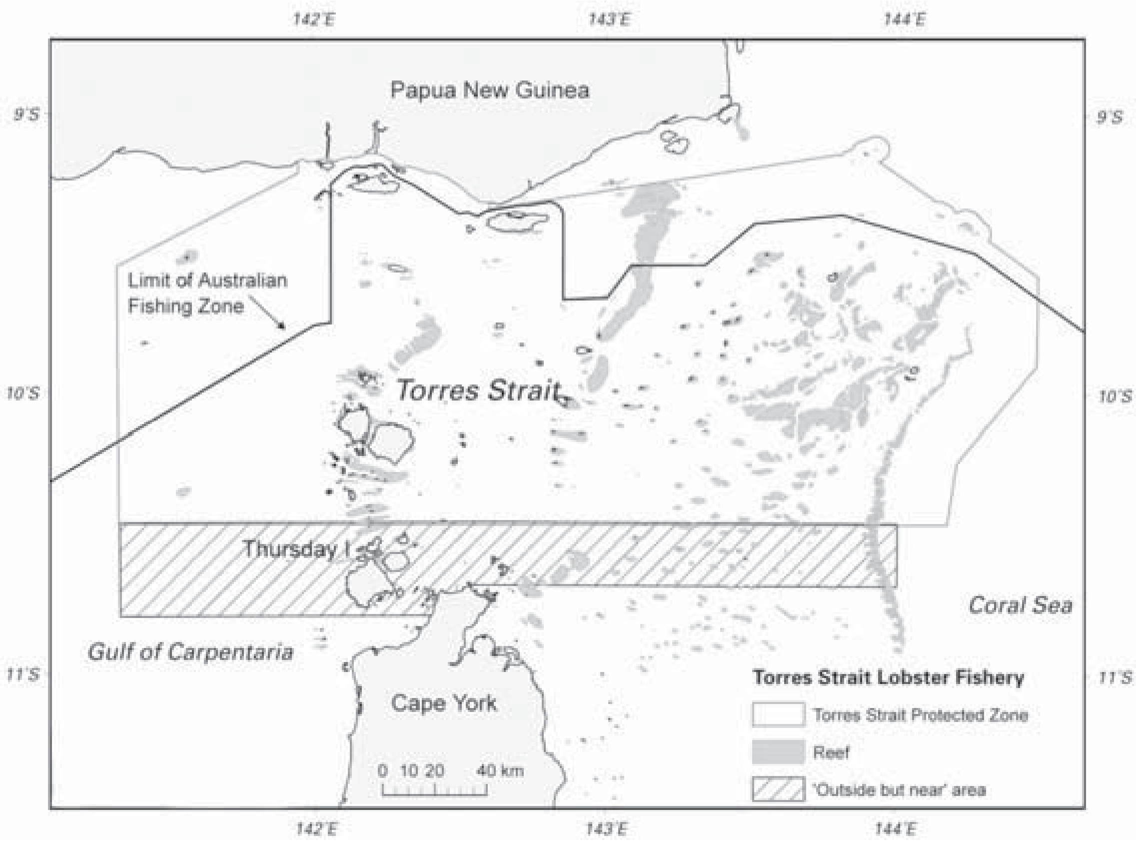

Fig. 11.3 The area in which the *Panulirus ornatus* fishery, jointly managed by Australia and Papua New Guinea, is located. Cape York and Thursday Island on the bottom of the figure is Australian territory; Papua New Guinea is in the northern part of the figure (adapted from Bureau of Rural Sciences, 2005 and courtesy of the Australian Fisheries Management Authority and Geoscience Australia).

the three-year-old animals migrate from the Torres Strait to north east and even the eastern reaches of the Gulf of Papua – a distance of up to 500 km (Moore & MacFarlane, 1984; Williams, 2004) (Fig. 11.3).

Recruitment to the fishery varies considerably and catches have fluctuated over the years (Fig. 11.4 and Table 11.2). Since 1989, the abundance of *P. ornatus* over the approximate 25 000 km^2 of the Torres Strait fishery has been estimated using a dive/transect technique (Pitcher *et al.*, 1992). *Panulirus ornatus* is found throughout this area except in the centre of the fishery where the habitat is unsuitable silt and mud (Pitcher *et al.*, 1992). It was estimated in 1989, that there were around 14 million lobsters in the Torres Strait, with about 8 million being legal size (Pitcher *et al.*, 1992). Ye *et al.* (2004) estimated the population size in 2002 at approximately 9 million animals of which the number of legal-size lobsters was between 1 and 1.5 million, or 17% of the numbers of legal size estimated in the 1989 survey (Ye *et al.*, 2004).

The informal reference limit for recruitment in this fishery is a fishing mortality that will produce 50% of the maximum recruitment (Williams, 2004). By controlling the amount of fishing, management has aimed to achieve a spawning stock that can produce a requisite number of recruits. In 2001, data showed that the lobster stock was overexploited relative to the reference limit and that the fishery was at significant risk. The stock had been fished down by excessive catches through the

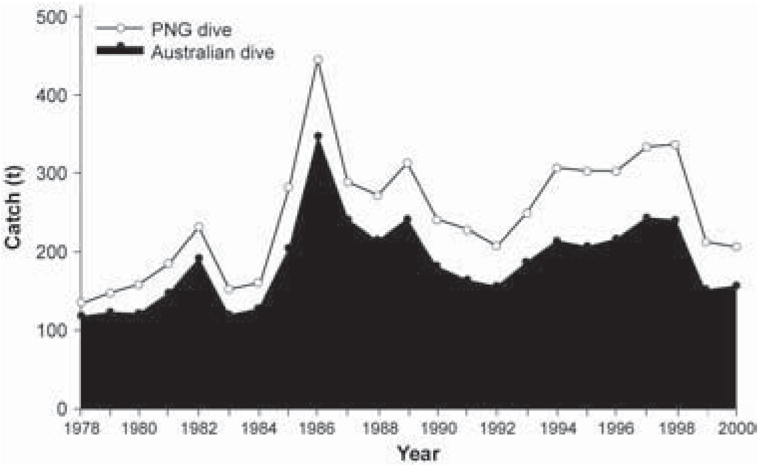

Fig. 11.4 Annual *Panulirus ornatus* catches taken by the Papua New Guinea (PNG) and Australian dive fisheries.

1990s, such that the estimated average fishing mortality rate to 2000 was 33% greater than the rate regarded as sustainable (Williams, 2004).

New regulations were introduced in 2002: an increase in the minimum size from 100 to 115 mm tail length; prohibition of commercial fishing in October and November; and banning the use of hookah gear from December to January (Ye *et al.*, 2004). Modelling results showed that these regulations would reduce the catch of age 1+ lobsters and increase the catch (or fishing mortality) of age 2+ lobsters. In addition, there will be a positive impact on the spawning stock and thus on recruitment under high fishing pressure (Ye *et al.*, 2004).

Near-average recruit abundances in 2002 ended declines that have been measured since 1999 (Ye *et al.*, 2004) and led the authors to conclude that the high variability in recruit abundance emphasises the great uncertainty in recruitment of this lobster species. The same authors have recommended a perpetual effort control regulation be introduced in both the indigenous and non-indigenous sectors of this fishery.

Australian catches in the Torres Strait have shown a dramatic increase since the low catches in 2001 and 2002 (Table 11.2). Latest figures (not shown in Table 11.2) indicate landings in 2004 were 692 t or over 500% greater than in the 2001 season.

These fluctuating catches are interesting when it is realised that only ten years ago the stock was considered under-exploited and an estimated sustainable catch of 600 t of tails (~1400 t whole weight) was considered possible (see Brown & Phillips, 1994). It clearly indicates how rapidly the situation can change.

11.6.2 Cuba[a]

Panulirus argus argus

The spiny lobster *Panulirus argus* is the most valuable single-species fishery in the Cuban archipelago. Lobster fishing is carried out over an area of 34 618 km^2, associated with shallow embayment and reef lagoons. The fishery involves 250 boats and 1300 fishermen operating 300 000 fishing gears (see Cruz & Phillips, 2000) during the eight-month coastal season (1 June to 31 January) in four management regions, which are divided into 10 smaller fishing zones, each controlled by a fishing company. The boats vary in length from 10 to 18 m and are concentrated on the south coast (75%), in the Gulf of Batabanó and south-eastern region, and 25% in the northern region (Cruz *et al.*, 1990).

The assignment of fishing zones, boats, fishermen, and industrial plants within the company is an important feature of the Cuba lobster fishery. Exports average US$70 million per year. About

[a] By courtesy of Dr Raúl Cruz Izquierdo, Centro de Investigaciones Marinas, Universidad de la Habana, Cuba.

75% of the catch is processed as cooked lobster, about 22% raw frozen, and about 3% live, in nine processing plants. These products are exported mainly to the markets of the European Union, Japan, Canada and Taiwan.

The Cuban fishery has been regulated for more than 70 years (García, 1919). The principal regulations governing it are a legal minimum size of 69 mm (carapace length) and a closed season of 120 days from February to May to safeguard the reproducing females during the spawning period of the population, to protect the new recruits, and to allow the growth and increase in weight of a major part of the population. Recruitment to the fishing grounds shows a pronounced seasonal cycle; from March to May it coincides with the decrease in the average size of lobsters and the arrival of the smallest lobsters (pre-recruits) into the fishery (Cruz *et al.*, 2001). Strict control is also exercised over the prohibition on the taking of berried females, number of fishing gears, boats, and boat replacement (Baisre & Cruz, 1994).

The majority (70%) of the fishing gears are artificial shelters, called 'pesqueros' (Cuban casitas) and are made from trunks of a coastal palm tree (*Coccothrina miraguana*) or from fibrocement sheets and palm trunks. The remaining 30% are 'jaulones' (rectangular traps joined by 40 m pieces of nets, which are trap-like set nets), which have replaced Antillean traps (Cruz *et al.* 1993; Cruz & Phillips, 2000). In Cuba, the catch rate is highest in June just after the beginning of the fishing season; 95% of pesqueros catches are made then because lobsters enter the pesqueros in the fishing area during the closed season, from February to May. Fishermen call the beginning of season, when 88% of the catch comes from the pesqueros, 'levante season' (June–September); during the mass migration season, called 'recalo season' (October–February), 70% of the catch comes from jaulones (Puga *et al.*, 1996; Cruz & Phillips, 2000). The seasonal migrations of *P. argus* are characteristic of adult populations, and the concentration and subsequent movements, which are influenced by meteorological processes (intensity of winter fronts, depressions, hurricanes, and continental cold-air mass), have a great influence on catch volumes (García *et al.*, 1991).

Lobster fisheries show high variation and from 1965 to 1977, a reduction of the closed season period to 45 days and the growth overfishing (18% annual sublegal catches) resulting in a 9000 t average catch. An extension of the closed season period to 90 days and strict observance of the minimal legal size from 1978 reduced the sublegal catches and changed the mean size at first capture (Cruz, *et al.*, 1991).

The fishery reached its maximum development in the 1980s and the abundance of juveniles in the years 1982–1987 sustained a catch that averages 12 037 ± 624 t. In 1984, the maximum observed recruitment took place and gave rise to a record catch of 13 584 t in 1985 (Cruz & Adriano, 2001). With the decrease in the abundance of juveniles after 1988, the catch showed a negative tendency and declined to an average catch of 7 025 ± 927 t in the beginning of this century, in spite of the Cuban fishery having been regulated for more than 40 years (Fig 11.5).

Since 1990, the fishery has experienced a marked decrease in catch, as a result of lower recruitment during a period of large increases in fishing effort and the consequent decline in catch per unit of effort (Fig. 11.5). The recruitment overfishing, in a period of intensive exploitation (Puga *et al.*, 1991; Phillips *et al.* 2000b; Cruz *et al.*, 2001), and hurricane phenomena that were more intensive from 1988 (hurricanes Gilbert, 1998; Mitchelle, 2001; Isidore & Lili, 2002; Charly & Iván, 2004), may be responsible for the recruitment decline since 1988. Nevertheless, we need a better understanding of the relationships between the life history stages and environmental effects, as well as more stock assessment research, to improve the management system.

11.6.3 USA (Florida)[b]

Panulirus argus argus

The Caribbean spiny lobster, *P. argus*, supports one of Florida's most valuable commercial fisheries as well as an intensive recreational fishery, with annual sales of recreational lobster fishing permits

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[b] By courtesy of Dr Michelle L. Braynard, Florida Fish and Wildlife Conservation Commission.

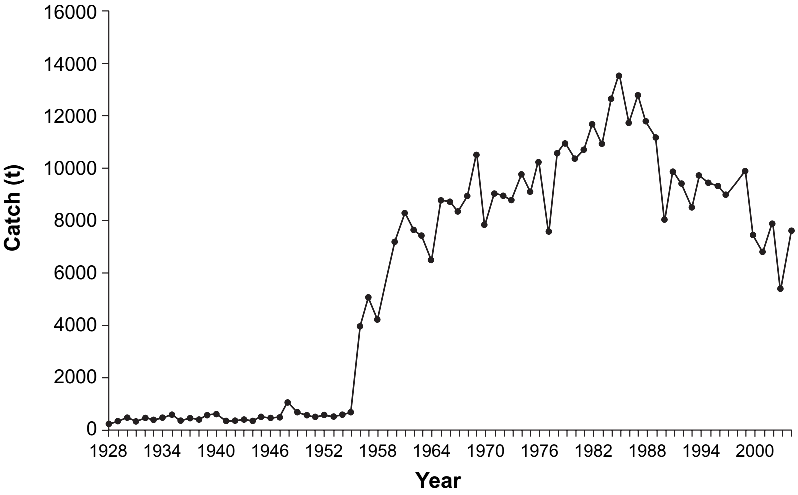

Fig. 11.5 Annual catches (whole weight) of *Panulirus argus* caught off Cuba from the late 1920s to 2004.

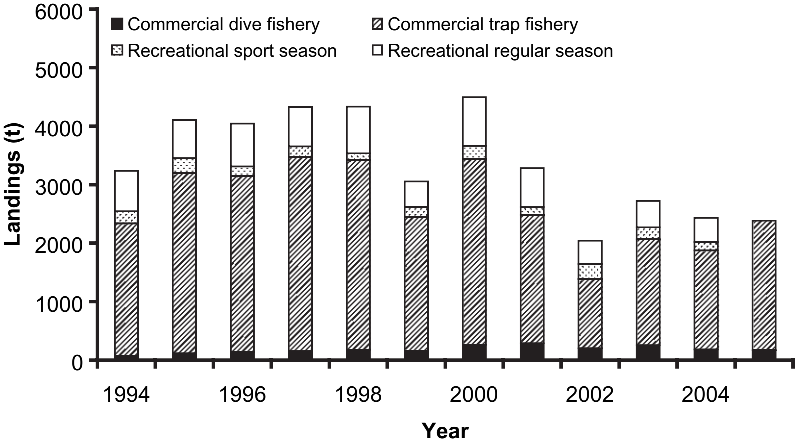

Fig. 11.6 Commercial and recreational spiny lobster landings of *Panulirus argus* in Florida, USA, from 1993/94 through to the 2003/04 fishing seasons. Landings for 2004/05 are preliminary and do not include recreational landings.

consistently in excess of 130 000. The fishery is located principally on Florida's extreme southeastern coast, especially along the Florida Keys archipelago, where approximately 90% of the State's landings occur. The rapid growth of this heavily capitalised fishery in the 1970s and 1980s evoked considerable management concern, which culminated in the implementation of management efforts in both the commercial and recreational sectors. Beginning in 1991, Florida required all amateur lobster fishers to possess a recreational spiny lobster permit, purchased as an additional endorsement to the State's saltwater fishing licence. Then, in 1993, the State implemented the Lobster Trap Certificate Program (LTCP) in the commercial sector with the goal of reducing fishing effort by reducing the number of lobster traps. These management efforts have shaped the course of the spiny lobster fishery in Florida in the past decade.

Prior to the 2001/02 fishing season, long-term total fishery landings statewide were consistently at or above approximately 3000 t (Fig. 11.6). However, since the record low landings in 2001/02, annual landings have remained well below this level. Whether or not this decline is a short-term trend or if it is indicative of a longer-term decline is naturally of concern to the fishery. Historically, landings have fluctuated in the short-term, and returned to previous reported levels over time. Though it is far too early to speculate, the increased preliminary landings estimates for the 2004/05 fishing season could be indicative of just such a return toward long-term landings trends. Alternatively, the lower harvests of the past four years could be indicative of a shift toward long-term trends of much lower average annual landings and in that scenario, the 2004/05 season would represent a very high-yield fishing season.

Evidence for both scenarios exists. A 15-year study of spiny lobster postlarval influx into the Florida Keys has indicated no pattern of a decrease in larval recruitment before or during the recent years of decreased adult landings. In contrast, the first naturally occurring pathogenic virus (PaV1) reported for any lobster species was discovered in juvenile *P. argus* in the Florida Keys in 1999 (Shields & Behringer, 2004). The virus is lethal with lobsters apparently dying within 90 days from metabolic wasting and loss of energy reserves. In semi-annual surveys of juvenile lobsters conducted since 1999 at 12 sites in the Florida Keys, prevalence of PaV1 infection has been as high as 30% with a mean prevalence of 7% per site (Shields & Behringer, 2004). Whether or not the apparent emergence of the PaV1 virus contributed to the decreases in recent landings warrants scrutiny.

During the 1993/94 fishing season, the first year that the LTCP-mandated reduction in the number of lobster traps in the Florida spiny lobster fishery was implemented, commercial lobster trappers accounted for 69% of total state-wide landings and landings by commercial divers accounted for approximately 2% of the total (i.e. commercial and recreational combined) state-wide landings (Fig. 11.6). After the inception of the trap reduction programme though, there was a progressive shift in total landings away from commercial trappers toward commercial divers, and by the 2001/02 season the latter group accounted for more than 10% of total landings. This shift in allocation was the result of a significant increase in dive-caught lobster during the first month of the fishing season in the Florida Keys and as commercial divers began to extensively use permanent underwater habitats to increase their catch efficiency. In an effort to limit this allocation shift, a bag limit regulation of 250 lobsters per day was placed on commercial divers beginning with the 2003/04 season. Since then, the relative proportion of landings attributed to the commercial dive sector has begun to decline.

A shift in the relative landings from the commercial fishery toward the recreational dive fishery has also been observed during recent years. Until the 1999/2000 season, the relative proportion of total landings accounted for by the recreational sector averaged 22%, and only exceeded 24% during one season (1993/94). Since the 2000/01 season though, the relative proportion of landings by the recreational fishery has averaged in excess of 25%. It is important to note that the years when relative recreational proportions were much higher than average coincided with those of record-low total landings. This is likely because nearly all of the recreational fishery effort occurs early in the season when abundance is highest, while the commercial sector effort is spread throughout the season. Though the shift in relative landings from the commercial to the recreational sector appears to have hit a plateau in the past few years, the relative proportion accounted for by the recreational sector is still above historic numbers.

By the end of the 2003/04 fishing season, the LTCP had reduced the number of traps to approximately 500 000 from a one-time high of almost 940 000. But user-group conflicts, several years of decreased landings, and shifts in the proportions of landings away from commercial trappers toward other user groups have led stakeholders to express concerns about the benefit of continued trap reduction. As a result, the reduction in trap numbers via the LTCP was suspended after the 2003/04 season pending a comprehensive fishery assessment. The outcome of this assessment, and management directions thereafter, will likely shape the course of the fishery for the decade to come.

11.6.4 Brazil

Panulirus argus argus, Panulirus argus westoni *and* Panulirus laevicauda[c]

The Brazilian fishery was the world's second largest producer of spiny lobsters. Two species, *P. argus*

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[c] By courtesy of René Schärer, Terramar Institute, Ceara, Brazil.

and *P. laevicauda* are landed. The fishery began in the mid-1950s with the catches made by artisanal (smallscale) sail-fleet fishers sold to industrial processors for export. With the help of government subsidies from 1967 to 1988 (Government Decree 221/67), the fishery quickly became the main export fishery in the country.

Catches, based on figures provided in Fonteles-Filho (2000), peaked at just short of 11 000 t in 1991, and from then up to 1997 have hovered at between about 6000 to 9000 t (Fonteles-Filho, 2000). More recent figures taken from FAO statistics (Fig. 11.7), show a substantial decline in landings in recent years, though it is likely that these landings may be under-reported; for example R. Scharer (personal communication) gives the estimated landings in 2001 as 9428 tonnes or 30% greater than the FAO figures used in Fig. 11.7.

All indications are that the Brazilian *Panulirus* lobster fishery is in serious risk of collapse due to overfishing (using highly efficient gill nets and diving, compared to traps) and inadequate management measures to protect the stocks. A prohibition on the retention of egg-bearing females was lifted in 1986 and the prohibition on gill nets in 1992. An unsuccessful attempt was made to reintroduce the ban on gill nets in 2003 when the negative effects of the use of gill nets in the fishery became clear. According to R. Scharer (personal communication) around 70% of motorised vessels in the fishery now catch lobsters with gill nets and 20% use hookah. He indicates that the nets have resulted in wastage of edible fish, by-catches of endangered turtles, high mortality and therefore quantity of lobsters caught and finally high fishing mortality of lobsters (indiscriminate of size and breeding condition), particularly when the nets are set across migration paths.

According to Chaffee (2001), in 2002 there were 1486 licensed boats fishing in this fishery, 2097 unlicensed boats fishing illegally, and of these an estimated 200 catching the lobsters by diving, which is an illegal commercial fishing method in Brazil and the cause of many accidental deaths and injuries of divers (Fonteles-Filho, 2000). Information from Chaffee (2001) indicates that catches in recent years in the fishery have been falling and competition for the resource has even led to some armed conflicts between hookah divers, and motorised and sailboat fishers, in recent times.

Whilst this fishery does have management regulations (see Table 11.1), there appears to be a lack of respect for, or enforcement of these regulations. According to C. Chaffee (Scientific Certification Services, USA, personal communication) some fishing, mainly hookah divers, is taking place during the closed fishing season, illegal fishing

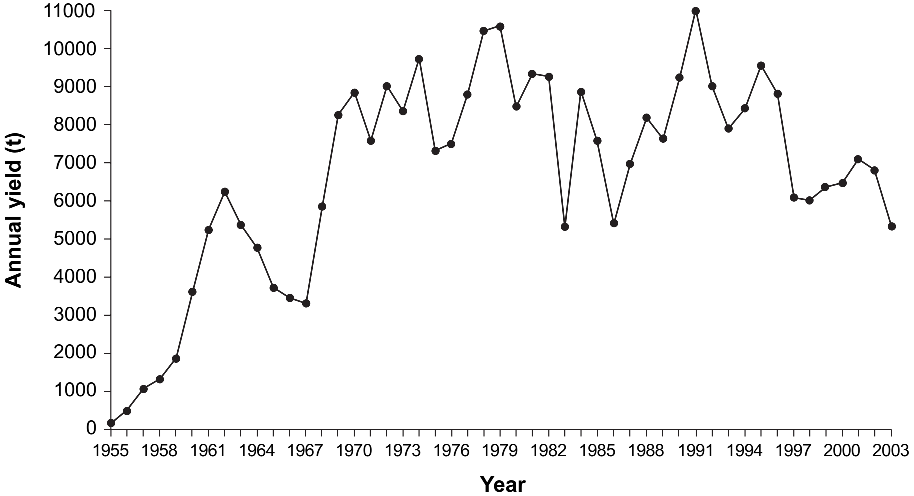

Fig. 11.7 Annual catches of spiny lobsters (*Panulirus argus* and *Panulirus laevicauda*) reported for Brazil (adapted from Fonteles-Filho, 2000 and FAO, 2005).

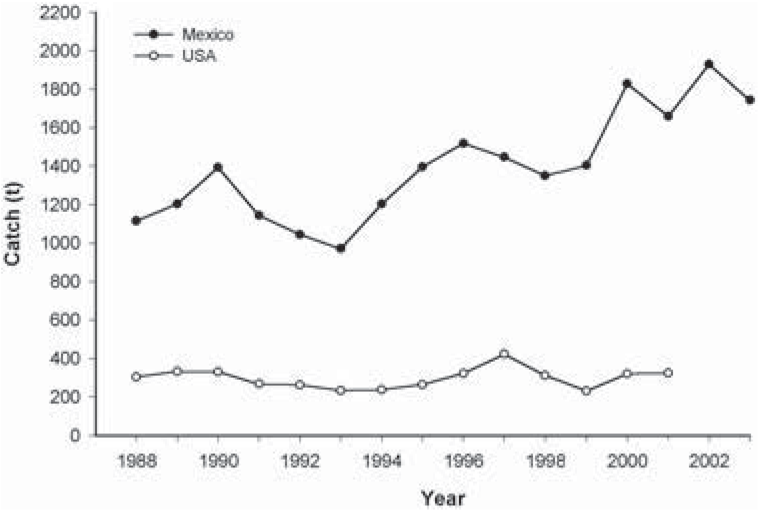

Fig. 11.8 Catches of *Panulirus interruptus* in Mexico and the USA between 1998 and 2001 (adapted from Scientific Certification Systems, 2004).

methods (diving) are being used and undersized lobsters are being caught and marketed locally as well as overseas.

11.6.5 Baja Mexico and USA (California)

Panulirus interruptus[d]

The *Panulirus interruptus* fishery in Baja California, for which Ayala *et al.* (1988), Vega and Lluch-Cota (1992) and Vega *et al.* (1996), have provided a thorough history, dates from the turn of the century. Also known as red lobster or California lobster, *Panulirus interruptus* is fished commercially in Mexico in an area from the border with the USA to Margarita Island. However, the main portion of the stock is between Cedros Island and Punta Abreojos along the coast of Mexico. Most of this area is part of the Vizcaíno Biosphere Reserve, except Cedros Island, with a 5 km band along the shore. *Panulirus interruptus* is also fished both commercially and recreationally in California in the USA.

In Baja California, 26 fishing cooperatives exploit *P. interruptus*. However, only 10 cooperatives operating in the central region of the Peninsula, from Punta Abreojos to Isla Cedros catch around 80% of the total catch of this species. Approximately 500 fishermen from nine fishing cooperatives distributed in ten villages set out wire traps using 5–7 m long skiffs with outboard motors.

Fishing rights were first exclusively allocated to fishermen's Cooperatives in 1936–1938, by assigning a group of species (lobster, abalone and others) within a delimited fishing territory for each organisation (Vega *et al.*, 1997). A unique scheme of limited entry originated from this system, which allows better control of effort and fulfilment of basic regulations (Vega *et al.*, 1997; Vega *et al.*, 2000). At present, 26 Cooperatives are authorised to harvest lobsters through concessions lasting 20 years. Each concession includes a clear description of the exclusive fishing zone allotted to the cooperative. This scheme is rigorously controlled by cooperatives and ensures a limitation on fishing effort within concessions as well as prevention of illegal fishing by poachers.

Catches by commercial fishers in Mexico and the USA have been monitored for long periods and usable data on catches and the number of traps are available since 1928 for Mexico, and 1916 for the USA. Catches over the last 14 years are shown in Fig. 11.8.

Phillips *et al.* (2000c) showed that changes in the catches of *P. interruptus* in Baja California over

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[d] By courtesy of Armando Vega, Instituto Nacional de Pesca, Mexico.

a long period tended to be higher four years after El Niño–Southern Oscillation (ENSO) episodes that cause high sea levels and a strong poleward flow. Vega and Lluch-Cota (1992) found evidence of a relationship between sea surface temperature and lobster catch.

Harvest control rules are established by official communications of the Mexican government. The actual control rule of this fishery since 1997 is to maintain the fishery at a level to harvest the maximum surplus production while maintaining the population biomass at values above the $B_0/2$ biomass estimate (B_0 = the estimated virtual population biomass). Regulations applied to this fishery are based on minimum size by species, limiting access by zone closures, and limiting fishing effort and trap design.

Annual voluntary quotas are followed by 95% of all fishermen who apply the harvest strategy established in 1993. The intent is not to increase fishing effort based on the number of boats, number of fisherman and number of traps. All of the fishers in the cooperatives fishing the central zone follow this harvest strategy without exception. This has led to a relatively stable fishery with catches driven mainly by varying recruitment levels driven by environmental fluctuations. Actual biomass in 2004 corresponds to 42% of the virgin population. The fishery was awarded Marine Stewardship Council certification as a well-managed fishery in March 2004 (Marine Stewardship Council, 2005).

11.6.6 India

Panulirus polyphagus

Commercial exploitation of lobsters began in the 1950s and targeted *Panulirus homarus*, *P. ornatus*, *P. polyphagus, P. versicolor* and also *Thenus orientalis* and the deepwater *Puerulus sewelli*. The peak landings occurred in 1985 (4075 t) but since then there has been a sharp fall in catches and growing instability in the stocks (Radhakrishnan *et al.*, 2005). We have chosen data on *Panulirus polyphagus* to present here, but the trends in the catches are similar for other *Panulirus* species in India. India is not the only country which catches *P. polyphagus*, a species which is widespread across South East Asia (Plate 11.1).

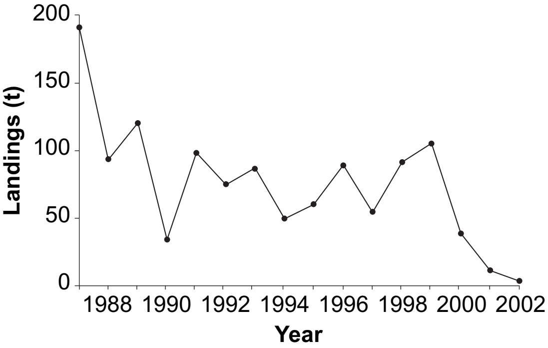

Fig. 11.9 Catches of *Panulirus polyphagus* in India in the trawl fishery at Veraval (Radhakrishnan *et al.*, 2005).

Panulirus polyphagus occupies a 1–10 m depth range along the south west coast and is caught by shrimp trawlers which catch about 75% of the lobster catch. The remainder of the lobster catch is taken by traps, gill nets and trammel nets in shallow water. Other species including *P. ornatus, P. homarus, P. versicolor, P. penicillatus* and P. *longipes* are also caught in small quantities, depending on the area.

P. polyphagus is heavily fished and overexploited (Fig. 11.9). Stock-assessment studies carried out at Mumbai indicate a high exploitation ratio (0.81 for males and 0.68 for females) and between 1996 and 2000 an exploitation rate of 78% on this slow growing species with 7–8 years of fishable life span (Radhakrishnan & Manisseri, 2003). Catches have declined by more than 50% over the peak catches of 1986–1990.

Currently, no management regulations are in force to control fishing of *P. polyphagus* in India, except that a minimal size for export of *P. polyphagus* of 300 g was adopted in 2003 (Radhakrishnan *et al.*, 2005). Minimum sizes for export were also introduced for *P. homarus* and *P. ornatus*, but other recommendations such as a minimum legal size, closure of the fisheries during the peak spawning season in the southern region of India, and a ban on trammel nets, have not been introduced.

11.6.7 Kenya and Somalia

Panulirus homarus megasculptus

Panulirus fisheries on the African coast generally have few regulatory controls. We have included lobster-fishing regulations in two countries, Kenya and Somalia, as examples (Table 11.1). According to A. Kulmiye (personal communication), most, but not all of the Somalian catch is *Panuliurus homarus* and landings are currently around 2100 t whole weight. The Kenyan catch is made up of at least five species (*P. homarus*, *P. longipes*, *P. ornatus*, *P. penicillatus* and *P. versicolor*) and the annual production is approximately 70 t.

11.7 Aquaculture and enhancement

11.7.1 Aquaculture

Countries involved in research in this area include Australia, New Zealand, Cuba, Brazil, Mexico, Singapore, India, Peoples Republic of China, Brazil, Japan, Vietnam and Thailand. Phillips and Liddy (2003) conducted a full review of this topic. Some highlights are given below.

Larval culture

The complete larval development under laboratory conditions has been achieved for several species of *Panulirus* (Table 11.4). *Panulirus japonicus* (the Japanese spiny lobster) has been cultured from egg through to the puerulus stage (Kittaka & Kimura, 1989). At least two other Japanese research groups have also been successful in culturing *P. japonicus* through its full larval cycle (Yamakawa *et al*., 1989; Sekine *et al*., 2000). Matsuda and Yamakawa (2000) reported the complete larval culture of *Panulirus longipes* (the long-legged spiny lobster).

The time required for larval development of the spiny lobsters under laboratory conditions in Japan varied considerably. *P. japonicus* took between 307–391 days and *P. longipes*, 281–294 days. These are about half the times it is estimated for the larvae to develop in the wild, and as these were only early attempts at larval culture, the prospects are exciting.

Table 11.4 Species of spiny lobster where complete larval development has been achieved in the laboratory.

Species	Number of instars	Duration of phyllosoma stages (months)	Duration of puerulus stage in the laboratory (days)	Author(s)
Jasus lalandii	15	10	>31	Kittaka (1988)
Jasus edwardsii	15–23	10.5–13.4	19	Kittaka *et al*. (1988), A. Ritar (pers. comm., 2004), Kittaka *et al*. (2005)
Sagmariasus verreauxi	16–17	6.1–11.6	25.5	Kittaka *et al*. (1997), Moss *et al*. (2000a)
Palinurus elephas	6–9	2.0–4.2	11–15	Kittaka & Ikegami (1988)
Panulirus japonicus	20–31	7.5–12.6	9–26	Kittaka & Kimura (1989), Yamakawa *et al*. (1989), Sekine *et al*. (2000)
Panulirus longipes	17	9.1–9.5	—	Matsuda & Yamakawa (2000)
Panulirus penicillatus	22	8.2–9.4		H. Matsuda, T. Takenouchi, J.S. Goldstein (pers. comm.)
Panulirus homarus				K. Murakami (pers. comm.)

In Australia, the main species being examined for aquaculture are *P. ornatus* and *Jasus edwardsii*, although some studies are currently underway on *Panulirus cygnus*. A considerable research effort is being expended to achieve this objective (Hart & van Barneveld, 2000a). Little of the research on *P. ornatus* has been published as it is considered 'commercial in confidence.' However, much of the research on *Jasus edwardsii* has been released (e.g. Ritar, 2001; Ritar *et al.*, 2002; Ritar *et al.*, 2003a, b).

Growout of pueruli and juveniles

Partial aquaculture involving raising wild pueruli or juveniles collected from the ocean is also an area of current interest. There is known to be a high mortality of wild pueruli and early juveniles (Phillips *et al.*, 2003), particularly in the first year post-settlement. If animals are ongrown in tanks, the mortality under laboratory conditions is usually minimal.

Growout of pueruli or juveniles is already possible in the laboratory. Australian experience with wild caught *P. cygnus* pueruli is that they can be raised in the laboratory, with up to 95% survival (Phillips, 1985). At a constant temperature of 25°C, *P. cygnus* juveniles can be raised under laboratory conditions from the puerulus stage (carapace length (CL) about 8 mm) to commercial size (76 mm CL) in about 2.1 years with very high survival (>95%). This is approximately half the time required in the wild, where juveniles take four years on average to reach the legal minimum size (Phillips, 1985). Glencross *et al.* (2001) determined the dietary protein and lipid requirements of post-puerulus western rock lobster.

Vietnam is currently producing more than 1000 t of cage-raised *Panulirus ornatus* (the ornate spiny lobster), *Panulirus homarus homarus* (the scalloped spiny lobster), *P. stimpsoni* and *Panulirus longipes longipes* annually, which are exported to China, Japan, Hong Kong and Thailand (Tuan *et al.*, 2000; K. Williams, personal communication). Some of these pueruli are being caught in Bangladesh and transported to Vietnam for growout.

As part of the *P. ornatus* studies in Australia, Jones (2001) investigated density effects on growout of juvenile (3.24 g) *P. ornatus* in a raceway system. Results showed survival and size were unaffected by the densities tested (14, 28 and 43/m^2), and growth rates were excellent, enough to allow growth to in excess of 1 kg in 18 months. Several recent studies in Australia have examined the protein and energy (lipid) requirements of spiny lobsters. *P. ornatus* fed dry-pelleted diets (Williams *et al.*, 2000; 2005) not only accept the diet but also have high survival rates (59%). Small juvenile *P. ornatus* were found to have a protein requirement of 43–47.4% and 53.3–55% in diets with 6% and 10% lipid respectively, for maximum growth (Williams *et al.*, 2000; Smith *et al.*, 2001). Growth of post-puerulus *P. cygnus* was found to be better in animals fed diets with protein levels greater than 50%, and significantly better in lobsters fed the lower-lipid diets, with survival in all treatments equal to or greater than 75%. Results indicate a very high dietary protein requirement and a low capacity to use dietary lipid (Glencross *et al.*, 2001). Other studies to develop artificial diets for *P. ornatus* have been undertaken by Barclay *et al.* (2004a, b), Smith *et al.* (2003, 2004, 2005) and Williams *et al.* (2004, 2005).

In India, it has been shown that juveniles of *P. homarus homarus* can be cultured to 200 g in 5–6 months with good survival (Vijayakuran & Radhakrishnan, 1984). Philipose (1994) also examined the rearing of undersized lobsters to attain a more valuable marketable size using *P. polyphagus*. Lobsters of around 50 g were ongrown to 100–125 g in 80–90 days.

Williams (2001) investigated feed development for rock lobster aquaculture with *P. cygnus*, *P. ornatus* and *Jasus edwardsii*, developing formulated diets for comparative trialling (dry moist and natural foods), and then using the diets for responses of post-puerulus/juveniles and adult rock lobsters to key nutrients (protein, lipid).

In reviewing the aquaculture potential of *P. argus*, Power *et al.* (2005) and Jeffs and Davis (2003) concluded that the species had positive aspects to its suitability for ongrowing, due to the availability of wild seed lobsters, combined with its rapid growth rates. Diaz-Iglasias *et al.* (2002) examined metabolic responses to natural and artificial feeding on the Caribbean spiny lobster *Panulirus argus* and Perera *et al.* (2005) evaluated practical diets for this species and measured the effects of protein sources and substrate metabolism and digestive proteases.

Other studies have been wide-ranging: from seeking explanations to explain early mortalities in puerulus culture (Pearce, 1997; Jeffs, 2001); to testing collector designs for commercial harvesting of puerulus (Phillips *et al.,* 2001); and estimating the effects on the wild stock of removing pueruli for aquaculture or other purposes (Phillips *et al.*, 2003); and studying disease (Handlinger, 2001).

Ongrowing of legal-size lobsters

In Florida, ongrowing of adults of *P. argus* (lobsters ranging in size from 100 to 1000 g) achieved an average increase in body weight of about 40% (Lellis, 1991; Blanco *et al.*, 2000).

11.7.2 Enhancement

Aquaculture could provide stock for reseeding and enhancement of the wild fishery (Hart & Van Barneveld, 2000a). Conan (1986) comprehensively reviewed enhancement of lobsters. It involves all types of protection of the early life history stages to increase yields from the fisheries. As pointed out by Conan (1986), 'References on recruitment enhancement are extremely scarce'.

Japan has pursued a plan for stock enhancement of the Japanese wild stocks of *P. japonicus* and in addition to encouraging culture of the larvae, has a programme of research into the best methods for safe release of pueruli and young juveniles into the wild.

Field experiments with *Panulirus argus* have clearly demonstrated that with appropriately designed artificial structures, recruitment to local populations can be increased (Butler & Herrnkind, 1997). Briones-Fourzán and Lozano-Álvarez (2001) have clearly demonstrated that artificial habitats (casitas) used by fishers increase the abundance and biomass and catch of lobsters (*Panulirus argus*) in habitat-limited environments in Mexico.

11.8 Management and conservation

The funding for research and therefore, by implication, the sincerity with which authorities manage their *Panulirus* fisheries, is variable over the distributional range of the species. There appear to be several regional localities where declining annual landings based on FAO by country statistics (reference) would indicate that the fisheries might be severely depleted. Catches in Taiwan declined to about 1 t per year in 2002 (FAO, 2005). The overall reported catches, for some of the more commonly caught species of this genus (Table 11.2), show no sign of decline. However, it is unclear whether this is as a result of more effort being applied to make the catches.

A lack of effort or total allowable catch (TAC) controls beyond relatively basic restrictions preventing the retention of berried animals or those below a minimum size, are quite widespread, even in some of the larger *Panulirus* fisheries (Table 11.1). Despite lobsters being relatively tolerant to intense fishing pressure, such weak management controls will inevitably result in stock collapses. Fortunately, the wide distributional range of most species in this genus, combined with their long and complex offshore larval phase, does provide an element of robustness to the likelihood of any species being fished beyond the possibility of recovery.

In recent times, there has been intense interest in the use of marine protected areas (MPAs) in managing fish populations (Roberts *et al.*, 2001; Pauly *et al.*, 2002; Hilborn *et al.*, 2004). Research into the response by rock lobster populations to MPAs has been a focus of attention, particularly in the *Jasus edwardsii* fishery in New Zealand (Kelly, 2000; Davidson *et al.*, 2002), but also in the *P. argus* fishery in Florida (Bertelson & Cox, 2001; Lipcius *et al.*, 2001; Acosta, 2002). It may be that this form of easily applied management restriction will be the solution to maintaining and restoring lobster populations in countries where effective input and output controls are too complex and/or expensive to manage and enforce.

11.9 Conclusions

Managing fisheries sustainability is a dynamic process. While some future questions in each lobster fishery have been identified here, it is inevitable that other unforeseen ones will arise. The challenge for fisheries researchers, managers, and industry, is to have the foresight to identify these potential problems and to have the continued means and ability to address them.

Change is inevitable, but not necessarily recognised as occurring. The global markets for lobsters have changed significantly, even in the last ten years. In Plate 11.2 we have illustrated changes in sales of live and cooked/frozen rock lobsters over the last ten years. Each country has its own special needs and requirements for lobster colour, size, form of delivery, price acceptability, etc., so these changes are much more than mere localities for delivery. These changes are brought about by many things such as: changes in affluence, availability of product, changes in community acceptance of product styles, economic downturns or upturns, and other phenomena such as the SARS virus. These types of changes also affect the needs for research by way of maintenance of supply, size of animals, and form of product sold.

Over the last 15–20 years we have seen an increasing call for sustainable management of fisheries. Initially, this was essentially management of the stock(s) of the fishery, and gradually the ecology of these resources. This has included economic and social aspects of the fisheries but in most cases without real objectives, collection of valid data, or performance measures. This is changing and lobster fisheries are increasingly finding that all of these aspects are now required for successful management in a modern world.

This is now expanding to ecosystem management. There are new calls for multiple-species models, and a complete raft of additional information, not just on the target species, to input to these models to make them operational.

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Chapter 12

Palinurus Species

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12.1 Species and distribution

The spiny lobster genus *Palinurus* (Weber, 1795) is the first named genus among the palinurid genera, and consists of five extant species (Holthuis, 1991). Two species, *Palinurus gilchristi* and *P. delagoae*, occur along the south-east African coast and in the south-west Indian Ocean, whereas the other three, *P. elephas*, *P. charlestoni* and *P. mauritanicus*, occur in the north-eastern Atlantic Ocean and Mediterranean Sea (Holthuis, 1991; Ceccaldi & Latrouite, 1994, 2000; Goñi & Latrouite, 2005).

12.1.1 The south-east African species

Palinurus off south-east Africa was long considered to be three varieties of the same species: *P. gilchristi* from southern South Africa, *P. gilchristi* var. *natalensis* from eastern South Africa, and var. *delagoae* from Mozambique. A revision of the genus in 1973 raised the latter two varieties to specific rank as *Palinurus delagoae* (Berry & Plante, 1973) – the diagnostic criteria of the two species are described by these authors and morphometric differences are highlighted by Groeneveld and Goosen (1996).

Palinurus gilchristi Stebbing (1900) is endemic to the south coast of South Africa, where it occurs on rocky substrata in moderately deep water (50–200 m) between Cape Point (18° E) and East London (28° E) (Pollock *et al.*, 2000). Locally known as south coast rock lobster, its distribution extends up to 250 km offshore on the Agulhas Bank, but further eastwards, the narrow, steep continental shelf restricts its distribution to within a few km offshore (Fig. 12.1).

Palinurus delagoae Barnard (1926) is a deeper-water species (150–600 m) distributed from 17° S (Mozambique) to 32° S (eastern South Africa) (Fig. 12.1) and off south-east Madagascar and submerged seamounts stretching southwards (Berry, 1971). It inhabits rocky areas and a substratum consisting of mud with a high organic content and varying quantities of sand and coral fragments (Berry, 1971). Morphological differences between the Madagascan and continental populations suggest that *P. delagoae* from Madagascar may be a separate species (Berry & Plante, 1973). The distributions of *P. delagoae* and *P. gilchristi* overlap off South Africa, however there is clear habitat partitioning because *P. delagoae* occurs deeper (150–600 m) than *P. gilchristi* (50–200 m).

12.1.2 The North Atlantic and Mediterranean species

The distributions of the European red spiny lobster *Palinurus elephas* (Fabricius, 1787) = *Palinurus vulgaris* Latreille, and the pink spiny lobster *P. mauritanicus* (Gruvel, 1911) overlap in many parts of the north-eastern Atlantic and western Mediterranean, although their ecological niches (i.e. depth distribution) differ (Ceccaldi & Latrouite, 1994, 2000; Goñi & Latrouite, 2005). *P. charlestoni* is

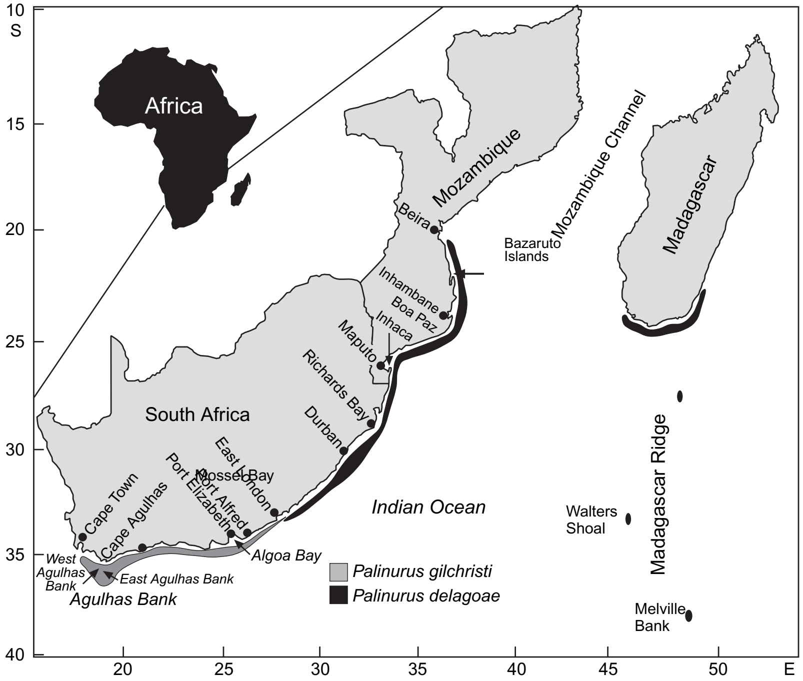

Fig. 12.1 Distribution of the south-west Indian Ocean spiny lobster species, *Palinurus gilchristi* and *P. delagoae*, along the offshore continental shelves of South Africa, Mozambique and Madagascar, and on isolated seamounts of the Madagascar ridge.

endemic to Cape Verde Islands (Latrouite & Alfama, 1996). Apart from their colouration, the three species can be distinguished morphologically based on characteristics of the first male pereiopod, the anterior carapace and the grooves on the abdominal somites (Holthuis, 1991).

Palinurus elephas is distributed widely in the Eastern Atlantic from the Hebrides and southern Norway (Tambs-Lyche, 1958) in the north to Cape Bojador (Morocco) in the south (Richie, 1912), including waters of Scotland (Wilson, 1952; Ansell & Robb, 1977), Ireland (Mercer, 1973), Wales, Devon (Bouvier, 1914), Cornwall (Hepper, 1967, 1977), the western part of the English Channel, along the coasts of Brittany (Latrouite, 1992), Spain, Portugal (de Vasconcellos, 1960), and off the occidental coasts of North Africa, including the Canary and Azores Islands (Goñi & Latrouite, 2005) (Fig. 12.2). In the Mediterranean, it occurs along the Spanish, French and Italian coasts, as well as in the Adriatic Sea (Gamulin, 1955; Soldo *et al.*, 2001), Aegean Sea (Moraitopoulou-Kassimati, 1973), and off the coasts of Tunisia, Morocco and Libya (Goñi & Latrouite, 2005) (Fig. 12.2). *P. elephas* lives between the shore and 200 m depth on rocky and coralligenous substrates where micro-caves and natural protective holes are numerous (Ceccaldi & Latrouite, 2000; Goñi & Latrouite, 2005).

Palinurus mauritanicus occurs in the Eastern Atlantic from western Ireland (53° N; Mercer, 1973) to southern Senegal (14° N; Vincent-Cuaz, 1966; Maigret, 1981) and in all the Western Mediterranean from Gibraltar to Sicily, west of 16° E (Holthuis, 1991) (Fig. 12.3). The greatest abundance occurs in the Atlantic along the coast of Mauritania (Maigret, 1978). *P. mauritanicus* is found at depths of 40–600 m, but the greatest densities occur between 200–400 m (Postel, 1966). It occurs along the edge of the continental shelf, especially in the canyons, and shows preference for muddy and coralligenous substrates near rocky outcrops (Postel, 1966). *P. mauritanicus* has been observed sheltering at the entrance of circular holes dug at the bases of compact mud cliffs (Latrouite *et al.*, 1999).

Palinurus charlestoni is named after the ship *Charleston* from which Forest and Postel (1964) obtained the type specimen. It is endemic to the Cape Verde Islands (14–17° N), roughly 600 km

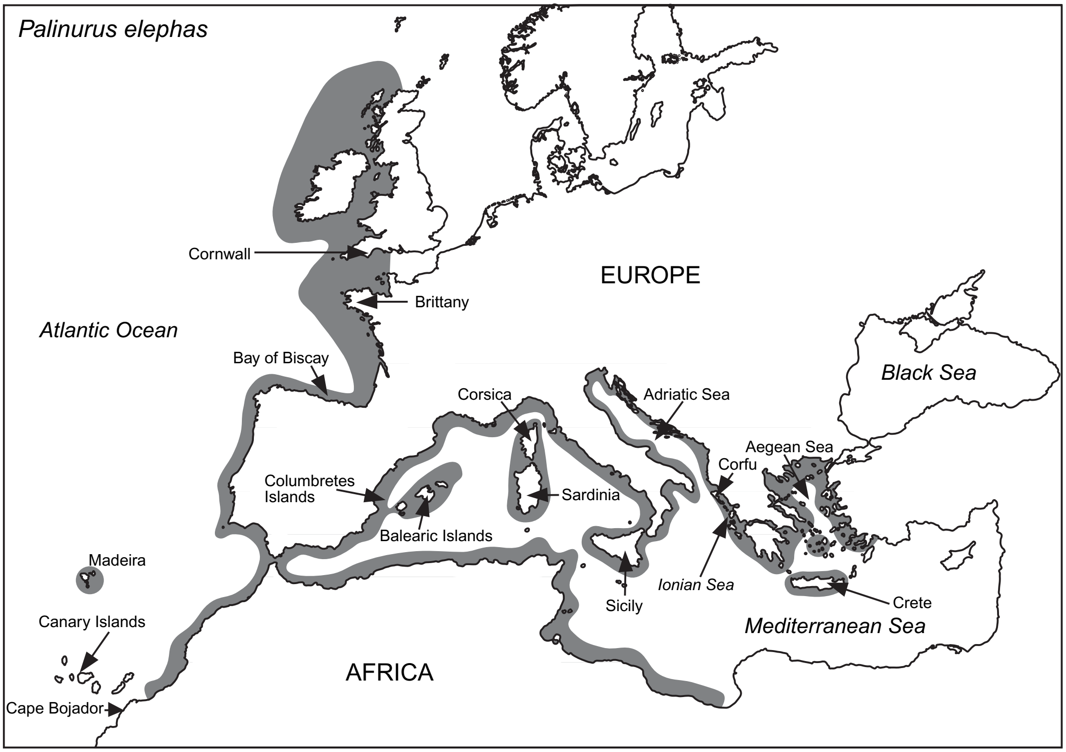

Fig. 12.2 Distribution of *Palinurus elephas* in the Western Mediterranean Sea and north-east Atlantic Ocean, including the occidental coast of North Africa, Canary Islands, and the Azores (not on map).

from the West African coast (Fig. 12.3), and occurs at depths of 50–400 m, with greatest densities at 100–250 m (Carvalho & Latrouite, 1992). Its preferred habitat is steep rocky grounds with an ambient water temperature of 13–14°C (Postel, 1966).

12.2 Biology, ecology and life history

12.2.1 Mating and fertilisation

Mercer (1973) describes the mating process of *P. elephas*. Stridulation by the female attracts males from distances of at least 15 m. Courtship starts with antennal contact and continues with rubbing and waving with the antennae and antennules. After a final stimulus, apparently triggered by a pheromonal release from the female, the male endeavours to overturn the female and copulation occurs, sternum to sternum, between intermoult individuals. The male deposits two spermatophores of a milky-white gelatinous texture on the sides of the female sternum, below the genital openings.

Berry (1969) similarly observed that mating in *P. delagoae* occurs between hard-shelled individuals, and that it involves the transfer of an opaque-white, soft, jelly-like spermatophoric mass from the male to the entire surface of the last sternal plate of the thorax of the female. In both *P. delagoae* and *P. elephas* (and in *P. mauritanicus*; Maigret, 1978) fertilisation is external and is achieved when the female scratches open the spermatophore during oviposition, using the fifth pair of walking legs. Oviposition occurs soon after mating (Berry & Heydorn, 1970; Mercer, 1973) and normally takes place in less than two hours in *P. elephas* (Mercer, 1973).

In none of the species does the spermatophoric mass have a specialised protective matrix (or

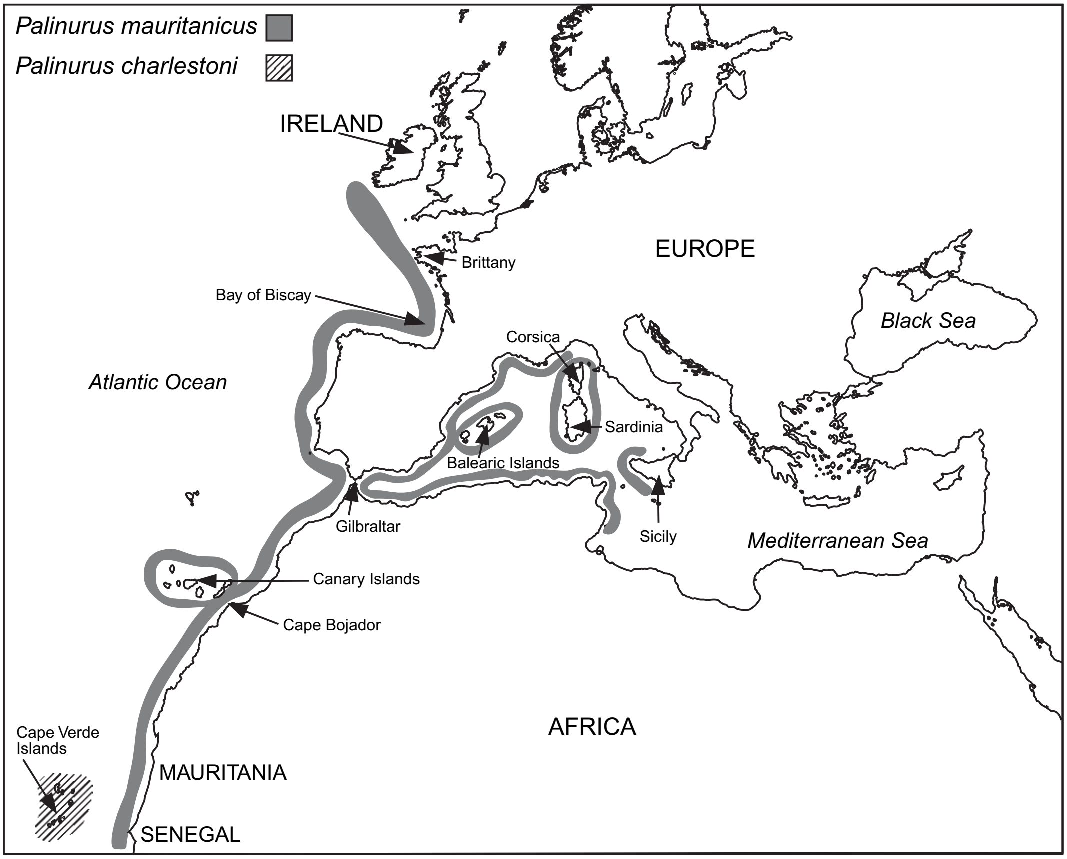

Fig. 12.3 Distribution of *Palinurus mauritanicus* in the Western Mediterranean Sea, north-east Atlantic Ocean, and occidental coast of North Africa. *P. charlestoni* (also shown) is endemic to the Cape Verde Islands.

tar-spot), as in the shallower water *Panulirus* genus, and this unprotected state may represent a more primitive evolutionary condition. Spermatophores in *P. elephas* disappear after a maximum of 10 days and thus they are infrequently observed (Hunter *et al*., 1996).

12.2.2 Breeding period

The breeding period of *P. gilchristi* is not clearly defined, with at least 20% of females caught in traps carrying eggs throughout the year. The ovaries of most adult females ripen in June, during the austral winter, with spawning taking place in July and August (Groeneveld & Rossouw, 1995). Egg-bearing percentages are highest between July and October (60–85% of females), with a slight decline towards November. Incubation of eggs therefore takes 4–6 months to complete. A large percentage of ovaries are either spent or inactive in October and November, in the period after spawning. More than 50% of females >80 mm in carapace length (CL) also bear eggs in March, suggesting that larger females may spawn twice per year, during autumn and spring.

The breeding period of *P. delagoae* is better defined with only one brood of eggs annually. Freshly-spawned eggs are first recorded in September, eggs about to hatch first occur in April, and hatched eggs are evident from May to July (Berry, 1973; Brinca & Palha de Sousa, 1983). Incubation of eggs takes about 5–6 months (Berry, 1973). The seasonal egg-bearing cycle can also be inferred from the ovarian cycle: in April, 90% of females have inactive ovaries and in November to December the highest incidence of ripe ovaries are recorded (Berry, 1973).

Egg-bearing in *P. elephas* in the Western Mediterranean may start in June and peaks in September (Gamulin, 1955; Campillo & Amadei, 1978; Marin, 1985; Goñi *et al.*, 2003a). In Greece, females with eggs have been observed from August to November (Moraitopoulou-Kassimati, 1973). In the Atlantic, mating occurs from June to October depending on the region (de Vasconcellos, 1960; Gibson & O'Riordan, 1965; Mercer, 1973; Hunter *et al.*, 1996) and egg-bearing peaks in September to October (Mercer, 1973; Hunter *et al.*, 1996; Latrouite & Noël, 1997). Egg incubation lasts 4–5 months in the Western Mediterranean (Campillo & Amadei, 1978; Marin, 1985; Goñi *et al.*, 2003a) and 6–10 months in the Atlantic (Mercer, 1973; Latrouite & Noël, 1997; Hunter, 1999). Hatching occurs during December to February in the Mediterranean (Gamulin, 1955; Campillo & Amadei, 1978; Goñi *et al.*, 2003a) and during March to June in the Atlantic (Mercer, 1973; Hunter *et al.*, 1996; Latrouite & Noël, 1997).

Egg-bearing females of *P. mauritanicus* are found year-round, although the main spawning season extends from August to January, roughly coinciding with breeding in *P. elephas*. Hatching of *P. mauritanicus* eggs in captivity may last 14 hours (Maigret, 1978). The breeding period of *P. charlestoni* starts in June, reaching a maximum during August to November. Hatching starts in November, peaks during December to January and ebbs in February. No egg-bearing females occur from March to May and incubation lasts for 4–5 months (Carvahlo & Latrouite, 1992).

12.2.3 Fecundity

Fecundity (external eggs carried on the female abdomen) in the two southern hemisphere *Palinurus* species and in *P. elephas* increases linearly with size (Fig. 12.4). *P. gilchristi* appears to be the most fecund, followed by *P. delagoae*. These species are much more fecund than *P. elephas* (Goñi *et al.*, 2003) where maximum relative fecundity (MRF) in Western Mediterranean populations is reached at intermediate sizes (100–110 mm CL) (Campillo, 1982; Goñi *et al.*, 2003a). Fecundity of *P. elephas* near Ireland (Mercer, 1973) compares well with the Western Mediterranean, where it is somewhat higher in a protected population at the Columbretes Islands (Goñi *et al.*, 2003a) than in an exploited population off Corsica (Campillo, 1982). The fecundity of *P. gilchristi* is lower at the easternmost limit of its distribution (Port Alfred; MRF = 72 mm CL) than between Algoa Bay and Cape Agulhas (MRF = 77 mm CL) (Groeneveld, 2005). Few data are available for *P. mauritanicus* and *P. charlestoni*, and fecundity–size relationships are

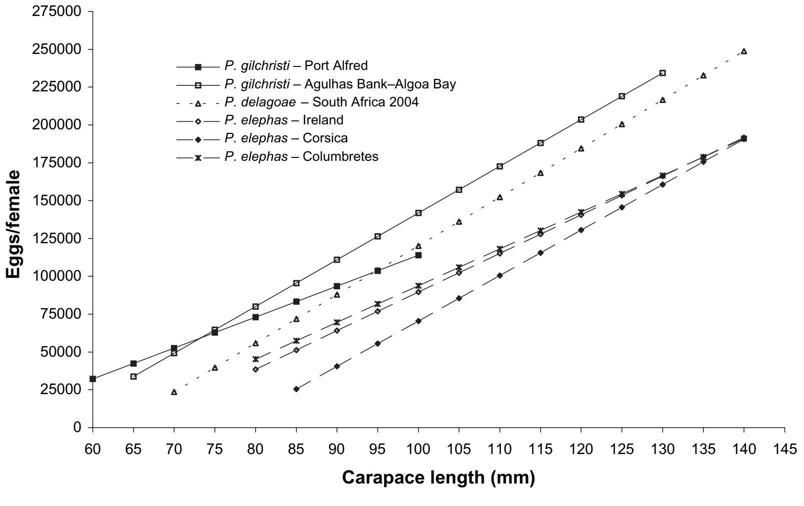

Fig. 12.4 Relationships between female fecundity and size of *Palinurus gilchristi*, *P. delagoae* and *P. elephas*.

still unclear. However, *P. mauritanicus* females with a CL of 140–157 mm carry only about 60 000 eggs (Maigret, 1978). Large *P. charlestoni* females (140–180 mm CL, n = 5) may spawn between 120 000 and 350 000 eggs (Carvalho & Latrouite, 1992), which compares well with *P. elephas*.

Egg loss during incubation in *P. gilchristi* is estimated at 14–17%, and is consistent over all size classes and among areas (Groeneveld, 2005). Egg loss in *P. elephas* was estimated at 10% in the Atlantic (Mercer, 1973) and 26–28% in the Western Mediterranean (Marin, 1985; Goñi *et al.*, 2003a), however, different capture methods used during sampling make these results difficult to compare.

12.2.4 Larval distribution and recruitment of pueruli

The larvae of *P. elephas* are leaf-like, transparent, planktonic zoeae called phyllosoma (Cunningham, 1892), which are adapted to a long offshore drifting life, and are poor horizontal swimmers. *P. elephas* larvae measure 2.9–3.9 mm total length (TL) at hatching (Willamson, 1983) and are larger than those of other species within the Palinuridae (Kittaka & Ikegami, 1988). Bouvier (1914) described 10 phyllosoma stages from natural plankton samples, and Kittaka *et al.* (2001) provides a full description of six phyllosoma stages (from hatching to puerulus) identified under culture conditions. Although the duration of the pelagic larval life of *P. elephas* is estimated to be from 5–6 and up to 10–12 months depending on the region, under culture conditions the larval cycle is much shorter, ranging from 65 days (six instars) to 149 days (nine instars), depending on culture conditions and food type (Kittaka & Ikegami, 1988; Kittaka *et al.*, 2001).

P. elephas pueruli are very rarely observed and the few existing records originate primarily from mid-water trawls or from the stomachs of pelagic fishes (Fage, 1927; Heldt, 1929). The puerulus has a well-developed abdomen and a translucent exoskeleton that acquires a darker colour and moults 10–15 days later into a benthic post-puerulus, which measures approximately 20 mm TL, and is the first juvenile stage with a similar appearance and habits to adults (Santucci, 1926; Orton & Ford, 1933). *P. elephas* post-larvae in the Western Mediterranean settle during June to July, a few weeks after the sea surface temperature starts to rise. According to Diaz *et al.* (2001) settlement occurs preferentially in holes and crevices in limestone rocks at depths of 5–15 m but early juveniles are commonly found at greater depths, suggesting that settlement probably occurs over a wider bathymetric range. Off Ireland, settlement occurs from late June to August (Mercer, 1973).

Larvae of *P. gilchristi* and *P. delagoae* are pelagic for at least four months (Pollock, 1995) and they are presumably widely dispersed by the south-westerly flowing Agulhas Current (Berry, 1974). Puerulus settlement hotspots have been inferred for *P. gilchristi* from the occurrence of a population of juveniles near Cape Agulhas, which is close to the downstream (westernmost) extreme of its range, beneath the Agulhas Current (Fig. 12.1) (Groeneveld & Branch, 2002). Such juveniles (CL <55 mm) are scarce on traditional fishing grounds where adults occur (Pollock & Augustyn, 1982). The absence of early juvenile *P. delagoae* from fishing grounds suggests that pueruli settle outside the 100–600 m fished depth range.

A single *P. mauritanicus* stage I phyllosoma of 2.9 mm TL was found by Maigret (1978) in December off Mauritania. The absence of larvae in the plankton during January to April, soon after hatching, suggests that phyllosoma are then offshore from the continental shelf. Maigret (1978) reports that fishermen have observed phyllosoma hanging from their pots, suggesting that the larvae may occur near the sea bottom, but no scientific observation currently confirms this behaviour. One puerulus was caught at 400 m depth.

12.2.5 Size at sexual maturity

The size at onset of sexual maturity in *P. gilchristi* varies geographically, with females at Port Alfred attaining maturity at a smaller size (59 mm and 62 mm CL, using setal and ovigerous methods respectively) than those at Algoa Bay to Cape Agulhas (64 mm and 71 mm CL) (Groeneveld & Melville-Smith, 1994). Female *P. delagoae* off South Africa reach 50% maturity at 67.3 mm CL (setal method) or 71.2 mm CL (ovigerous method)

(Groeneveld, 2000). Off Mozambique, 50% egg-bearing is also reached at approximately 70 mm CL (Brinca & Palha de Sousa, 1983). A moult between attaining the primary characteristics of maturity (ovigerous setae) and functional maturity (bearing eggs) accounts for the difference between estimates using the two methods.

The mean size at maturity of *P. elephas* also varies regionally. *P. elephas* in Brittany becomes functionally mature at 95 mm CL (Latrouite & Noël, 1997; smallest berried female = 92 mm CL). In Ireland, Mercer (1973) estimated physiological maturity of females at 82 mm CL (presence/absence of ovigerous setae) and of males at 84.5 mm CL. In the Western Mediterranean, a recent study of the reproductive biology of a protected *P. elephas* population concluded that physiological and functional maturity of females were attained simultaneously at a mean size of 76–77 mm CL, while males attained physiological maturity at 82.5 mm CL, but at the same age (Goñi *et al.*, 2003a). However, off Corsica, Marin (1987) observed a one-year lag between female physiological and functional maturity, and estimated male physiological maturity (testis weight/body size) at a mean CL of 76 mm.

P. charlestoni females begin to bear eggs at 90–100 mm CL, and the mean size of functional maturity is 110 mm CL (Carvalho & Latrouite, 1992).

Discrepancies between maturity estimates may be explained on the basis of geographical variation in growth rates, which depend on food availability, population density, or water temperature (Goñi *et al.*, 2003a). Furthermore, estimates in the literature vary as a result of the criteria used by different authors, as well as the sampling period, and number and size range of the specimens (Chubb, 2000). Despite these discrepancies, it is clear that the northern hemisphere *Palinurus* species achieve maturity at a larger size than their southern hemisphere counterparts.

12.2.6 Moulting and growth

Palinurus gilchristi exhibits a clear size-dependent moulting season during summer when the water temperature at 100 m depth is cooler than during winter because of an intense seasonal thermocline (Groeneveld & Branch, 2001). Setagenic development of the pleopods divide the moulting cycle into seven discrete moulting stages and substages showing that the proportions of premoult lobsters in catches peak in September (25%), October (35%) and November (22%) (Groeneveld & Branch, 2001). Tagging data confirm the summer moult season, with an increase in proportions of small postmoult lobsters in catches in October (43%), November (60%) and December (98%), and in larger (>70 mm CL) postmoult lobsters in December (61%). The single seasonal moulting cycle agrees with the general pattern suggested for macruran decapods (Conan, 1985), i.e., in regions with little seasonal variation and cold water there appears to be only one moulting season shifted towards the cooler season. *P. delagoae* adults off South Africa and Mozambique moult once per year, during August to October (Berry, 1973) and August to January (Brinca & Palha de Sousa, 1983), respectively. A minor peak in April is probably a continuation of moulting of subadults, which moult more often (Berry, 1973).

Tagging data show that adult *P. gilchristi* and *P. delagoae* grow slowly, that annual growth increments decrease with increasing CL, and that females grow progressively slower than males after reaching sexual maturity (Fig. 12.5) (Groeneveld, 1997, 2000). Moult increments of *P. gilchristi* are smaller at Port Alfred (1.5 mm/year for a male of 70 mm CL) compared to Algoa Bay to Cape Agulhas (3.5 mm/year). Maximum observed CLs are 110 mm (males) and 97 mm (females) at Port Alfred compared to 130 mm (both sexes) between Algoa Bay and Cape Agulhas. The theoretical maximum lengths (CL_∞) of the von Bertalanffy growth function grossly underestimate these values, but growth coefficients (K) are smaller at Port Alfred than elsewhere. In *P. delagoae*, the observed maximum CL is 180 mm, compared to length-based Powell–Wetherall estimates of 160–163 mm CL. The low value of K reflects slow growth towards CL_∞, which is consistent with a slow-growing and long-lived life strategy.

In the Mediterranean, mature female *P. elephas* moult one to two times per year, mainly during April to May (Marin, 1987), and possibly also in winter after hatching (Cuccu *et al.*, 1999; Goñi,

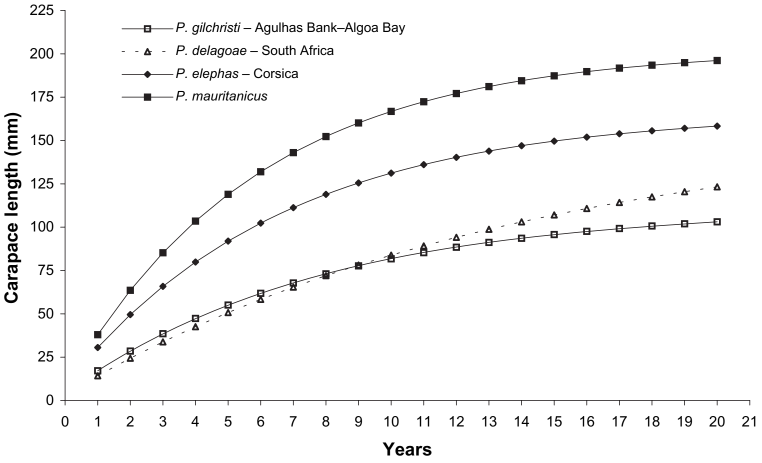

Fig. 12.5 Von Bertalanffy growth curves calculated for *Palinurus gilchristi*, *P. delagoae*, *P. elephas* and *P. mauritanicus*.

unpublished data). In the Atlantic, mature females appear to moult only once per year during June to August prior to mating (Mercer, 1973; Latrouite & Noël, 1997). According to Mercer (1973), mature males off Ireland follow the same pattern but with a more extended moulting season. Off the Columbretes Islands (Western Mediterranean) males were seen moulting *en masse* in February, and data from captive males show another moulting peak in the fall (Goñi *et al.*, unpublished data). Moult frequency is related to size with juveniles moulting two to five times per year (Corral, 1968; Marin, 1987; Cuccu *et al.*, 1999). Moult frequency decreases faster in females than in males after reaching sexual maturity, and large adults moult once per year or less (Cuccu *et al.*, 1999; Follesa *et al.*, 2003).

Tagged male *P. elephas* in Corsica grew faster than females, with respective von Bertalanffy growth parameters of $CL_\infty = 166$ mm, $K = 0.151$, $t_0 = -0.348$ for males; and $CL_\infty = 136$ mm, $K = 0.189$, $t_0 = -0.342$ for females (Fig. 12.5) (Marin, 1987). *P. elephas* attains a larger maximum size in the Atlantic (200 and 170 mm CL for males and females off Brittany; Latrouite & Noël, 1997) than in the Mediterranean (175 and 160 mm CL respectively off Corsica; Campillo & Amadei, 1978). These estimates should be taken with caution as maximum sizes observed in different areas depend on the level and pattern of exploitation and may be influenced by factors such as sample size, sampling method, habitat, season and depth.

Adult *P. mauritanicus* from Mauritania moults once per year between September and December (Maigret, 1978). Moult increments from a few tagged males of initial size 25–27 cm TL, were 3–4 cm. Using Maigret's data, Boitard (1981) proposed the von Bertalanffy growth parameters of $CL_\infty = 202.8$ mm, $K = 0.169$, $t_0 = -0.227$ for females (Fig. 12.5).

No data is available on the moult season or increment of *P. charlestoni* in nature, but moulting in commercial tanks has been observed in February and March (T. de Carvalho, personal communication).

12.2.7 Population structure, size composition and sex ratios

The CLs of *P. gilchristi* caught in commercial traps range from 50–130 mm, but lobsters >125 mm are scarce. Long-term size composition differs markedly between sites (Fig. 12.6). At Cape Agulhas, catches almost exclusively comprise small immature lobsters (mean CL = 62.5 mm), compared to West Agulhas Bank, where the population has a mean CL of 71.3 mm and consists mostly of a mixture of immature lobsters and small mature lobsters. At East Agulhas Bank (mean CL = 75.8 mm) the size-frequency distribution is bimodal, suggesting that a cohort of small sexually mature lobsters (mode = 65 mm CL) coexist with a cohort of larger sexually mature lobsters (mode = 77 mm CL). The size-frequency distributions at the

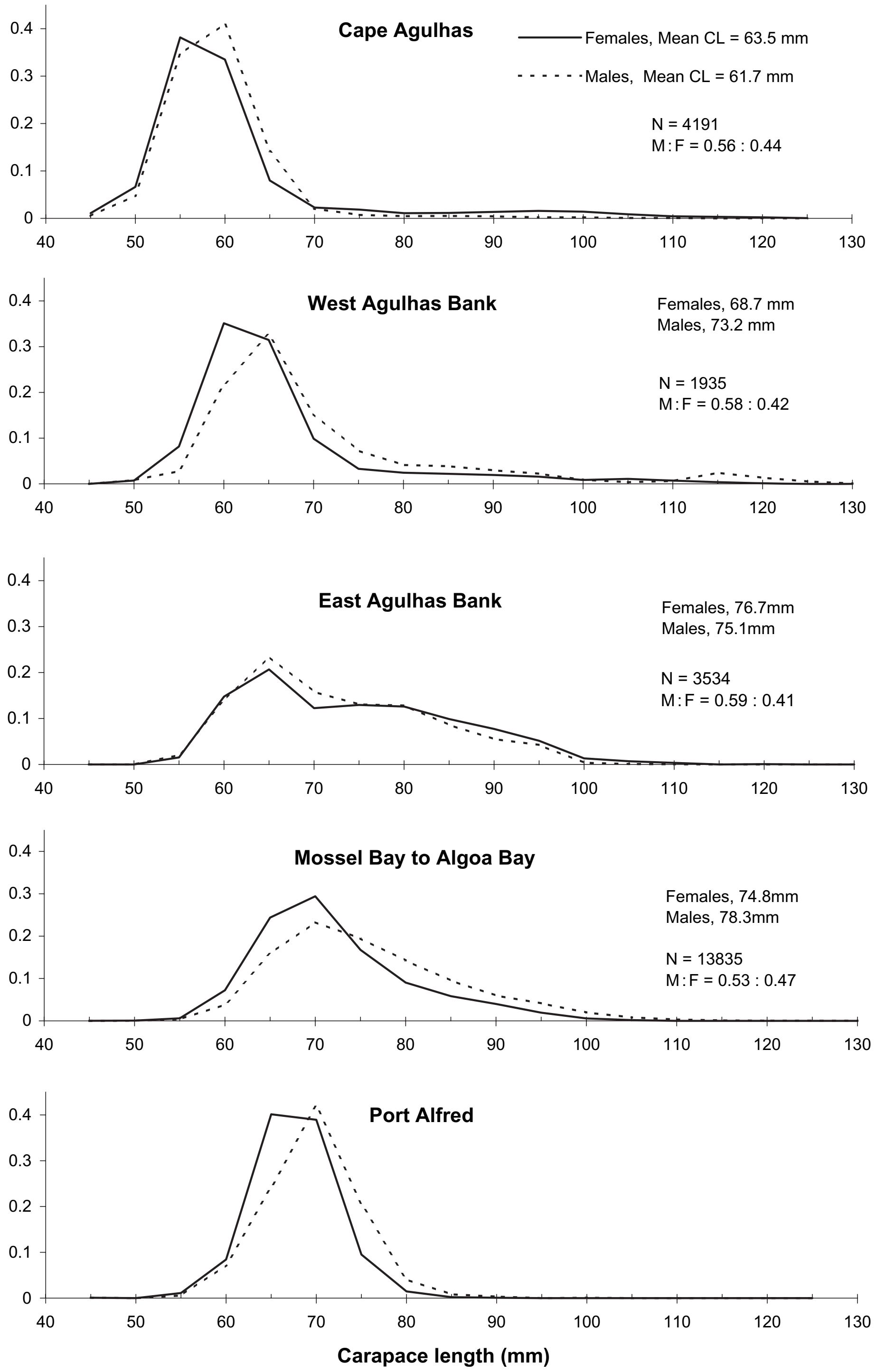

Fig. 12.6 Size composition and sex ratio of *Palinurus gilchristi* captured at five sites along the South African south coast (from Groeneveld & Branch, 2002).

remaining two sites are both unimodal. The mean CL at Mossel Bay (76.5 mm) continues the trend of increasing size from west to east, but the mean size at Port Alfred (70.7 mm) is 5.8 mm smaller. Sex ratios vary with season, but generally there is parity or males outnumber females at all sites except Port Alfred, where females often outnumber males (Pollock & Augustyn, 1982; Groeneveld & Branch, 2002).

The population structure of south-east African continental *P. delagoae* is well studied, but little is known about the insular Madagascan population. The CLs of *P. delagoae* caught in trap and trawl fisheries range from 50–185 mm, with a marked absence of juveniles <50 mm. Off South Africa and Mozambique, depth and latitude strongly influence size composition, with average CL increasing as depth decreases from 400–150 m (Cockcroft *et al.*, 1995; Palha de Sousa, 1998). The latitudinal trend shows a smaller average CL south of Durban (Fig. 12.1), and large variations in size composition in other areas (Cockcroft *et al.*, 1995). Trap fishing between 1994 and 1997 reduced the average CL in three areas off South Africa (Groeneveld & Cockcroft, 1997). Males dominate in length classes above 125 mm CL, and sex ratios of catches during the non-reproductive season (May to September) are fairly evenly spread across depth, with the percentages of males per depth interval being 54% (112–200 m), 46% (201–275 m), 51% (276–325 m), 51% (326–375 m) and 50% (376–425 m).

Information on the population structure of *P. elephas* originates from a variety of gear types, including traps/pots, diving, and trammel nets (Hepper, 1977), which together with the scattered nature of the data hamper temporal and spatial comparisons (Hunter *et al.*, 1996; Goñi & Latrouite, 2005). In general, Atlantic *P. elephas* attain larger modal and maximum sizes than in the Mediterranean, and at all fishing grounds, reductions in size have been registered over the past four decades. Male *P. elephas* caught in trammel-nets off Scotland and Cornwall in 1965–1975 had mean CLs of 145–160 mm compared to 122–134 mm for females (Ansell & Robb, 1977; Hepper, 1977). Later studies (Hunter *et al.*, 1996) showed a decline to 125.6 mm CL in Cornish male *P. elephas*, and concluded that it was caused by the replacement of pots by trammel nets during the 1970s. Corsican *P. elephas* caught in trammel nets in 1977 recorded modes of 95.6 mm and 103.7 mm CL, and maxima of 175 mm (male) and 160 mm (female) (Campillo, 1982). Eight years later, the modal size had declined to 75 mm CL (both sexes) and maxima to 140 mm (male) and 120 mm (female) (Marin, 1987). Goñi *et al.* (2003b) showed that pots used in the Western Mediterranean exclude and thus protect large *P. elephas* (mostly males) and suggest that trammel nets removed this component during the late 1970s and early 1980s.

Maigret (1978) used commercial data (1972–1974) from Mauritania and recorded recruitment of *P. mauritanicus* at 73–82 mm CL, male modal sizes at 96 mm and 119 mm (max. 217 mm CL) and female modal size at 83 mm (max. 195 mm CL). Experimental catches in 1975 indicated a size range of 77–198 mm CL (males) and 75–197 mm CL (females). Boitard (1981) measured maxima of 170 mm CL (males) and 155 mm CL (females). Half of the catches from a sporadic trammel-net fishery in the Bay of Biscay in the 1990s comprise individuals >2 kg (CL >155 mm), with some males weighing up to 7 kg (D. Latrouite, unpublished data). Sex ratio and size appear to be depth-dependent; males are more abundant at 150–250 m depth, whereas large females and juveniles predominate between 250–300 m (Maigret, 1978).

The size of *P. charlestoni* caught in commercial traps ranges from 60–270 mm CL for males and 60–210 mm CL for females, but males over 220 mm and females over 170 mm represent <5% of landings. The size composition of females is unimodal around 130 mm CL while males exhibit a scattered distribution. Mean lobster weight at landing is around 1.25 kg. The size structure of catches does not appear to have changed much over time (T. de Carvahlo, unpublished).

12.2.8 Migrations

Long-term movement patterns of juvenile *P. gilchristi* and *P. delagoae* against the westerly-flowing Agulhas Current, have been shown in tagging studies (Groeneveld, 2002; Groeneveld & Branch, 2002). In *P. gilchristi*, over 97% of tagged juveniles at Cape Agulhas migrated >50 km, either south-eastwards offshore to the outer reaches of the Agulhas Bank, covering a mean distance of 154 km, or eastwards longshore up to Algoa Bay, a mean distance of 461 km (Fig. 12.7). The greatest straight-line distance recorded was 790 km, by a male lobster tagged at Cape Agulhas and recaptured at Algoa Bay. The fastest 5% of migrants moved at 0.43–0.78 km d^{-1}. In general, Cape Agulhas migrants reached the outer Agulhas Bank within one to two years, and Algoa Bay within three years. No westwards or return migration was observed and the easternmost (upstream) Port Alfred population is non-migratory and receives no immigrants from elsewhere. The Cape Agulhas area is now considered an important postlarval settlement area, from where juveniles migrate eastwards against the current to recruit to adult habitats.

Juvenile *P. delagoae* tagged near their southern range limit (eastern South Africa; Fig. 12.1) migrated up to 495 km, north-eastwards, longshore and counter to the Agulhas Current between Durban and southern Mozambique (Groeneveld, 2002). Some 48.3% of juvenile lobsters (CL <65 mm) but only 2.1% of larger lobsters migrated further than 20 km, and the fastest 5% of migrants achieved 0.43 km d^{-1}. Both *P. gilchristi* and *P. delagoae* appear to have evolved long-distance countercurrent migrations as a retention mechanism to maintain populations off South Africa and Mozambique.

Apart from the longshore migration by juveniles, *P. delagoae* exhibits two other migratory life-history strategies (Groeneveld, 2002). Size composition shows that juveniles inhabit deep, offshore waters (400–600 m) and gradually move shallower as they grow larger to recruit to the adult population at depths of 150–350 m (Berry, 1973; Cockcroft *et al.*, 1995). Egg-bearing females tend to concentrate in dense aggregations in shallower strata (150–275 m) in summer, and then move deeper (>300 m) in autumn and winter after their eggs have hatched (Koyama, 1971; Berry, 1972, 1973; Kondritskiy, 1976). These inshore juvenile and reproductive migrations occur over relatively short distances because of the narrow continental shelf.

Palinurus elephas undertakes a pre-reproductive onshore migration during spring and a reverse post-reproductive offshore migration in late autumn (Mercer, 1973; Ansell & Robb, 1977; Goñi *et al.*, 2000, 2001b). Foraging and change of shelter also motivate movements. Tag–recapture studies from the Atlantic and Mediterranean indicate that distances moved by adults are generally 5–20 km after 1–8 years at large (Hepper, 1967, 1970; Marin, 1987; Goñi *et al.*, 2001b), however there are two reports of movements of 50 and 70 km in the Mediterranean (Relini & Torchia, 1998; Cuccu *et al.*, 1999).

Palinurus mauritanicus migrates during several life-history stages. Off Mauritania, the mean size composition is smaller north of Cape Blanc (20° 45′ N) than in the south, suggesting a northern nursery area created by northward drift of larvae on bottom currents, followed by juvenile migrations southward (Maigret, 1978). Other migrations are linked to moulting and reproduction – large groups concentrate in autumn along canyon edges and then disperse over the shelf. Females undergo migrations in late autumn, linked to spawning during August to January (Maigret, 1978).

Seasonal movements of *P. charlestoni* have been inferred from catch rates, which indicate that the bulk of the population occurs at 100–200 m depth in summer, compared to 150–250 m in winter (Carvahlo & Latrouite, 1992).

12.2.9 Predators and natural mortality

Natural mortality in *Palinurus* is primarily because of predation, particularly on larvae, during juvenile stages and during moulting. *P. gilchristi* is sometimes found in the stomachs of Cape fur seals (*Arctocephalus pussilus*) (Berry, 1971), and giant octopus, *Octopus magnificus*, regularly enter traps and predate on captured lobsters (Cochrane *et al.*, 2004; Groeneveld *et al.*, 2006). Predators of *P. delagoae* include dogsharks *Dalatius licha* and *Cephaloscyllium sufflans* (Berry, 1973). Both *Octopus vulgaris* and dusky grouper (*Epinephelus marginatus*) are known predators of *P. elephas* in the Western Mediterranean (Quetglas *et al.*, 2001), and other fish predators of juveniles in the region are *Labrus* spp., *Scorpaena* spp., and *Serranus* spp. (Marin, 1987). *P. elephas* defended itself against fish predators by pointing or trapping the attacker between the two antennae, where they could whip and lunge at the fish to scrape or scratch it (Barshaw *et al.*, 2003). A study of *P. elephas* diet did not reveal cannibalism under natural conditions (Goñi *et al.*, 2001a), but it has been observed in captivity (Marin, 1987).

Natural mortality estimates are 0.11 y^{-1} (Hepper, 1977) and 0.15–0.3 y^{-1} (Marin, 1987) for *P. elephas*, 0.09–0.15 y^{-1} for *P. delagoae* (Groeneveld, 2000) and 0.1 y^{-1} for *P. gilchristi* (Pollock & Melville-Smith, 1993). These low values reflect a long-lived, slow growing life strategy. The longevity of *P. elephas* has been estimated at 15 years (Marin, 1987) but this may be an underestimate. *P. mauritanicus* can attain 21 years (Maigret, 1978). Based on tagged individuals recaptured up to 13 years after tagging, Groeneveld (unpublished) estimates that both *P. gilchristi* and *P. delagoae* may live for >30 years.

12.2.10 Diet

Palinurus elephas preys nocturnally on a variety of benthic organisms, including molluscs, echinoderms and crustaceans (Mercer, 1973; Goñi *et al.*, 2001a). Food preference appears to change according to prey abundance, and decapod crustaceans, ophiuroids or coralline algae are consumed when molluscs and echinoderms are scarce (Goñi *et al.*, 2001a). *P. mauritanicus* feed primarily on fish carrion, molluscs (bivalves and gastropods), crustaceans, polychaetes and echinoderms (ophiuroids and echinoids) (Maigret, 1978). The gastric mills of *P. delagoae* contained 46% (by volume) cephalopod remains that could be matched to a single common, but unidentified cuttlefish (Berry, 1973). Teleost remains (33%) and crustaceans (6%; largely brachyuran exoskeletons) made up the remainder.

12.2.11 Evolutionary phylogeny and genetic population structure

A recent analysis of the mitochondrial DNA cytochrome oxidase I subunit (COI) suggests that a *P. elephas* type ancestor gave rise to *P. mauritanicus* (likely in a broad Tethys Sea environment encompassing the contemporary North Atlantic and Mediterranean), and to the progenitor of the Indian Ocean species (Molecular Genomics Unit, University of Stellenbosch, South Africa). These two lineages may have been isolated with the closure of the Levant (Red Sea passage between the Mediterranean Sea and the Indian Ocean). COI sequences further suggest that *P. gilchristi*, *P. delagoae* and *P. charlestoni* are closer related to each other than to *P. elephas* and *P. mauritanicus*, and that the closest relative to *P. charlestoni* is *P. delagoae*. This finding suggests that speciation of the Indian Ocean lineage (including *P. charlestoni*) followed current-driven dispersal pathways clockwise around Africa, and that the *P. charlestoni* ancestor rounded the Cape of Good Hope before dispersing northwards to settle at the Cape Verde Islands. The absence of contemporary *Palinurus* in tropical waters on either side of the African continent suggests cool temperatures as a selective factor. The role of glacial and inter-glacial sea level changes, water temperature and sea current shifts in explaining the above mechanism are still unclear. Nevertheless, the mtDNA analysis suggests that, despite the close geographic proximity of present-day *P. charlestoni* and *P. mauritanicus* populations (*c.* 600 km between the Cape Verde Islands and Mauritania), these two species are only distant relatives within the genus, having reached their present locations along two entirely different routes, clockwise and anti-clockwise around Africa.

Analysis of the hypervariable mtDNA control region of *P. gilchristi* suggests that there is no significant genetic population structure, and that it is therefore panmictic (Tolley *et al.*, 2005). Likely factors contributing to panmixia are larval exchange within the environment of the Agulhas Current and long-distance countercurrent migrations between Cape Agulhas and Algoa Bay (Fig. 12.7). The mtDNA region also suggests that there has been a relatively recent demographic change, and that the population is not at equilibrium. The demographic change is probably due to a historical increase in population size, coupled with an increase in range size, possibly between *c.* 5300 and 10 600 years ago. The most likely explanation for the range expansion is an increase in available habitat when the Agulhas Bank (average depth <200 m) became submerged by rising sea levels (>150 m) after the

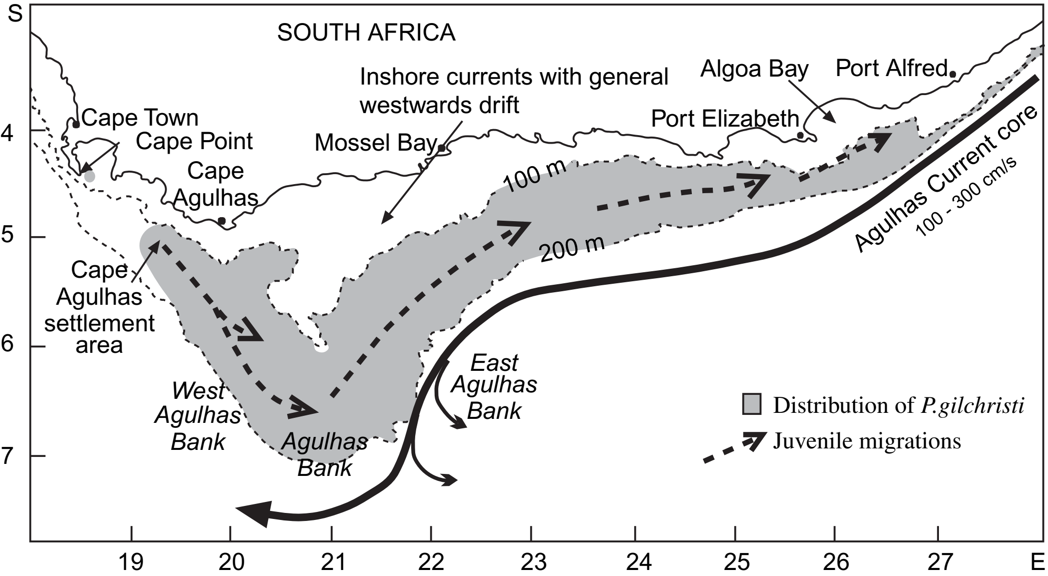

Fig. 12.7 Migration route of *Palinurus gilchristi* juveniles along the south coast of South Africa (from Groeneveld & Branch, 2002).

Last Glacial Maximum (*c.* 18 000 years ago). Thus the lack of genetic structure could be the result of a leading edge effect coupled with contemporary larval mixing (Tolley *et al.*, 2005).

12.3 Harvest of wild populations

12.3.1 Palinurus gilchristi

Palinurus gilchristi is fished exclusively with traps on rocky patches along the edge of the southern South African continental shelf (50–200 m depth) and up to 250 km offshore on the Agulhas Bank (Fig. 12.1). Commercial exploitation by local and foreign fishing vessels began in 1974, but in 1976, foreign vessels withdrew when the species was recognised as endemic to the South African continental shelf (Pollock & Augustyn, 1982). Effort, catch and catch rates from 1974–2005 can be subdivided into four periods (Fig. 12.8): 1974–1979/80 – fishing effort and catches increase above sustainable levels followed by a near collapse of the resource; 1980/81–1983/84 – effort and catches are drastically reduced and the resource recovers; 1984/85–1999/2000 – effort gradually increases and catch rates decline by 5–10% per year; 2000/01 to 2004/05 – the number of vessels is reduced by 30% (to nine vessels) in 2001, and smaller catches of <1000 t per year result in an average 9% per year increase in catch rates (Groeneveld, 2003).

Fishing gear initially consisted of single buoyed traps set from small vessels (Pollock & Augustyn, 1982), but the fleet soon converted to using plastic top-entry barrel-shaped traps set in strings of 100–200 traps (Fig. 12.9). Larger fishing vessels (30–60 m length) were rigged to carry 2000 or more traps, and to set up to 20 long lines per day. Some vessels carry recirculating seawater tanks to transport live lobsters, whereas others carry a factory for on-board processing and freezing of lobsters.

12.3.2 Palinurus delagoae

Exploratory trawling in 1920 first revealed the existence of *P. delagoae* concentrations off eastern South Africa (Gilchrist, 1920). Jackpot catches of up to 5 t in a single trawl (Fig. 12.10) (Berry, 1972; Koyama, 1971) gradually became rare and after the 1960s the lobster-directed trawl fishery diversified to catch deep-water prawns, langoustines, red crabs and several fish and cephalopod species (Groeneveld

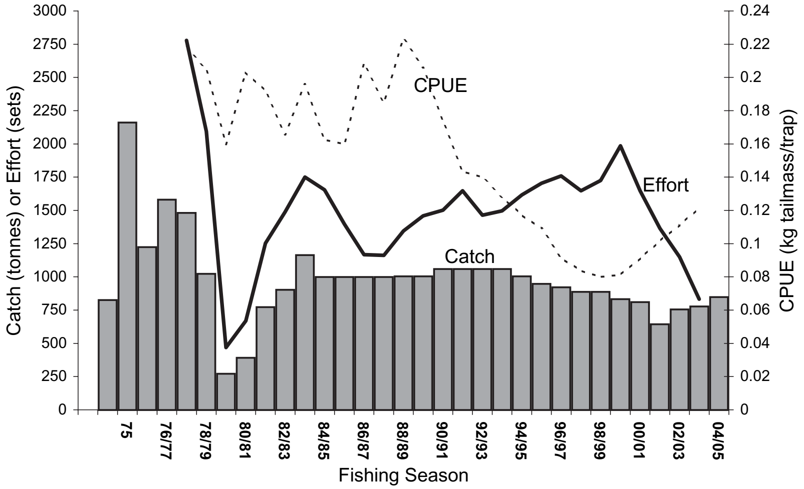

Fig. 12.8 *Palinurus gilchristi*: trends in fishing effort (number of long lines set), total catches (tonnes whole mass) and catch rates (kg tailmass/trap) between 1975 and 2005. (CPUE = catch per unit effort.)

Fig. 12.9 Long-line system with top-entry plastic traps used in the fisheries for *Palinurus gilchristi* and *P. delagoae*.

& Melville-Smith, 1995; Fennessy & Groeneveld, 1997). Small quantities of *P. delagoae* are landed as a by-catch (5–10 t per year since 1995). A similar multi-species trawl fishery in Mozambique has been active since at least 1960, attracting fishing vessels from South Africa, Japan, Spain, Russia and East Germany (Berth *et al.*, 1984; Torstensen & Pacule, 1992; Palha de Sousa, 1998). Much of the catches have gone undeclared.

Trap fishing for *P. delagoae* commenced in 1980 in Mozambique and rapidly expanded to cover extensive fishing grounds between Inhaca (27° S) and the Bazaruto archipelago (21° S) (Fig. 12.1) (Palha de Sousa, 1992, 1998). Initial catches of >300 t per year decreased to 100–200 t per year by 1994, thereafter increased effort resulted in rapid declines (102–48 t) by 1999. Catch rates declined from 0.74–0.33 kg per trap haul, and the fishery was curtailed in 2000 (Palha de Sousa, 2001). Experimental trap fishing in South Africa was undertaken between 1994 and 1997, recording initial catches of 89.5 t of *P. delagoae* and ~30 t of slipper lobster *Scyllarides elisabethae* (Groeneveld *et al.*, 1995). Catches declined sharply to 50 t in 1995, 30.5 t in 1996, and 7.8 t in 1997, and catch rates also declined by ~75% relative to 1994 (Groeneveld, 2000). The fishery was discontinued during 1997–2004. Exploratory trapping for *P.*

Fig. 12.10 Jackpot catches of up to 5t of *Palinurus delagoae* per trawl were made during the 1960s (from Berry, 1972).

Fig. 12.11 Various types of pots used in the fisheries for *Palinurus elephas*, particularly prior to the 1970s.

delagoae off southern Madagascar (Roullot, 1988; Holthuis, 1991), and on submerged seamounts to the south of Madagascar (Fig. 12.1) recorded occasional good catches, but not commercially viable quantities.

12.3.3 Palinurus elephas

Palinurus elephas has been fished for centuries and reports of commercial activity exist at least since the nineteenth century (e.g. Von Salvador, 1895). In France, a dedicated fleet developed and expanded to England, Ireland, Scotland, Spain, Portugal, Morocco and Tunisia in the first years of the twentieth century (Ceccaldi & Latrouite, 2000).

Traditionally, *P. elephas* was captured mainly by means of traps/pots (Fig. 12.11) and sometimes by diving (Hepper, 1977; Hunter *et al*., 1996; Goñi *et al*., 2003a; Gristina & Gagliano, 2004). A major

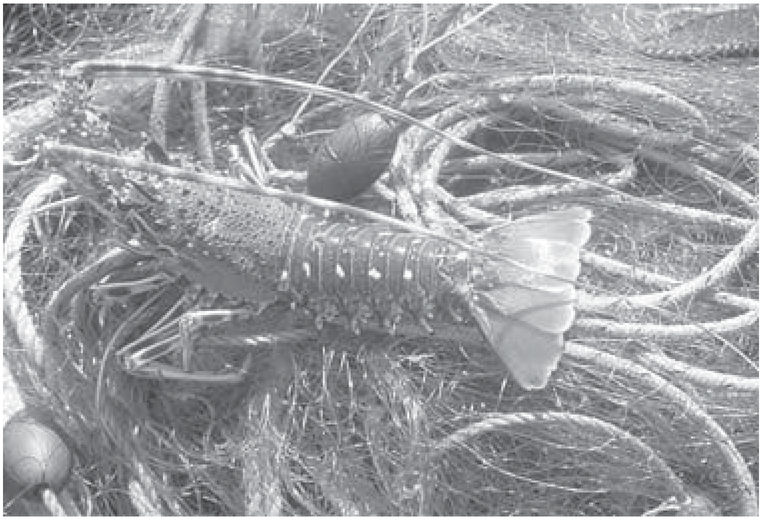

Fig. 12.12 *Palinurus elephas* caught in a trammel net. These nets gradually replaced pots as the gear of choice after the 1960s and 1970s.

change in exploitation strategy occurred during the 1960s and 1970s with the progressive introduction of trammel nets (Fig. 12.12) that virtually replaced other fishing methods. This change in fishing strategy not only had an impact on exploitation levels, demography and sex composition of the exploited populations (e.g. Hunter *et al*., 1996; Goñi *et al*., 2003b), but also on sampling of commercial catches, because samples are influenced by gear selectivity and catchability. A study comparing traps and trammel nets (Goñi *et al*., 2003b) showed reduced catchability of large males in traps relative to trammel nets. The same study indicated that small lobsters of <70 mm CL are poorly retained in traps and that large ones of >130 mm CL are less likely to enter traps due to behaviour, physical limitations or because they are able to feed without entering.

Overfishing of *P. elephas* populations was noted as early as the 1930s (e.g. Ninni, 1934), but the widespread decline of the fisheries may be traced back to the 1960–1980 period (Marin, 1985; Ceccaldi & Latrouite, 2000; Hunter, 1999). Fishing effort then increased dramatically as pots were replaced by trammel nets and hauling gear and other technological advances were introduced. However, lack of reliable historical catch and effort data prevents testing of the hypothesis that gear changes led to overfishing. In all European and African countries where *P. elephas* and *P. mauritanicus* are fished, Food and Agriculture Organization (FAO) landing statistics between 1984 and 1996 are registered as '*Palinurus* spp.' (distinction only in France). Official statistics show declines between 1988 and 1996, from 8710 t per year to 4242 t per year. Unfortunately, irregular reporting by most countries, or inclusion of other species in catch records make data difficult to interpret. Rough estimates of 2004 landings of *P. elephas* range between 500–800 t per year in the Mediterranean and between 150–300 t per year in the Atlantic. These values contrast strikingly with landings of several thousand tonnes in the first half of the twentieth century (e.g. French landings alone reached 3000 t in the 1940s).

Table 12.1 summarises current *P. elephas* fisheries by country. Published data on *P. elephas* fisheries are scant despite their past and present socio-economic importance, and most of the information appears only in unpublished reports or had to be sourced through personal communications (O. Tully, Ireland; M. Castro, Portugal; H. Masski, Morocco; C. Mytilineou, Greece). We are confident that the major historic and present fisheries are reported here, nevertheless, smaller fisheries of local importance may have been overlooked. In general, landing figures are considered to be underestimates.

Table 12.1 Current fisheries for *P. elephas*. No. boats = number of boats targeting *P. elephas* during all or part of a season; Season = open fishing season; Landings = official statistics(1), or best estimates/published information(2); Regulations = national legislation; MLS = minimum legal size; and ND = no data.

Country	No. boats	Season	Main gear	Landings (period)	Regulations including MLS
Ireland	20–25	May–Sep	Trammel nets	175 t (1990) 33 t (2000)	110 mm CL 2 areas closed to net fishing
United Kingdom	ND	ND	Tangle or trammel nets (rarely traps)	Declining	110 mm CL in Cornwall
France (Atlantic)	By-catch	Year-round	Tangle and trammel nets	50 t (2003)(2)	95 mm CL
France (Mediterranean)	Corsica 200	Apr–Aug	Trammel nets	65 t in Corsica (2004)(2)	80 mm CL 8 closed areas (80 km^2) Ban on landing berried females Closed season
Portugal	40 (SE)	Year-round	Tangle or trammel nets	400 t (1990–1992) 6 t (2000–2002)	95 mm CL Ban on landing berried females
Spain (Atlantic)	By-catch			2 t (2000)(2)	95 mm CL
Spain (Mediterranean)	600	Mar–Aug	Trammel nets (rarely traps)	98 t (2000)(2)	80 mm CL 1 closed area (44 km^2) + several small marine reserves Ban on landing berried females Closed season 4500 m net or 350 traps/boat
Italy	Sardinia 250	May–Dec	Trammel nets (rarely traps)	ND	107 mm CL Ban on landing berried females Closed season
Croatia	ND	May–Sep	Tangle and trammel nets	83 t (1953) 23–43 t (1985–1998)	82 mm CL Ban on landing berried females Closed season
Greece	ND	Jan–Aug	Tangle and trammel nets	23 t (1990s)(1)	85 mm CL Ban on landing berried females Closed season
Tunisia	56	Mar–mid-Sep	Trammel nets (rarely traps)	74 t (1993) 33 t (2002)	67 mm CL Ban on landing berried females Closed season
Morocco	ND	Year-round	Nets or traps	17 t (1967)(2)	170 mm TL

12.3.4 Palinurus mauritanicus

Commercial fishing for *P. mauritanicus* originated along north-west Africa when Spanish and Portuguese trawlers incidentally discovered stocks as shallow as 40 m depth. From 1955 onwards, a French fleet operated along the Mauritanian coast (Fig. 12.3), expanding to >40 boats (length 25–38 m) in the 1960s, and using cylindrical baited traps and bottom trawls along the shelf edge at 150–300 m depth and occasionally down to 600 m (Maigret, 1978). French landings peaked at 3600 t in 1961 but the fishery shrank to 200 t per year in 1970 as a result of overfishing and habitat destruction by trawlers (Maigret, 1978). Reduced effort allowed stocks to recover, and by 1986 landings had increased to 900 t (10 boats), close to the maximum sustainable yield (MSY) estimate (Boitard, 1981). In a 1987 agreement with Mauritania, the European Commission allocated lobster-netting rights to Portugal and an escalation of poaching rapidly led to a new collapse. French boats abandoned the fishery in 1990. After 1995, *P. mauritanicus* was reduced to a by-catch of boats trawling or netting for demersal fish and cephalopods (M. Diop, personal communication).

In the Bay of Biscay, sporadic netting for *P. mauritanicus* by one or two boats occurs on coral grounds at 300–400 m depth, but low catch rates have made targeted fishing uneconomical. Trawlers occasionally land *P. mauritanicus* as a by-catch. In the Western Mediterranean, *P. mauritanicus* is also sometimes taken by bottom trawlers as by-catch (Holthuis, 1991), and is occasionally targeted with trammel nets or epibathyal fixed nets (Addis *et al.*, 1998); however, as in the Atlantic, yields have declined rapidly.

12.3.5 Palinurus charlestoni

Fishing for *P. charlestoni* started in 1963 when three French vessels involved in the fishery for *P. mauritanicus* off Mauritania prospected Cape Verde waters (Fig. 12.3; Forest & Postel, 1964). French involvement ceased in 1966 when the Portuguese administration extended its territory to 12 nautical miles offshore, however, Portuguese vessels continued fishing even after 1975, when the Cape Verde archipelago became independent. No data are available on landings of *P. charlestoni* up to 1982, except for an estimate of 50 t in 1976 (Moal, unpublished). Sources differ on actual landings after 1982, and the statistics are therefore indicative: 20–60 t per year between 1982 and 1990; a maximum of 85 t in the 1991/92 fishing season, followed by a downward trend with 14 t in 1996/97, and 35 t in 1998/99 (Medina *et al.*, 2003).

Palinurus charlestoni is fished exclusively with traps, which have evolved from traditional barrel-shaped top-entry traps (0.6 m high, 0.7 m long, wooden frame) set in strings, to half-cylindrical top-entry Cape Verdian traps (1.5–2 m long, 1.15–1.5 m wide, 0.5 m high, metal frame covered by wire netting) set singly (Carvalho & Latrouite, 1992). Traps are baited with mackerel and horse mackerel, and are set overnight. Currently five vessels (12–22 m long), rather old and with no onboard storage facility, are active (A. Medina, personal communication). Standardised fishing effort expressed as the number of Cape Verdian traps hauled annually was around 10 000 at the end of the 1980s, 67 000 in 1992/93 and 20 000 in 1998/99 (Medina *et al.*, 2003).

12.3.6 By-catch and ecological impacts of fisheries

Traps set for *P. gilchristi* also catch *Octopus magnificus*, when they enter traps to prey opportunistically on trap-caught lobsters (Groeneveld *et al.,* 2006). Other by-catches are negligible, and ghost fishing is not considered a major problem, because traps that are retrieved after a long period at sea are invariably empty. Traps set for *P. delagoae* also catch slipper lobster *Scyllarides elisabethae* (Groeneveld *et al.*, 1995) and red crab *Chaceon macphersoni*. Apart from spider crabs, very little is discarded overboard. *P. delagoae* forms only a small by-catch in deep-water crustacean trawl fisheries, which are notorious for their large discards of unwanted fish, sharks and crustaceans.

Trammel-net fishing for *P. elephas* generates by-catch, much of which is made up of finfish, molluscs and crustaceans that are increasingly relied upon to supplement dwindling lobster yields.

Common by-catch species in the Western Mediterranean trammel-net fisheries are scorpionfish (*Scorpaena scrofa*), rays (*Raja* spp.), dogfish (*Scyliorhinus canicula*), monkfish (*Lophius* spp.), and torpedo (*Torpedo marmorata*) (Quetglas *et al.*, 2004). Traps generate much less by-catch than trammel nets; by numbers, an average of 61% of trap catches are lobsters, whereas this proportion declines to 46% in trammel nets (Goñi *et al.*, 2003c). By-catch from trap and trammel-net fisheries can be divided into two categories: retained by fishers and discarded at sea. Discards of stronger species such as *Scyliorhinus* and *Raja* spp. may survive capture and return, but soft-bodied fishes such as *Merluccius* spp. decay rapidly and thus their discarded fraction, especially from trammel nets soaked over several days, is high (Quetglas *et al.*, 2004). Ongoing studies show that trammel nets also have greater physical impacts on benthic habitats than traps, through the incidental catch of vulnerable, structure-forming species such as sponges, bryozoans, corals and coralline algae, are nearly absent from trap catches (Goñi *et al.*, 2003c).

12.4 Management controls and regulations

The fishery for *P. gilchristi* is limited to South African fishing vessels, which may operate year-round. No minimum legal size (MLS) is enforced, but egg-bearing females must be released. The total allowable catch (TAC) management regulation that was historically used to control the fishery failed to address over-harvesting as a result of poor compliance. A combined TAC and TAE (total allowable effort) management strategy was therefore introduced in 2000 to restrict fishing effort (days at sea) on the basis of quota size and vessel efficiency (Groeneveld, 2003). Days at sea are monitored using global satellite positioning technology, and authorities at landing sites weigh all catches. Thus, only drastic management intervention (the removal of a rogue fishing company responsible for unreported over-harvesting; a reduction in total fishing effort by *c.* 30%; reductions in the overcapacity of vessels and other infrastructure; a change in management strategy to a combined TAC and TAE; and improved compliance) succeeded in turning the fishery around, and substantial gains have been made between 2000 and 2005 (Fig. 12.8; Groeneveld, 2003).

Palinurus delagoae straddles the border between South Africa and Mozambique (Fig. 12.1), and is currently managed separately by the two countries. A trans-boundary trapping survey to determine a sustainable off-take and to promote regional management is underway. Small by-catches of *P. delagoae* made by prawn trawlers are not restricted by an MLS or ban on egg-bearing females in either country. Occasional fishing for *P. delagoae* in Madagascar and in international waters on the submerged seamount at Walter's Shoal in the south-west Indian Ocean (Fig. 12.1) is not regulated.

Except for a MLS in the Atlantic Ocean (95 mm CL), which is decided at the European Community level, all *P. elephas* fisheries are managed at national level. No TAC or quotas exist, as the reliability of landing statistics in most countries would make this strategy difficult to apply. Regulations are based on technical measures and/or effort limitations. In most fisheries the MLS is equal or larger than the mean size at maturity and in all Mediterranean fisheries, landing of berried females is forbidden (Table 12.1). Fishing effort in the Mediterranean is limited by an annual seasonal closure, which covers all or part of the egg-bearing season. In the Spanish Mediterranean, fishing at weekends is prohibited, and the amount of fishing gear per boat is capped. The mesh size of nets (inner and outer panels in trammel nets) and the size of the traps may also be regulated. Despite the multiplicity of controls imposed in some fisheries, many regulations are difficult to enforce. *P. elephas* is targeted by a large number of artisanal vessels, typically distributed in many ports along the coastline, or is a by-catch of bottom trawl or finfish netting. Therefore, at-sea effort control is problematical and regulations are often ignored. Trammel nets may be left in the water for several days resulting in loss of catch and loss of condition of undersized specimens to be returned to the sea. The by-catch of benthic structure-forming species also increases with soak time.

Palinurus mauritanicus exploitation is managed only through a MLS, which is 95 mm CL in

European Atlantic waters (EC regulation), 24 cm TL in French and Spanish Mediterranean waters and 17 cm TL in Morocco. *Palinurus charlestoni* occurs entirely within Cape Verdian national waters and legislation includes a restricted number of fishing licensces (currently five), a MLS of 24 cm TL and a five-month seasonal closure (July to November). Until recently, landing of egg-bearing females was banned and the seasonal closure was restricted to three months. However, the decision was made to lift the ban on egg-bearing females and extend the seasonal closure.

12.5 Assessments and current status of the stock and fisheries

Annual numerical assessments of *P. gilchristi* rely on an age-structured production model (ASPM), which projects abundance for management purposes (Johnston & Butterworth, 2001). The most important inputs to the ASPM are population size structure (collected by observers at sea), total catches, somatic growth rate and a relative abundance index obtained by standardising daily catch rates to account for the influences of vessel characteristics, trap soak-times, month, year, location and depth (Glazer, 1999). An experimental assessment of the impact of gear saturation showed only a very small probability that saturation would affect the standardised abundance index (Groeneveld *et al.*, 2003). However, the index was affected significantly by under-reporting of catches over the past decade – this malpractice increased sharply between 1997 and 2000. Eliminating the under-reported information from the input data and including the adjusted index and estimated over-catches for the 1991–2000 period as input data in the ASPM, increased the MSY by 8% (Groeneveld, 2003). Recent estimates of biomass, as a percentage of pristine, range between 0.28 and 0.36 (Johnston & Butterworth, 2004). The outlook for the fishery is now positive with recorded catch rates increasing by 9% per year over the past four years (Johnston & Butterworth, 2004).

Palinurus delagoae stocks in South Africa and Mozambique appeared to be heavily depleted by 2000 (Groeneveld, 2000; Palha de Sousa, 2001). *Palinurus elephas* populations declined rapidly during the 1960–1980 period and now most, if not all stocks are overfished or depleted (Massuti, 1973; Marin, 1985; Petrosino *et al.*, 1985; Latrouite & Noël, 1997; Hunter, 1999; Gristina *et al.*, 2002; Goñi & Latrouite, 2005). The multi-national composition of *P. elephas* fisheries and lack of a reliable data series precludes rigorous assessments.

Following a collapse late in the 1960s and a partial stock recovery, *P. mauritanicus* off north-west Africa has been prone to unreported fishing. The stocks collapsed again after 1987, and since then the species is mainly a by-catch of boats trawling or netting for demersal fish and cephalopods (M. Diop, personal communication). Even at this lower level of exploitation, excessive fishing and capture of undersized specimens have delayed stock recovery.

An evaluation of *P. charlestoni* stocks using a Fox surplus production model suggested over-exploitation, and that a MSY of about 40 t per year could be attained at 60% of the fishing effort expended in 1999 (Medina *et al.*, 2003).

12.6 Culture, enhancement and marine reserves

Complete larval culture from egg stage to puerulus of *P. elephas* was first achieved in 1988 (nine instars, 132 days; Kittaka & Ikegami, 1988), and subsequently repeated in 1996 (seven instars, 65 days; Kittaka, 1997) and in 1999 (six instars, 65–72 days; Kittaka *et al.*, 2001). These studies showed that *P. elephas* phyllosomas hatch at an advanced stage and are generally larger than in *Jasus* and *Panulirus*. More important, however, is that *P. elephas* under culture conditions has an exceptionally short larval cycle (65–2 days) compared to *Jasus* (205–319 days) and *Panulirus* (306–341 days) (Kittaka *et al.*, 2001), a factor that would circumvent a major constraint on commercial cultivation of lobster larvae. *P. elephas* is therefore one of the best candidates for aquaculture because of its short larval life, rapid growth from the puerulus (Archer & Nickell, 1997) and high market value. Current research in Japan is focused on further reducing the larval period by providing appropriate foods, developing an artificial diet for cultured phyllosomas, and on reducing larval mortality through control of pathogenic microflora levels (Kittaka *et al*., 2001).

Obtaining large quantities of pueruli from the wild is problematical, and precludes most enhancement strategies based on growout and restocking. Marine reserves or marine protected areas (MPAs) may provide an alternative for recovery of over-exploited populations by permanently closing certain fishing or spawning grounds, or proclaiming areas in which only pots may be used. The latter option is being considered in the Balearic Islands, Corsica, Ireland and Brittany. In Corsica, eight sanctuaries cover an 80 km^2 cumulative area, and in Spain, a marine reserve at the Columbretes Islands has provided scientists with several leads on stock recovery methods, i.e. that relatively small MPAs can be used to enhance *P. elephas* adult stock biomass (Goñi *et al*., 2001b), because this species undertakes relatively short migrations after settlement, during foraging and for reproduction. The potential of marine reserves was highlighted at Columbretes, where a recovery in *P. elephas* modal size to 130 mm (male) and 100 mm CL (female), and to maximum CLs of 173 mm and 148 mm respectively, were achieved 10 years after the establishment of the reserve (R. Goñi *et al*., unpublished). Nevertheless, proclamation of MPAs for *P. elephas* should be based also on genetic population structure (Cannas *et al*., 1998) and a good understanding of its metapopulation structure and of how metapopulations are connected within the ocean environment (Tuck & Possingham, 2000).

12.7 Conclusions

12.7.1 Biology

One of the most interesting aspects of the *Palinurus* genus is its present-day geographic distribution, with three species (*P. elephas, P. mauritanicus* and *P. charlestoni*) occurring only in the north-eastern Atlantic and Mediterranean, far removed from the other two species (*P. delagoae* and *P. gilchristi*) which are restricted to the south-western Indian Ocean. Recent analyses of mitochondrial DNA relationships within the genus provide a possible explanation, assuming that ancestral *P. elephas* inhabited the broad Tethys Sea region (present-day North Atlantic and Mediterranean), and that it gave rise to *P. mauritanicus* (which spread to deeper water and lower latitudes along north-west Africa) and to the progenitor of the Indian Ocean species (including *P. charlestoni* from the North Atlantic). It appears that the latter lineage dispersed through the Levant (Red Sea region) and clockwise around the African continent, establishing the present-day populations of *P. delagoae*, *P. gilchristi* and *P. charlestoni*. The role of glacial and inter-glacial sea level changes, water temperature and sea current shifts in explaining the above mechanism is still unclear, nevertheless, based on the close genetic relationship of *P. charlestoni* with *P. delagoae* (relative to *P. mauritanicus*) it appears that the genus circumnavigated the African continent.

Comparisons of the biological characteristics of the North Atlantic/Mediterranean species versus their Indian Ocean counterparts offer a number of interesting parallels. (1) All of the species (except *P. elephas*) occur only in relatively deep water (50–600 m), and none of them have a specialised protective matrix over the spermatophoric mass. These characteristics, together with a scant fossil record, suggest a more primitive evolutionary condition than many of the shallow-water spiny lobster genera. (2) The Atlantic and Mediterranean species appear to grow faster, reach sexual maturity at a larger size, and attain a much larger maximum size than their southern counterparts. Conversely, fecundity is much higher in the two Indian Ocean species, possibly as an adaptation to high loss of larvae in the strong Agulhas Current regime, which dominates oceanographic features along south-east Africa. (3) Adults of all five species appear to moult only once per year, over an extended period during spring and summer (*P. gilchristi*, *P. elephas* and *P. delagoae*) or fall and spring (*P. mauritanicus* and *P. charlestoni*). (4) *Palinurus* females generally produce a single batch of eggs per year, with incubation lasting between four and ten months. This characteristic differs from the more frequent moulting episodes and multiple broods produced by warmer-water genera. (5) Under culture conditions (but not necessarily in the wild) *P. elephas* has an exceptionally short larval cycle (65–72 days) compared to *Jasus* (205–319 days) and *Panulirus* (306–341 days), and phyllosoma larvae are comparatively large and well developed. This factor may, in future, make it a good choice for commercial cultivation. (6) Only the juveniles of the Indian Ocean species undertake long-distance migrations, against the direction of the prevailing currents. This is apparently an adaptation that was not required by the Atlantic and Mediterranean species, although some reproductive and short-distance ontogenetic migrations (*P. elephas, P. mauritanicus*) do occur. (7) It is suggested that the root cause of the differences in biological characteristics (size, fecundity and migrations) between the Indian and Atlantic Ocean *Palinurus* species is the adaptations that *P. gilchristi* and *P. delagoae* had to undergo to maintain their populations in the strong unidirectional Agulhas Current regime.

12.7.2 *Fisheries*

The commercial fisheries for the *Palinurus* lobsters have much in common: high product value; diminished catches; multi-national fishing fleets; multiple gear types; unreliable fisheries information and ineffective management strategies. Generally, intense exploitation of the Atlantic and Mediterranean species throughout the twentieth century and the introduction of trammel nets in the 1970s have depleted stocks to a fraction of pristine. Exploitation of the Indian Ocean species started much later (1960s and 1970s), and in the case of the South African endemic, *P. gilchristi*, access could from the onset be restricted to local vessels only. The local fleet could more easily be controlled through enforcing quotas, restricting gear to traps only, and timely management interventions, and at present *P. gilchristi* is the only species in this genus for which the outlook for fisheries is positive. Recent assessments, followed by a restriction on the number of boats fishing for the Cape Verde endemic, *P. charlestoni*, is a promising step after a period of over-exploitation, and stocks are now considered to be recovering. Attempts are being made to recover stocks of *P. delagoae*. Commercial fishing for *P. delagoae* has been suspended for five years, and a survey was undertaken in 2004 and 2005 to assess stock recovery off South Africa and Mozambique. Marine reserves appear to be the only new method envisaged so far for recovery of *P. elephas* stocks, and apart from a total ban on fishing (such as at Columbretes Islands Marine Reserve) this concept aims to include areas where use of trammel nets will be prohibited. *P. mauritanicus* in Mauritania remains over-exploited, without a clear strategy aimed at stock recovery.

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Chapter 13

Nephrops Species

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13.1 Introduction

With total catches exceeding 55 000 tonnes annually, the Norway lobster, *Nephrops norvegicus*, is the most important commercial crustacean in Europe. Not surprisingly, its biology, fisheries and management have been the subject of several reviews already (Farmer, 1975; Chapman, 1980; Dow, 1980; ICES, 1982; Sardà, 1995; Graham & Ferro, 2004). In the present review, the focus is primarily on recent developments (broadly speaking, over the past 20–25 years) in our knowledge of the species' natural history, population dynamics, exploitation and management. However, this approach is not rigorously pursued in all sections of the review, and some of the older literature is also being revisited, whenever this was considered relevant in light of our current understanding of *Nephrops*.

13.2 The species

13.2.1 Species description

Nephrops norvegicus (Linnaeus, 1758), is a member of the family Nephropidae, sub-family Nephropinae, and has the typical physiognomy of a clawed lobster, albeit with a slenderer body shape and longer claws than the 'true' lobsters *Homarus americanus* and *Homarus gammarus* (Fig. 13.1). Other distinguishing characteristics include: a carapace with a distinct post-cervical groove and longitudinal spinose keels; a long and spinose rostrum; an abdomen with transverse grooves; and large, well-pigmented and kidney-shaped eyes (hence the genus name *Nephrops*, which means 'kidney-eye'). Its colour is pale to reddish orange (Holthuis, 1950; Hayward & Ryland, 1990).

Nephrops from the Mediterranean Sea is sometimes referred to as *Nephrops norvegicus* var. *meridionalis* (e.g. Zariquiey Alvarez, 1968), the distinction with the type species being based on a small difference in morphology of the second maxilliped, but the validity of this sub-species is controversial (Holthuis, 1945; Crnkovic, 1969).

The morphometrics of *Nephrops* are well documented throughout its distributional range (see Farmer, 1975; Sardà & Fernandez, 1981; ICES, 1982, 2003, for synoptic overviews), but it is beyond the scope of the present contribution to review these in detail. Biometric relationships most frequently used, particularly for data collection and stock assessment purposes, are the length–weight relationships and the relationship between abdominal width (usually the second or the fift segment) and carapace length. The first is commonly used to calculate mean weights-at-age and total weights from size-frequency distributions, and the second to convert tail measurements into carapace lengths (CL) in fisheries where part of the landings is taking place as tails only (ICES, 1996). Although biometric relationships do differ between populations, there is no hard evidence of spatial gradients in morphometrics, and environmental factors are considered to be most likely to explain the observed differences (Castro *et al.*, 1998a).

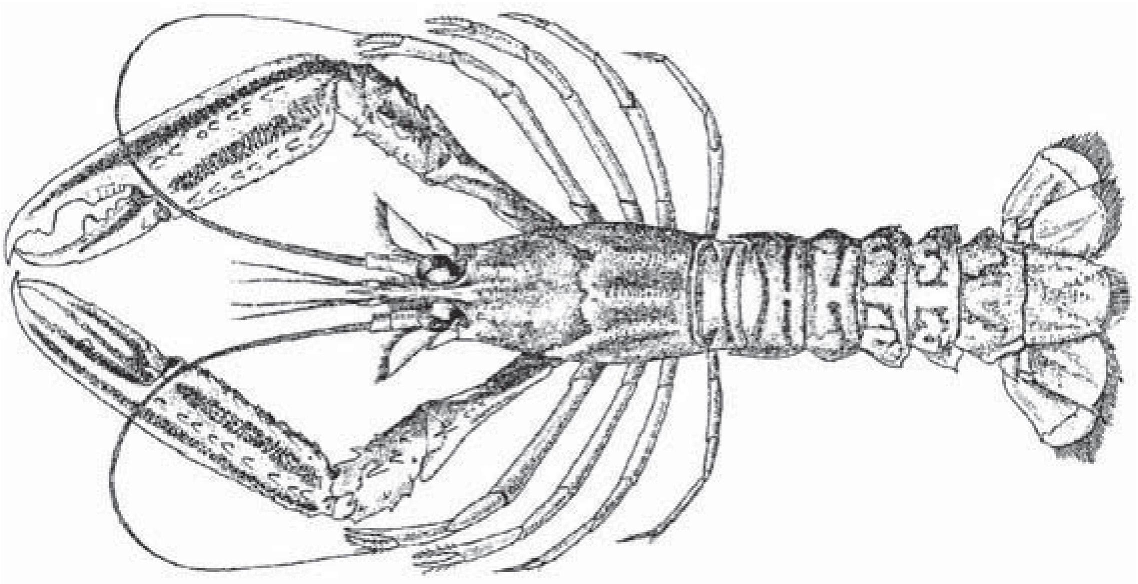


Fig. 13.1 General appearance of the Norway lobster, *Nephrops norvegicus* (L.) (after Holthuis, 1950).

13.2.2 Geographical distribution

Nephrops norvegicus is widely distributed on the continental shelves and upper continental slopes of the north-east Atlantic and the Mediterranean, from Iceland and Norway in the north, to Morocco and Greece in the south, at depths from 20 to 800 m (Fischer *et al.*, 1987; Holthuis, 1991; Ardizzone *et al.*, 1999; Abello *et al.*, 2002). The species is absent from the Baltic Sea, the Black Sea and the Levantine coast. Occasional records of *Nephrops* have been reported outside its main distributional area (e.g. Canary Islands; Greenland) (Farmer, 1975; Barquin *et al.*, 1998), but these should be considered incidental.

Nephrops is fished wherever it is found in exploitable quantities and is one of the commercially most important demersal species in the north-east Atlantic. Table 13.1 and Figure 13.2 give an overview of the major *Nephrops* populations and fishing grounds, their average landings figures for the years 2000–2002, and the countries that take most of the catches (figures based on ICES, 2003, and FAO Fisheries Statistics, http://www.fao.org/fi/figis/tseries).

Since *Nephrops* is dependent on particular types of seabed sediment (see Section 13.2.3), its overall geographical distribution is highly discontinuous. In the European waters, there are at least 30 different *Nephrops* populations, which are all physically isolated from each other, most often by large stretches of unsuitable sediment (coarse sand, gravel, bedrock, etc.). *Nephrops* is also very sedentary and only rarely migrates over distances longer than a few hundred metres (Jensen, 1965; Chapman, 1982). Except possibly during the planktonic larval stage, exchanges between neighbouring stocks are virtually non-existent, and this raises the question of genetic differentiation. So far however, there is no conclusive evidence of genetic divergence or genetic isolation in *Nephrops* (Passamonti *et al.*, 1997; Maltagliati *et al.*, 1998).

Even within areas that are considered to be inhabited by the same unit stock, the distribution of *Nephrops* can be very heterogeneous, depending on sediment characteristics such as grain size and redox potential (Tully & Hillis, 1995; Maynou *et al.*, 1996; Maynou & Sardà, 1997). A stock may thus be divided into a (large) number of smaller ‘stocklets’, with different population densities, size and sex compositions, and also different biological features (growth rate, size at first maturity, etc.) (see Sections 13.3.1 and 13.3.2).

Table 13.1 *Nephrops* landings by fishing area and stock (averages for 2000–2002), and countries taking most of the landings.

Stock/Fishing area[1,2]	Area code	Landings 2000–2002 ('000 t)	Principal countries[3]
Iceland (1)	ICES Va	1.4	Iceland
Faeroe (2)	ICES Vb	<0.1	Faroes
Northern North Sea	ICES IVa	9.1	
Noup (3)		0.3	UK
Moray Firth (4)		1.4	UK
Fladen (5)		6.1	UK, Denmark
Norwegian Deep (6)		1.2	Denmark, Norway
Central and Southern North Sea	ICES IVbc	6.6	
Firth of Forth (7)		1.5	UK
Farn Deeps (8)		2.2	UK
Botney Gut – Silver Pit (9)		1.2	Netherlands, Belgium, UK, Denmark
Off Horn Reefs (10)		0.7	Denmark
Skagerrak and Kattegat	ICES IIIa	4.4	
Skagerrak (11)		2.7	Denmark, Sweden, Norway
Kattegat (12)		1.7	Denmark, Sweden
West of Scotland	ICES VIa	10.8	
North Minch (13)		3.3	UK
South Minch (14)		3.7	UK
Clyde (15)		3.3	UK
Irish Sea	ICES VIIa	8.1	
Irish Sea West (16)		7.5	UK, Ireland
Irish Sea East (17)		0.6	UK, Ireland
North, West and South of Ireland	ICES VIIbcjk	3.3	
Aran Islands (18)		1.0	Ireland
Porcupine Bank (19)		1.1	Ireland, France, Spain, UK
Ireland SW and SE coast (20)		0.9	Ireland, France
Celtic Sea (21)	ICES VIIfgh	4.7	France, Ireland
Bay of Biscay	ICES VIII	3.7	
Bay of Biscay North (22)		3.2	France
Bay of Biscay South (23)		0.3	France
Cantabrian Sea (24)		<0.1	Spain
North Galicia (25)		0.1	Spain
Iberia Atlantic coast	ICES IXa	0.6	
West Galicia and North Portugal (26)		0.1	Spain
SW and S Portugal (27)		0.3	Portugal
Gulf of Cadiz (28)		0.2	Spain
Morocco Atlantic coast (29)		0.3	Spain
Western Mediterranean		1.0	
Catalan Sea (30)	FAO 1.1	0.5	Spain
Ligurian and N Tyrrhenian Sea (31)	FAO 1.3	0.4	Italy
Adriatic Sea (32)	FAO 2.1	0.9	Italy, Croatia
Eastern Mediterranean		1.5	
Ionian Sea (33)	FAO 2.2	1.2	Italy
Aegean Sea (34)	FAO 3.1	0.3	Greece
Grand total NE Atlantic		52.9	
Grand total Mediterranean		3.3	
Grand total all areas combined		56.2	

1. Numbers in brackets refer to location of fishing ground as shown in Fig. 13.2.
2. Shaded cells represent distinct stocks (or groupings of stocks, in the case of the Mediterranean) within preceding larger sea areas. Note that landings figures for the larger areas may exceed the sum of the figures for the distinct stocks, owing to landings taken within the larger areas but outside the individual stocks.
3. Countries taking at least 100 t of total international landings, in order of importance. Countries are given by their FAO three-letter code.

Fig. 13.2 *Nephrops norvegicus* stocks and fishing grounds in European waters (see Table 13.1 for details).

13.2.3 Habitat requirements

Nephrops has a preference for muddy seabed sediments, with >40% being of silt and clay. In areas where sediment composition and *Nephrops* densities have been studied in detail (e.g. around the British Isles and in the Adriatic Sea), there is a close relation between the distribution of *Nephrops* and the nature of the bottom deposits (Alfirević, 1968; Farmer, 1975; Bailey *et al.*, 1993; ICES, 2001). This knowledge, combined with the introduction of instruments for seabed detection and classification on commercial fishing vessels, has led to the rapid expansion of *Nephrops*-directed fisheries in areas of 'suitable' sediment, which were formerly unexploited or only lightly exploited. This has notably been the case on the Fladen Ground (northern North Sea), where the landings increased from about 1000 t in the mid-1980s to 5000–6500 t in the mid-1990s, and in both the Horn Reefs area (south-eastern North Sea) and the Norwegian Deep, where they rose from less than 50 t in the late 1980s to over 800 t ten years later (ICES, 2003).

13.2.4 *Similar species*

Apart from *Nephrops norvegicus*, the family *Nephropidae* comprises another 40 species with physical features that resemble *Nephrops* (a slender body shape and elongated claws), and with a similar preference for muddy seabeds. Species of the genera *Eunephrops* and *Metanephrops* are mostly found on the upper part of the continental slope, at depths between 200 and 600 m, while species of the genera *Acanthacaris*, *Nephropides*, *Nephropsis*, *Thymopides*, *Thymops* and *Thymopsis* are mostly found in deeper waters, between 400 and 1000 m (Holthuis, 1991). Of these, only a few are of importance to the commercial fisheries: *Metanephrops armatus* (Taiwan), *M. australiensis* (NW Australia), *M. challengeri* (New Zealand), *M. formosanus* (Taiwan), *M. japonicus* (Japan), *M. mozambicus* (SE Africa), *M. thomsoni* (Korea, Taiwan) and *M. velutinus* (NW Australia) (Holthuis, 1991; Ingle, 1997). However, their catches (a few hundred tonnes each, at the most), are by no means comparable to those of *Nephrops norvegicus* (55 to 60 thousand tonnes annually).

13.3 Life history and population dynamics

13.3.1 *Moulting and growth*

Moulting pattern

As with all decapod crustaceans, growth in *Nephrops* is the combined effect of moult frequency and size increment at moult. Although growth rates vary widely between and even within stocks (see below), there is a general pattern of moult frequency that applies to most. After having passed to the benthic stage and up to the autumn of their first year of life, juvenile *Nephrops* grow very rapidly, with moult frequencies around one moult per month (Conan, 1978). In their second and third year, the intermoult periods get longer and moult frequency gradually decreases to 3–4 moults per year, usually in late winter or spring, in summer and in autumn. After the onset of sexual maturity, growth slows down even further, and moult frequency is reduced to 1–2 moults per year in males (usually in late winter or spring, and in late summer or autumn) and 0–1 moults per year in females (in late winter or spring, after the hatching of the eggs) (e.g. Hillis, 1971a; Farmer, 1973; Charuau, 1975; Conan, 1975, 1978; Sardà, 1991; Talidec & Reyss, 1993). There is no evidence of terminal anecdysis in *Nephrops* (Farmer, 1973).

Published data sets on absolute size increments at moult show different types of relationships, from positively to negatively correlated with premoult size, but relative size increments are usually inversely related with premoult size (Farmer, 1973; Charuau, 1975, 1977; Bailey & Chapman, 1983; Sardà, 1985; González-Gurriarán *et al.*, 1996; Verdoit *et al.*, 1999). Increments at moult typically range between 1.0 and 2.5 mm CL (which corresponds to a relative size increment of 3–12 %), but considerably larger and smaller values have been recorded in many populations. Scottish studies, which covered the full size range of both immature and mature *Nephrops*, show evidence of a change in growth pattern at the onset of sexual maturity (Bailey & Chapman, 1983). In a recent laboratory study using wild-caught *Nephrops* from the south coast of Portugal, Castro *et al.* (2003) found no systematic relationship between moult increment and premoult size. They concluded instead that moult increment could be modelled as a random Normal variable, with mean values not significantly different between the sexes.

Actual moulting takes 20–30 min (Sardà, 1983) and is a laborious process during which the animals are very vulnerable to predation and cannibalism. The period between successive moults can be subdivided into four main stages, which can be recognised from morphological alterations in the setae of the pleopods (Charuau, 1973; Sardà 1983). According to Sardà's subdivision of the intermoult period, there are two postmoult stages, a so-called 'resting stage' and a premoult stage, the relative duration of which changes as the animals grow older (Sardà, 1983).

Growth curves

Growth curves for *Nephrops* have been established for many stocks throughout the geographical range of the species, by means of a variety of techniques: the analysis of modal progression in length-frequency distributions, tagging, and the combination of moult frequency and size increment data from animals held in captivity. Immature males and females have similar growth patterns and hence similar growth curves. After the onset of sexual maturity however, females grow considerably slower than males and this results in much flatter growth curves tending towards much lower size asymptotes (von Bertalanffy's L_∞) than for males (Figure 13.3). The slower growth in females also explains why the largest size classes of commercial *Nephrops* catches almost entirely consist of males, even at the time of the year when female catch rates are highest, while in the smallest size classes, both sexes are usually present in more or less equal numbers.

Von Bertalanffy's growth function is frequently used to model growth in *Nephrops*, but suffers from several shortcomings. This is particularly true for females, where the combination of a low value of L_∞ and a relatively high value of K (growth coefficient) is inclined to produce a gently sloping curve that tends to underestimate the size-at-age of the youngest, immature age classes. To resolve this problem in the context of stock assessment, when growth functions are used to convert size compositions to age compositions, the ICES Working Group on *Nephrops* Stocks has introduced the concept of 'combined' growth curves, where growth of the immature females up to the size of 50% maturity is represented by the steeper 'male' growth curve, and that of the mature females by the typical, much flatter 'female' growth curve (ICES, 1994) (see Figure 13.4 for an example).

Variations in growth rate

As already shown (Figure 13.3), growth rates vary widely between *Nephrops* stocks, and numerous arguments have been put forward in the literature to explain the differences. The exact reasons for the variability in growth rates, however, are difficult to establish, since they are likely to be the combined effect of several driving forces (temperature, sediment particle size, food availability, population density, fishing pressure, etc.), each of which may have different and possibly interactive effects.

It is also known that within the same biological population, there may be major differences in the size structure and growth parameters of patches of *Nephrops* inhabiting smaller areas with different environmental and/or population characteristics (de Figueiredo, 1984; Tully & Hillis, 1995; Tuck *et al*., 1997a; Thompson *et al*., 1998). In the Clyde (west Scotland), the K values for male *Nephrops* were found to range between 0.16–0.22 yr^{-1}, and the values of L_∞ between 45.5–65.5 mm CL (Tuck *et al*., 1997a), while on the Portuguese south and south-west coast, they ranged between 0.21–0.28, and 61.5–71.5 mm CL (de Figueiredo, 1984). These ranges are wider than the reported differences in growth parameters between, for example, the Icelandic and the Bay of Biscay *Nephrops* stocks.

In view of the above, it is impossible to draw firm conclusions on the reasons why growth differs – or seems to differ – between *Nephrops* stocks on a wider geographical scale. Some of the growth curves reported in the literature may not be representative for the stock as a whole, and may well have appeared different if the underlying data had been obtained from another location within the same stock, with other environmental and/or population characteristics. The high level of intra-population variability also poses a problem for the analytical stock assessments where inferences about the age composition of fishery catches are drawn by applying growth curves to size-frequency data (see Section 13.5.2).

Methodological problems to establish growth

Growth studies on *Nephrops* are very difficult in terms of both data collection and analysis, and the levels of uncertainty on the estimates of K and L_∞ can be considerable (regardless of the problems associated with intra-population variability). Although there has been some progress in the calibration of age with the concentration of the 'age pigment' lipofuscin in the neural tissues (Tully, 1993; Belchier *et al*., 1994), there remains no

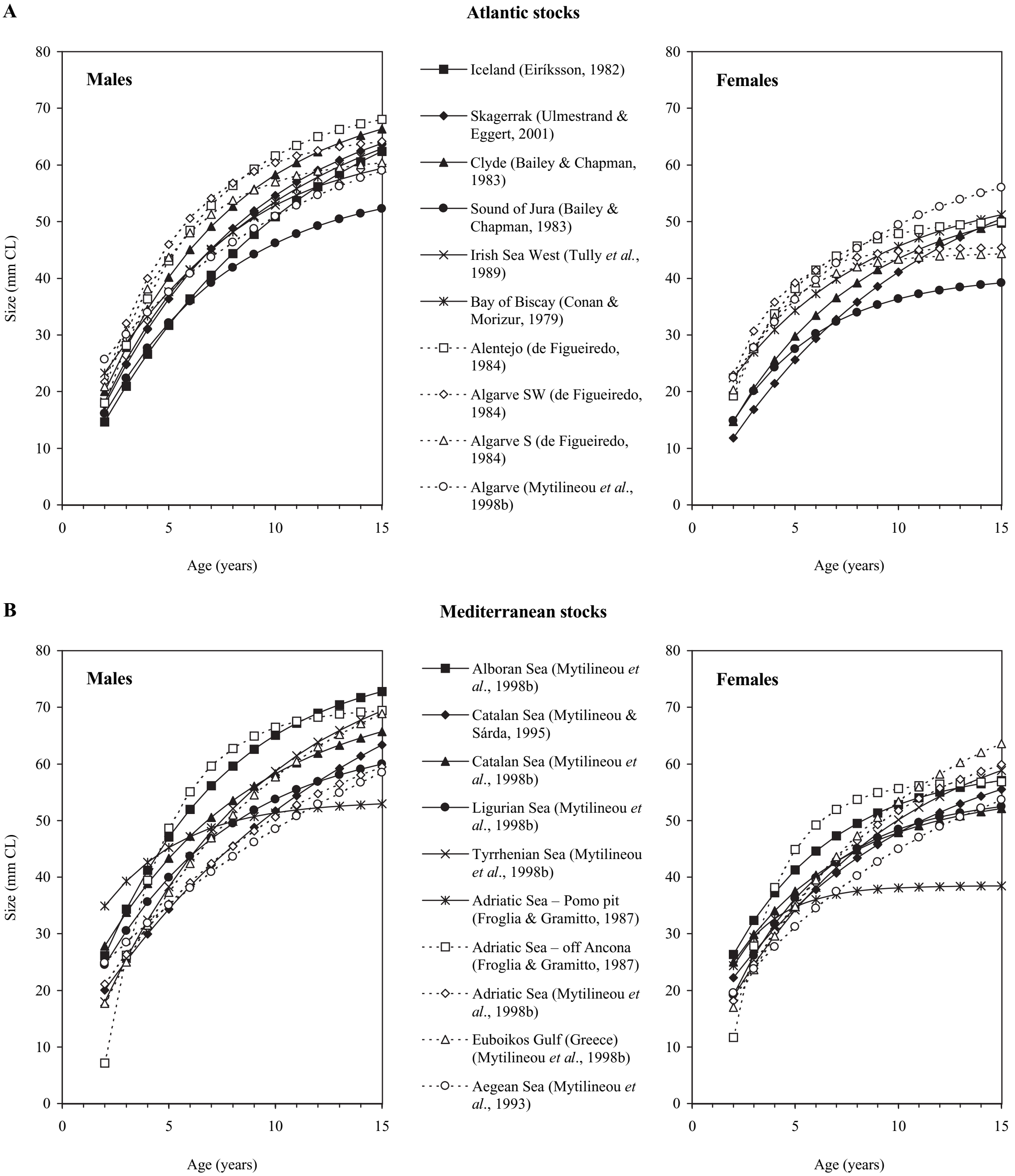


Fig. 13.3 (A) Growth curves of male (left) and female (right) *Nephrops norvegicus* – Atlantic stocks; (B) Growth curves of male (left) and female (right) *Nephrops norvegicus* – Mediterranean stocks.

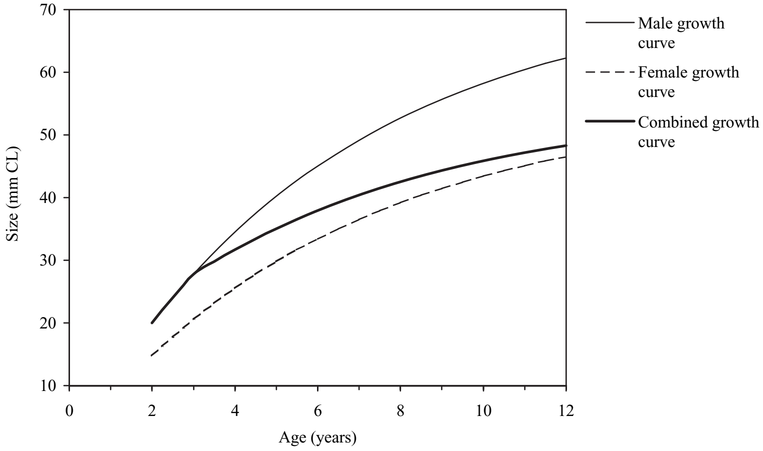


Fig. 13.4 Example of a 'combined' growth curve for female *Nephrops norvegicus*, following the approach of the ICES Working Group on *Nephrops* Stocks (ICES, 1994). The combined curve applies male growth parameters to growth of immature females, and female parameters thereafter. The unadjusted female growth curve underestimates size-at-age for the younger age classes.

reliable or routine method for direct age determination of *Nephrops* (see also Farmer, 1973). The consequence is that growth curves need to be established through indirect methods: the progression of modes corresponding to age cohorts in length-frequency distributions and/or the combination of data on moult frequency and size increments at moult obtained from tagging experiments or from animals held in captivity. The proper identification of age cohorts in length distributions however, becomes problematical after the onset of sexual maturity, when growth rates drop and the modes of successive age classes start to convolute. Computer-aided methods for resolving distribution mixtures into individual components (such as Elefan, Mix, Multifan, etc.) can be of help to identify modes in length-frequency data, but their use is often interpretative and the outcome not always unambiguous (see e.g. Mytilineou & Sardà, 1995; Castro *et al.*, 1998b). For the time being, tagging seems to be the only alternative in order to collect growth data on adult *Nephrops*, but tagging experiments are laborious and costly, and recapture rates are usually low, in the order of 2–20% (Jensen, 1965; Chapman *et al.*, 1989; de Figueiredo, 1989). Finally, the choice of a proper L_∞ to plot the von Bertalanffy growth curve, may also pose problems. Quite often, the maximum size of the animals in a population is used as a proxy for L_∞, but in unexploited populations, the maximum size may be much larger than the theoretical L_∞, whereas in heavily-exploited populations it may be much smaller (owing to the constant removal of the largest animals by the fishery) (Tuck *et al.*, 1997a; Figure 13.5).

13.3.2 Reproduction

Size at maturity

Estimates of the size at 50% maturity (L_{50}) are available for many *Nephrops* stocks, albeit mostly for females only. Estimates of the L_{50} for female *Nephrops* differ between stocks but also depend on the method used: ovary maturation stage, the presence of spermatophores, or ovigerous (berried) condition (Table 13.2). Estimates of L_{50} derived from data on the proportions of berried females are usually larger than those based on the other criteria. Berried females retreat very effectively into their burrows shortly after spawning and therefore their true proportions are likely to be underestimated, especially in samples that are collected by trawling. This results in a shift of the maturity ogive to the right and an overestimate of the size at 50% maturity (Redant, 1994).

Generally speaking, female *Nephrops* mature at a size between 23 and 30 mm CL in the relatively shallow-water populations of north-western and northern Europe, and at a size between 30 and 36 mm CL in the deep-water populations off Portugal and in the Mediterranean (Table 13.2). The corresponding age at 50% maturity (viz. 3–4 years), however, is roughly the same in all areas.

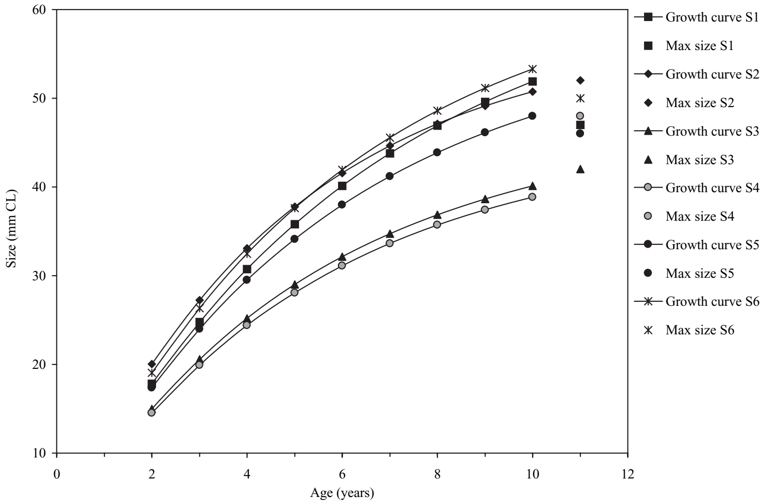


Fig. 13.5 Growth curves of male *Nephrops norvegicus* at different locations in the Firth of Clyde (S1–S6), and corresponding maximum sizes in the catches (after Tuck *et al.*, 1997a).

In some populations, there is evidence of a decrease in the proportions of mature females in the largest size classes, which suggests that not all of the older females spawn every year (Sardà, 1991; Redant, 1994).

As for growth, there can be major differences in sexual maturity parameters within the same biological population. In the Clyde (west Scotland), L_{50} estimates for female *Nephrops* (based on oocyte counts) were found to vary between 22.5 and 33.5 mm CL (Tuck *et al.*, 2000), i.e. over a range that is wider than the overall range of L_{50} estimates reported for all north-western and northern *Nephrops* stocks combined (Table 13.2). In all parts of the population concerned however, females appeared to mature at the same age (3–3.5 years), which seems to confirm that maturation is age-dependent rather than size-dependent (Tuck *et al.*, 2000).

So far, the only comprehensive study on male sexual maturity has been on Irish Sea *Nephrops*, using both primary (presence of spermatophores in the vasa deferentia) and secondary sexual characteristics (allometric changes in the morphology of the appendix masculina and the cutter claw) (McQuaid, 2002). Although in the Irish Sea, 50% of the males are capable of producing spermatophores at a size of 15 mm CL, they only develop a fully-grown appendix masculina – and hence become physically capable of mating with a female – at a size of 24–27 mm CL and an age of 3 years (Farmer, 1974a; McQuaid, 2002; McQuaid & Briggs, 2004).

Reproductive cycle

An overview of the geographical differences in the reproductive cycle of *Nephrops* is given in Table 13.3. The periods of hatching and spawning, and the length of the incubation period, vary with latitude and the breeding cycle changes from annual to biennial as one moves from south to north.

In populations where the reproductive cycle is essentially annual (such as in the Mediterranean, around the Iberian peninsula, in the Bay of Biscay, the Irish Sea and most of the North Sea), it can be summarised as follows. Mating takes place in winter or spring, while the females are still in the soft, immediate postmoult condition (Farmer, 1975). Throughout the spring and summer months, the ovaries mature – a process that is associated with marked changes in the biochemical composition of the ovaries and the hepatopancreas (Tuck *et al.*, 1997c; Rosa & Nunes, 2002) – and egg-laying takes place in late summer or early autumn. Immediately after spawning, the berried females hide in their burrows, where they stay until the next hatching period in late winter or early spring (Table

Table 13.2 Size (mm CL) at 50% maturity of female *Nephrops*.

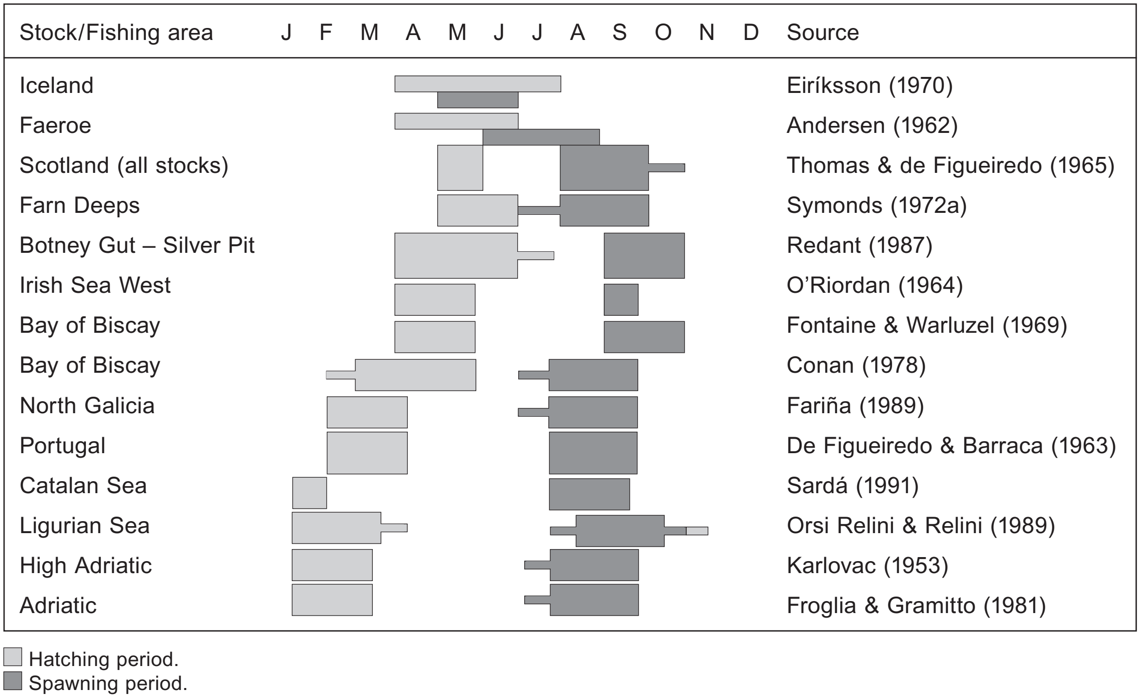
Stock/Fishing area	Method used A	B	C	D	Source
Iceland				25	Eiríksson in ICES (1982)
All Scottish stocks	25–27				Afonso-Dias & Bailey (1998)
Clyde	27–28				Bailey (1984)
Clyde	22–34				Tuck *et al.* (2000)
Sound of Jura	23				Bailey (1984)
Irish Sea West			25–26		Hillis (1979)
Irish Sea West			23.5		Briggs (1988)
Botney Gut – Silver Pit	27.5				Redant (1994)
Bay of Biscay	24–25				Fontaine & Warluzel (1969)
Bay of Biscay	23–24	22–23			Morizur (1983)
Algarve	29				De Figueiredo (1982)
Algarve	30				Orsi Relini *et al.* (1998)
Algarve			29.5		Arrobas (1982)
Alboran Sea	36				Orsi Relini *et al.* (1998)
Catalan Sea	30–31		32.5		Sardá (1991)
Catalan Sea	30				Orsi Relini *et al.* (1998)
Ligurian Sea	32				Orsi Relini *et al.* (1998)
Tyrrhenian Sea	32				Orsi Relini *et al.* (1998)
Strait of Sicily			30–32		Bianchini *et al.* (1998)
Adriatic Sea	30				Orsi Relini *et al.* (1998)
Adriatic Sea – Pomo Pit				′ 26	Froglia & Gramitto (1981)
Adriatic Sea – off Ancona				′ 32	Froglia & Gramitto (1981)
Euboikos Gulf (Greece)	33				Orsi Relini *et al.* (1998)

A = Ovary maturation stage (plus ovigerous condition).
B = Presence/absence of spermatophores.
C = Ovigerous condition.
D = Unknown or not specified.

13.3). Shortly after hatching, the females moult and mate again, and the cycle resumes.

Incubation of the abdominal eggs is strongly temperature-dependent, and increases from approximately 5.5 months at 15°C to approximately 10 months at 8°C (Dunthorn, 1967). As the average temperature decreases, the duration of the incubation period increases, hatching is delayed until it starts to overlap with the spawning season (which means that there is insufficient time left for the females to take part in that year's reproductive cycle), and the breeding cycle becomes biennial (Table 13.3). Biennial breeding cycles are typical for the cold-water *Nephrops* stocks around Iceland

Table 13.3 *Nephrops* spawning and hatching periods.



and the Faeroe Islands (Andersen, 1962; Eiríksson, 1970, 1993; Nicolajsen & Eiríksson, 1990). Also in warmer temperature regimes however, there is evidence that not all females reproduce annually (Bailey, 1984; Sterk & Redant, 1989; Sardà, 1991; Redant, 1994). As a female grows older, spawning is delayed by the combined effects of recovery from moulting and then ovary maturation, until a point is reached where ovary resorption occurs and the female misses out a year of egg carrying (Bailey, 1984). Whether reproduction proceeds biennially from then onwards is not clear.

It is tempting to view temperature as the regulatory factor of the breeding cycle, and most observations seem to confirm this assumption. The fact however, that also in isothermal environments, the breeding cycle of *Nephrops* is closely phased, with clear-cut spawning and hatching seasons (Orsi Relini & Relini, 1989), suggests that there may be other driving forces as well, although there is no indication what these forces might be.

Potential and effective fecundity

Potential and effective fecundity have been studied in many *Nephrops* stocks. Estimates of potential fecundity are derived from oocyte counts in the ovary, and estimates of effective fecundity from the numbers of eggs close to hatching (so-called stage D). The latter however, should be treated cautiously, especially when trawling collects the samples, since this may cause abrasion of the abdominal egg clump and hence additional loss of eggs, in the order of 10–20% (Chapman & Ballantyne, 1980).

Potential fecundity is exponentially related to female body size (Figure 13.6), and increases from 600–1200 oocytes in females of 25 mm CL, to 3200–4800 oocytes in females of 45 mm CL. Effective fecundity is substantially lower than potential fecundity in all *Nephrops* stocks, but the level of egg loss differs widely between areas. In the Bay of Biscay and the Mediterranean, the loss of eggs from ovary to stage D is 40–50% (Gramitto &

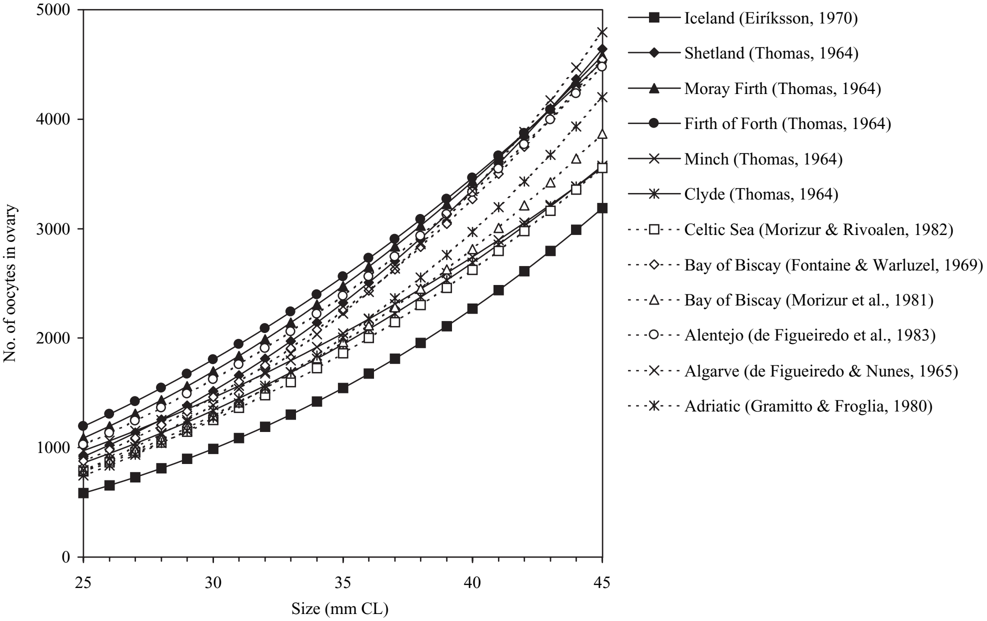


Fig. 13.6 Potential fecundity of female *Nephrops norvegicus* in different areas or stocks.

Froglia, 1980; Morizur, 1981; Morizur *et al.* 1981; Mori *et al.*, 1998), while on the Portuguese coast it is as high as 70–75% (de Figueiredo *et al.*, 1963, 1983). Extrusion failure and failure to adhere to the pleopods have been put forward as the main reasons for the loss of eggs between ovary and first abdominal stage, and unsuccessful embryonic development, predation and cannibalism (on the abdominal egg clumps) as the main reasons for the loss of eggs during the actual incubation period (de Figueiredo & Nunes, 1965; Morizur *et al.* 1981).

Larval development and confinement

The planktonic larvae of *Nephrops* pass through three developmental stages (first, second and third zoea) before they acquire their postlarval benthic life form and move to the seabed (Farmer, 1975). Larval development is temperature-dependent, and takes from approximately seven weeks at 8°C to approximately three weeks at 18°C (Farmer, 1975; Dickey-Collas *et al.*, 2000a).

Larval settlement is a critical phase in the life history of *Nephrops*, especially since the larvae need to settle in areas of suitable sediment to be able to survive (Bailey *et al.*, 1995). When dispersion of the larvae is high, or when the area inhabited by the parental stock is very small, it may not be possible to sustain a self-regenerating population against the losses during the planktonic larval stages (Hill & White, 1990). In the western Irish Sea, hatching of the *Nephrops* larvae was found partly to coincide with the formation of a cyclonic near-surface gyre, centred on the mud patch of their parental population. The gyre retains the larvae over the area of suitable sediment and thus provides a mechanism that helps to reduce the loss of larvae when they return to the seabed (Brown *et al.*, 1995; Hill *et al.*, 1996). There are indications of similar retention mechanisms in several other areas, including the Kattegat and Skagerrak (between Denmark and Sweden), the North Sea, the Minches (on the west coast of Scotland) and the Celtic Sea (Bailey *et al.*, 1995; Brown *et al.*, 1995; Hill *et al.*, 1997; Øresland, 1998). The existence of such retention mechanisms however, also has important implications for stock management, since it means that the stocks concerned are physically isolated from each other, and that the chances for replenishment of a depleted stock with larvae from a neighbouring stock are virtually non-existent (Brown *et al.*, 1995).

13.3.3 Burrowing and emergence behaviour

Diurnal and seasonal variations in catch rates are a common feature in all *Nephrops*-directed fisheries (also see Section 13.4.2). Both are associated with the burrowing and emergence behaviour of the species, which is governed by a variety of driving forces, including environmental conditions, the need to forage and the reproductive cycle.

Structure and densities of Nephrops *burrows*

It was not until the mid-1960s that evidence was produced of the existence (Priestley & Thomas, 1964) and the semi-permanent nature (Dybern & Höisæter, 1965) of *Nephrops* burrows. Before that, two hypotheses were advanced to explain the diurnal and seasonal variations in catchability (viz. migrations and temporary burrows, or a combination of the two), although there was no supporting evidence for either (Dybern & Höisæter, 1965).

Nephrops burrows vary in structure and size, from simple U-shaped tunnels with a main entrance and a narrow rear-opening, to complex structures with three or more large openings and several small vertical shafts. Typical *Nephrops* burrows are 20–30 cm deep and have a distance between main entrance and rear-opening of 50–80 cm (Rice & Chapman, 1971; Hillis, 1974). Newly-settled postlarvae and early juveniles do not seem to make their own burrows, but to live in association with larger animals (Tuck *et al.*, 1994).

Burrow densities have been studied with underwater television cameras on various Atlantic and Mediterranean *Nephrops* grounds (ICES, 2003, 2004; Smith *et al.*, 2003; Aguzzi *et al.*, 2004; Lordan *et al.*, 2004; Tuck *et al.*, 2004). Mean densities generally range between 0.1 and 1.6 m^{-2} (Table 13.4), but much lower densities (0.004 to 0.1 m^{-2}) have been recorded in the Aegean Sea (Smith *et al.*, 2003). Methodological problems associated with underwater television surveys and the interpretation of video images are discussed in Section 13.5.2, Underwater television surveys.

Several studies indicate that burrow density is related to sediment particle size. In Scottish *Nephrops* populations, high burrow densities are usually seen on coarse muds with high proportions of sand, and low burrow densities on fine muds with a low sand content (Chapman & Bailey, 1987). Similar studies in the Irish Sea, albeit on a different range of sediment types, found the converse (Hillis, 1987, 1988; Tully & Hillis, 1995), suggesting that the relationship between *Nephrops* burrow density and sediment particle size is not simply linear. To reconcile the two data sets, it has been suggested that burrow density is a non-linear function of sediment structure, with the highest densities of *Nephrops* occurring at intermediate sediment particle sizes (ICES, 1988).

Diurnal activity patterns

Nephrops spend most of their time inside their burrow or lying at its entrance, and only leave the safety of their shelter to forage and, presumably, to mate (Chapman & Howard, 1979; Chapman, 1980). There is some evidence of homing behaviour in *Nephrops*, but also of shifts from one burrow to another, and fighting over the possession of burrows is a common feature, particularly amongst larger males (Chapman & Rice, 1971).

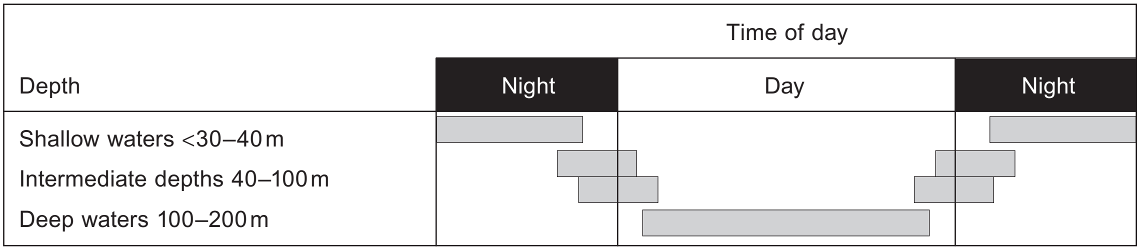
A considerable part of our initial knowledge on diurnal activity patterns in *Nephrops* was based on observed patterns in trawl catch rates, in both the commercial fisheries and research vessel surveys (primarily in north-western European waters). In addition, there was also substantial evidence from direct *in situ* investigations, albeit mostly in shallow waters, by means of underwater TV and scuba diver observations. The combined data show that the diurnal activity patterns are clearly depth-related (Table 13.5). In shallow waters (<30–40 m), peak emergence occurs during night-time, and catch rates are at their lowest during daytime (e.g. Chapman & Rice, 1971; Hillis, 1971b; Chapman *et al.*, 1972; Chapman & Howard, 1979). At intermediate depths (40–100 m), the single night peak splits into two periods of peak emergence, one around dawn and the other around dusk, which gradually move from the nightly into the daytime hours as depth increases (e.g. Höglund & Dybern,

Table 13.4 *Nephrops* burrow densities for different stocks, estimated by underwater television surveys.

Area	Stock	Range of mean burrow density (m^{-2})	Reference
North Sea	Fladen Ground	0.13–0.30	Tuck *et al.* (2004)
	Noup	0.30–0.63	ICES (2003)
	Moray Firth	0.14–0.39	Tuck *et al.* (2004)
	Firth of Forth	0.38–0.80	Tuck *et al.* (2004)
	Farn Deeps	0.25–0.67	ICES (2003)
West of Scotland	North Minch	0.25–0.64	Tuck *et al.* (2004)
	South Minch	0.23–0.44	Tuck *et al.* (2004)
	Stanton Bank	0.24–0.27	ICES (2003)
	Sound of Jura	0.50–1.24	ICES (2003)
	Firth of Clyde	0.33–0.83	Tuck *et al.* (2004)
Irish Sea	Western Irish Sea	1.5*	Lordan *et al.* (2004)
	Eastern Irish Sea	0.12–0.35**	J.M. Elson (pers. comm.)
West of Ireland	Aran Grounds	0.84–1.6	ICES (2003)
Western Mediterranean	Catalan coast	0.81	Aguzzi *et al.* (2004)
Aegean Sea	Mytilini	0.046	Smith *et al.* (2003)
	Limnos	0.025	Smith *et al.* (2003)
	Thasos	0.014	Smith *et al.* (2003)
	Skyros	0.019	Smith *et al.* (2003)
	Skiathos	0.017	Smith *et al.* (2003)
	Pagasitikos	0.12	Smith *et al.* (2003)
	Evoikos	0.004	Smith *et al.* (2003)

*Preliminary estimate.
**Possibly includes some burrows of *Goneplax rhomboides.*

Table 13.5 Periods of peak emergence of *Nephrops* from burrows.



1965; Simpson, 1965; Hillis, 1971b; Chapman *et al.*, 1972; Farmer, 1974b; Chapman & Howard, 1979; Redant & De Clerck, 1984). In deeper waters (100–200 m), the two peaks merge into a single peak during daytime, and catch rates are at their lowest during night-time (e.g. Höglund & Dybern, 1965; Simpson, 1965; Hillis, 1971b). The patterns described here are generalised patterns, and there are many examples of data sets where single or successive 24-hour cycles depart from the general pattern, for reasons which are not always clear.

In the 1970s, it was assumed that hunger state and light intensity were the triggering factors for the circadian activity rhythm in *Nephrops*, with hunger state being the driving force and light intensity – or changes in light intensity – being the regulatory factor for the actual emergence from the burrows (Chapman, 1980). At depths between 20 and 200 m, maximum emergence was observed at light intensities between 10^{-5} and 1 lux (Hillis, 1971b; Chapman *et al.*, 1972), and this was considered to be the 'optimum light intensity range' to allow foraging and avoid predation, while at the same time avoiding retinal damage due to exposure of the highly sensitive eye to excessive light (Chapman, 1980).

Since then, however, increasing evidence has shown that the regulatory mechanisms of emergence and hiding behaviour are much more complex, and probably not entirely exogenous. First, observations on animals held in captivity suggested the existence of endogenous activity rhythms (Atkinson & Naylor, 1973, 1976; Naylor & Atkinson, 1976; Hammond & Naylor, 1977). Second, observations on Mediterranean deep-water stocks of *Nephrops* revealed the existence of diurnal activity patterns that did not match the abovementioned 'optimum light intensity range', which suggests that (1) *Nephrops* may be sensitive to changes in the intensity of particular wavelengths (probably around 480 nm), rather than to light intensity as such, and (2) external factors other than light (e.g. the availability of nycthermal prey species) may play a role as triggering factor of the diurnal emergence behaviour (Froglia, 1972; Froglia & Gramitto, 1981, 1985; Aguzzi *et al.*, 2003).

Seasonal activity patterns

Seasonal activity patterns are most pronounced in female *Nephrops* and are closely related to the reproductive cycle. Shortly after spawning, the berried females retreat into their burrows, and they mostly stay there for the entire duration of the incubation period (in the majority of stocks, from late summer or autumn until late winter or spring – see Section 13.3.2, Reproductive cycle). Reduced commercial catch rates of immature females and males during the winter in some areas (e.g. southern North Sea, Celtic Sea, Bay of Biscay), suggest that these also tend to spend more time in their burrows during winter than during the rest of the year, but this pattern is much less pronounced than in berried females. As a combined result of these seasonal activity patterns: (1) fishery catch rates are usually lower in winter than in summer, (2) winter catches predominantly consist of males, certainly in the larger, adult size classes, and (3) berried females are virtually absent from the winter catches (e.g. Thomas & de Figueiredo, 1965; Arrobas, 1982; Redant, 1987; Sardà, 1991; Briggs, 1995).

In late winter or spring, the females reappear from their burrows to hatch their eggs. In some areas, there is a small dip in female catch rates shortly afterwards, which may be associated with the spring moult (Redant, 1987). After the hatching and mating season, the females spend at least as much of their time as the males and maybe more, foraging outside the burrows. This results in: (1) increased overall fishery catch rates throughout the summer, and (2) sex ratios in the catch close to 1 : 1 or in favour of the females up to the next spawning period in late summer or autumn (Thomas & de Figueiredo, 1965; Arrobas, 1982; Redant, 1987; Sardà, 1991; Briggs, 1995).

The seasonal patterns described here apply to populations where spawning is essentially annual. In populations where spawning is biennial, the female part of the stock falls into two fractions, spawning in alternate years. Each fraction will show the typical hiding behaviour when berried, but since this affects only half (or thereabouts) of the adult female population, the associated changes in, for example, sex ratios in the fishery catch will be much smaller than in stocks where the majority of adult females spawn every year (ICES, 1982). Another striking exception to the general pattern is the Farn Deeps stock (south-western North Sea), where female catch rates peak during the winter months and are at their lowest in the summer (Symonds, 1972a; ICES, 2003).

Effects of hypoxia

Hypoxic conditions occasionally observed, for example, in the Kattegat and the Adriatic (Froglia & Gramitto, 1982; Bagge, 1988; Hallbäck & Ulmestrand, 1990), can cause severe disruption of the natural emergence patterns and even mass mortality in *Nephrops* populations. When oxygen saturation in the bottom water layers drops below about 50%, *Nephrops* are forced up from their burrows, in search of oxygen (Bagge & Munch-Petersen, 1979). Under moderate hypoxia, locomotory activity declines and the animals raise their bodies on stilted legs to increase oxygen availability. Oxygen saturation levels below about 25% are lethal within 24 hours, particularly in juveniles which are more sensitive to hypoxia than adults (Eriksson & Baden, 1997). Moderate hypoxia and its associated behavioural responses, makes *Nephrops* much more vulnerable to trawling, and the increased catch rates may, at least in the beginning, give the false impression that stock density is increasing. Severe hypoxia can wipe out entire *Nephrops* populations, and it may take years before the stock recovers to the pre-hypoxia situation (Hallbäck & Ulmestrand, 1990; ICES, 1990).

13.3.4 Food and feeding

Nephrops is an opportunist predator and scavenger (Thomas & Davidson, 1962), making short foraging excursions in the vicinity of its burrow (Chapman & Rice, 1971; Chapman *et al.*, 1975). Feeding mainly occurs during periods of subdued light (see Section 13.3.3), although it is likely that larger individuals spend a greater proportion of their time in foraging (Chapman, 1980). Descriptions of feeding methods are given by Yonge (1924) and Thomas and Davidson (1962), based on aquarium observations. Active prey is captured by grasping with chelipeds and walking legs, and the walking legs are also used to close around passive food items. Food is conveyed to the mouth using the anterior walking legs assisted by the maxillipeds.

Similar to many other decapods, *Nephrops* possesses a 'gastric mill' – a set of calcareous ossicles operated by gastric muscles in the cardiac-foregut (stomach). The actions of the mouthparts and gastric mill, breaking up food and grinding into a fine powder, are described in detail by Yonge (1924) (see also Farmer, 1974c). As noted by Höglund (1942), this vigorous mastication of the food makes it difficult to identify food items from examination of stomach contents. Despite this difficulty, several studies have described the diet of *Nephrops* in various parts of its range, relying on fixing with formaldehyde to prevent further digestion of stomach contents before examination (Parslow-Williams *et al.*, 2002). Organisms with hard parts are likely to be slightly over-represented in the stomach samples, partly for reasons of identifiability, but also because of shorter digestion times for soft tissues. Sardà and Valladares (1990) calculated that soft prey items such as polychaetes are likely to be underestimated by about 10%. For the purposes of drawing broad conclusions about diet composition, this source of bias can probably be ignored.

The results of stomach contents analyses indicate that *Nephrops* is an unselective feeder, and representation of different items in the stomach appears to be governed by prey abundance rather than any feeding preference. Crustaceans, polychaetes, molluscs and, to a lesser extent, echinoderms appear to make up the bulk of the diet. In Scottish samples, Thomas and Davidson (1962) found 67% of *Nephrops* stomachs to contain crustaceans, 66% to contain polychaetes, 64% to contain molluscs and 50% to contain echinoderms. A wide range of species was represented within each of these groups. For example, the most abundantly represented crustacean groups were ostracods, amphipods and decapods up to the size of *Nephrops* itself. For *Nephrops* in the Firth of Clyde, Parslow-Williams *et al.* (2002) showed that up to half of the total weight of ingested items comprised crustaceans. Crustaceans in the diet appear to give a lower energetic return than soft-bodied prey items such as polychaetes, but do serve as a source of essential minerals such as calcium (Parslow-Williams *et al.*, 2002).

Generally, similar results have been obtained in various other parts of the geographical range: Andersen (1962) lists various polychaetes and molluscs in *Nephrops* stomachs from the Faeroes; Fontaine (1967), Fontaine and Warluzel (1969) and Lagardère (1977) list molluscs, crustaceans, polychaetes and some other groups from the Bay of Biscay; Gual-Frau and Gallardo-Cabello (1988), Cristo (1998) and Cristo and Cartes (1998) list crustaceans, molluscs, polychaetes, echinoderms, fish and some other groups from the south of Portugal and in the Mediterranean. Comparison at the higher taxonomic levels in the studies of Thomas and Davidson (1962) and Cristo and Cartes (1998), shows similar diet composition in Scottish,

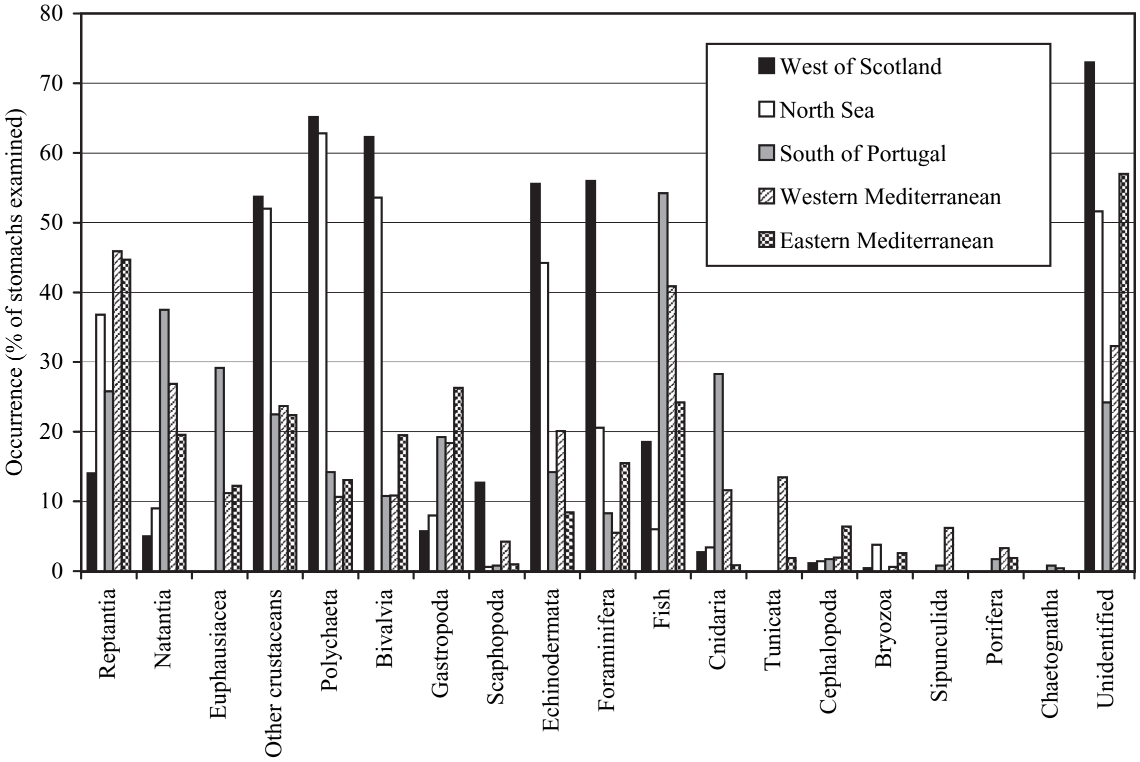


Fig. 13.7 Diet of *Nephrops norvegicus* in different parts of its range: occurrence of food items identified in the contents of the gastric-foregut (stomach). Data for west of Scotland and the North Sea from Thomas & Davidson (1962); data for Portugal and the Mediterranean from Cristo & Cartes (1998).

Portuguese and Mediterranean samples (Fig. 13.7). Some differences are also apparent, such as the absence of Euphausiacea and greater importance of echinoderms in the Scottish samples, but the overall picture is one of relatively constant diet composition. Cristo and Cartes (1998) came to similar conclusions with regards to different areas of the Mediterranean and southern Portugal, and also confirmed the previous finding by Gual-Frau and Gallardo-Cabello (1988) (for southern Portugal) that the diet does not vary seasonally. As would be expected, the similarity across geographical areas does not extend to the level of species. Whereas, for example, *Crangon* spp. were found in the stomachs of Scottish *Nephrops* (Thomas & Davidson, 1962), the closest counterparts in southern European samples would be species of *Aristeus*, *Sergestes* and *Solenocera* (Lagardère, 1977; Gual-Frau & Gallardo-Cabello, 1988; Cristo, 1998; Cristo & Cartes, 1998).

Suspension feeding appears to be rare in larger decapods, and Thomas and Davidson (1962) suggested that *Nephrops* does not ingest particles below 1 mm in diameter. Farmer (1974c) noticed that the exopodites of the mouthparts in *Nephrops* are continuously waving, and speculated that the function of their plumose setae might be to remove suspended food particles that might otherwise foul the mouthparts during feeding. The results of Loo *et al.* (1993) suggest instead that *Nephrops* are capable of active suspension feeding by this method. In experiments where *Nephrops* were offered planktonic food items, these authors found evidence that *Nephrops* are able to retain particles down to a size of 200 m. Both *Nephrops* and European lobster (*Homarus gammarus*) were able to clear water of brine shrimp nauplii about 600 μm in size, and *Nephrops* appeared also to ingest rotifers averaging 2000 μm in size. Haemocyanin concentration in the blood (an index of nutritional state) declined more slowly in *Nephrops* held in unfiltered seawater than in those held in filtered seawater, indicating a significant nutritional gain from suspension feeding. It is possible that this contributes to the nutrition of ovigerous females, which appear not to emerge from their burrows to forage (see Section 13.3.3).

No account of feeding behaviour in *Nephrops* would be complete without mentioning cannibalism. Sardà and Valladares (1990) found that mortality due to cannibalism in groups of *Nephrops* held in laboratory tanks was 12% over 16 days if the animals were provided with other sources of food, and 36% in starved *Nephrops*. It is not known how significant a contribution cannibalism makes to the feeding of *Nephrops* in the wild, but it is widely considered that it acts as a factor constraining the recruitment of juveniles to the stock under conditions of high adult stock density.

13.3.5 Predators

Cod (*Gadus morhua*) is generally identified as the most important predator of *Nephrops* in the northern parts of its range (e.g. Farmer, 1975). Symonds and Elson (1983) estimated that cod accounted for 88% of the predation on *Nephrops* by fish in the western Irish Sea, and concluded that this was the only species to exert significant predation mortality. Other studies have confirmed the importance of cod as a predator of *Nephrops* in areas to the north of the English Channel (e.g. Thomas, 1965; Rae 1967a, b, 1968; Warren, 1976; Björnsson & Dombaxe, 2004). Brander and Bennett (1986, 1989) modelled the interactions between cod and *Nephrops* in terms of predation and fishing mortality, and suggested that maximum fishery yield of *Nephrops* would be achieved with fishing pressure increased on cod and decreased on *Nephrops*. Brander and Bennett (1989) noted that catch rates of *Nephrops* in the Irish Sea were negatively correlated with cod stock biomass, but there is little evidence that *Nephrops* stocks have benefited from the declines in cod stocks observed over recent years (Bennett & Lawler, 1994). This may be because the alleviation of cod predation pressure is offset by increased predation of juvenile *Nephrops* by small fish that are themselves preyed upon by cod (Armstrong *et al.*, 1991). The importance of *Nephrops* to cod can, perhaps, be overstated. Bromley (1991) found that the rate of energy intake by cod was six times higher whilst feeding on sprat than whilst feeding on *Nephrops*. Björnsson and Dombaxe (2004) also noted the poor quality of *Nephrops* as food for cod, and suggested that the predation of cod on *Nephrops* in Icelandic waters could be reduced by increasing stocks of alternative prey species such as capelin (*Mallotus villosus*).

Despite the undoubted primacy of cod in northern areas, many other species are known to prey upon *Nephrops* at least occasionally. Thomas (1965) found *Nephrops* in the stomachs of thirteen species of fish trawled from Scottish waters, of which the most important are summarised in Figure 13.8. *Nephrops* has even been recorded in the stomachs of giant squid (*Architeuthis* sp.) off the west of Ireland (Lordan *et al.*, 1998), although there is no suggestion that this is a major *Nephrops* predator. See Farmer (1975) for a comprehensive list of fish species for which *Nephrops* has been recorded as prey. Armstrong (1982) examined the stomachs of cod and two smaller gadoid species in the Irish Sea and found a strong positive relationship between fish length and the size of *Nephrops* taken (Figure 13.9A). *Nephrops* comprised 5% of the average daily intake of poor-cod (*Trisopterus minutus*), 16% of the intake of pouting (*T. luscus*) and 43% of the intake of cod (weighted averages calculated from tables in the Appendix of Armstrong, 1982). Warren (1976) reported a similar predator–prey size relationship for *Nephrops* taken by cod in the North Sea and Irish Sea (Figure 13.9B). The size distribution of *Nephrops* in cod stomachs was similar to that observed in a small-mesh trawl, but with a slight bias towards more small and fewer large individuals taken by cod.

Information on the predators of *Nephrops* in the southerly parts of its distribution is scantier, but it is presumed that cod is replaced by other large demersal fish species that co-occur with *Nephrops*. Gauss-Garady (1912, 1913; cited by Farmer, 1975)

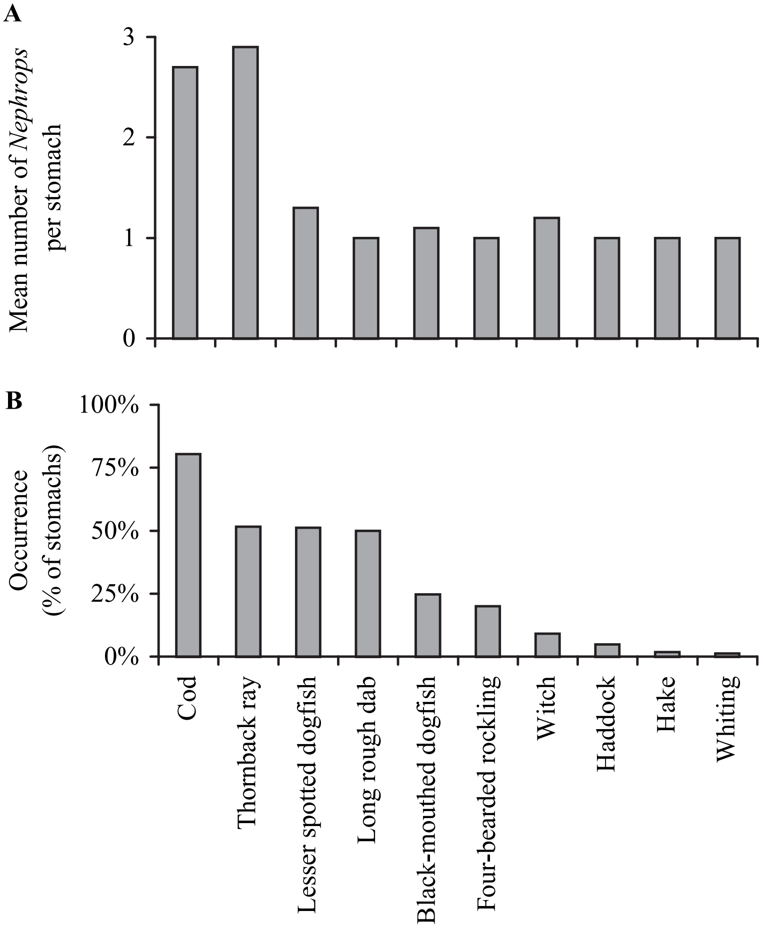


Fig. 13.8 Predators of *Nephrops norvegicus* in Scottish waters, from Thomas (1965): A, mean number of *Nephrops* per stomach; B, percentage of stomachs examined that contained *Nephrops*.

reported a range of fish species as major predators of *Nephrops* in the Adriatic Sea, including anglerfish (*Lophius* spp.), various elasmobranchs, hake (*Merluccius merluccius*), weevers (*Trachinus* spp.), gurnards (*Trigla* spp.), scorpionfish (*Scorpaena* spp.) and small gadoids. The gadoid species included Mediterranean poor-cod (*Trispoterus minutus capelanus*), which has also been reported as an important predator of *Nephrops* off the east coast of Spain (Planas & Vives, 1952) and in the Euboikos Gulf, eastern Greece (Politou & Papaconstantinou, 1994). Presumably, this species accounts for predation only of the smaller size classes of *Nephrops* (cf. Figure 13.9A). Gauss-Garady (1912, 1913) also reported the harbour crab (*Liocarcinus depurator*) and the musk octopus (*Eledone moschata*) as feeding on *Nephrops*, although neither is likely to be a major predator. Quetglas *et al.* (1999) found a very low incidence (<1%) of *Nephrops* in the stomachs of the European flying squid (*Todarodes sagittatus*) in the western Mediterranean.

13.3.6 Parasites and diseases

Stewart (1984) noted that the list of parasites and diseases known to afflict lobsters is not extensive, and this is certainly true of *Nephrops*. Epizoa including polychaetes, bryozoans, hydrozoans, molluscs, cirripedes and exceptionally, Foraminifera have been noted on the exoskeleton of *Nephrops* (Barnes & Bagenal, 1951; Farmer, 1977), but individuals in commercial and survey catches are generally very clean-shelled. The extent to which this

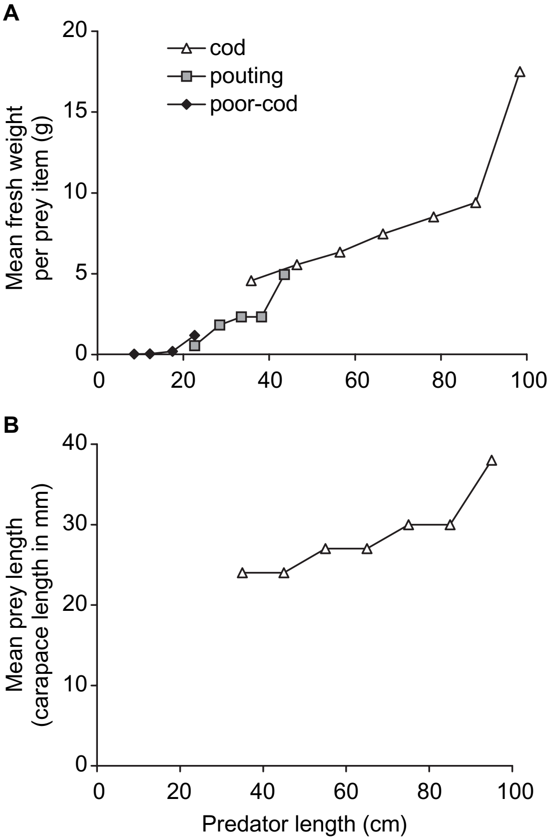


Fig. 13.9 Relationship between predator size and mean size of *Nephrops norvegicus* recorded in stomachs: (A) mean fresh weights of *Nephrops* recorded in stomachs of poor-cod (*Trisopterus minutus*), pouting (*Trisopterus luscus*) and cod (*Gadus morhua*) in the Irish Sea by Armstrong (1982); (B) mean carapace lengths of *Nephrops* recorded in stomachs of cod in the North Sea and Irish Sea by Warren (1976).

is due to grooming, burrowing behaviour or relatively high moult frequency is unknown, but heavy epibiont loads are seen only rarely, usually in exceptionally large individuals which presumably moult with less than annual frequency.

Shell and muscle necrosis

'Shell disease' caused by fungal and bacterial agents and characterised by chitinolysis and necrosis of the exoskeleton has been recorded in a number of decapod crustacean species (Rosen, 1970; Stewart, 1984), but there are no documented reports of its occurrence in *Nephrops*. Possibly this is also because of the relatively high frequency of moulting, although shell disease has been reported in some small species of peracarid crustaceans with much higher moult frequency (Rosen, 1970).

A brown-coloured necrosis of the exoskeleton is frequently observed where *Nephrops* has been injured. Farmer (1975) considered this to be the result of chitinoclastic bacteria destroying the exoskeleton at the site of the injury.

A rapid-onset abdominal muscle necrosis was first noted in creel catches of *Nephrops* taken from the west coast of Scotland in the summer and autumn of 1999 (Stentiford & Neil, 2000). Individuals were reported to be dying or moribund during live transport, and the opaque appearance of the tail meat caused some catches to be refused at market. Stentiford and Neil (2000) found that 8% of individuals in a trawl-caught sample from the Firth of Clyde showed signs of necrosis in at least one abdominal muscle fibre immediately after capture, this proportion rising to 29% after four hours. Death of the affected individuals occurred within days. The condition is characterised by degeneration and disruption of muscle fibre organisation, infiltration of damaged muscle with granulocytes and a loss of contractile proteins from affected tissues. No causative agent has been identified, although Stentiford and Neil (2000) noted the presence of unidentified bodies in some severely damaged muscle tissues, which may have been viruses. They suggested that the condition is most likely to be ideopathic (host-induced), caused by a combination of damage to the exoskeleton and stress during and immediately after capture. Similar conditions caused by microsporidians in other species are characterised by much slower progression (e.g. Breed & Olsen, 1977). The overall incidence of the condition in *Nephrops* populations is unknown, but Stentiford and Neil (2000) speculated that it may well contribute to the high mortality of fishery discards returned to the sea after trawl capture.

Larger parasites

Stewart (1980) lists some of the larger parasites that have been recorded on lobsters, including some on *Nephrops*. The immature stage of the aspidobothrid trematode *Stichocotyle nephropis*, which in its adult form is a parasite of skates and rays, has frequently been found encysted in the stomach and intestinal wall of *Nephrops*, but its incidence appears to be very variable in time and space. Symonds (1972b) reported incidences between zero and 20% in samples taken from the coasts of Britain during the early 1960s. In samples taken about the same time, Mackenzie (1963) found the parasite to be absent from populations on the east coast of Scotland, including the Firth of Forth (the type locality), where Cunningham (1887) had described it as 'fairly common' during the late nineteenth century. Other parasites recorded in *Nephrops* include the gregarine protozoan *Porospora nephropis* from the digestive tract and a lernaeopodid copepod found in the vas deferens (references in Sinderman, 1970; Farmer, 1975; and Stewart, 1980). Choniostomatid copepods of the genus *Nicothoe*, which includes the 'gill maggot' of *Homarus gammarus*, have been found on the gills of several Pacific lobster species similar to *Nephrops* but now assigned to the genus *Metanephrops* (Sinderman, 1970). In none of these cases is there information on the pathology in *Nephrops*, but the impact is generally assumed to be small (Stewart, 1980).

Dinoflagellate infections

Recent studies have highlighted the importance of dinoflagellates as parasites of crustaceans, including many species of commercial importance (Shields, 1994). Syndinid dinoflagellates of the genus *Hematodinium* have been identified as the causative agents for a number of crustacean diseases, such as 'bitter crab disease' in some majid crabs (Meyers *et al*., 1987; Taylor & Khan, 1995) and 'pink crab disease' in the edible crab *Cancer pagurus* (Stentiford *et al*., 2002). In the early 1980s, a low incidence of lethargic, abnormally-coloured *Nephrops* was observed during routine biological sampling off the west coast of Scotland. Affected individuals were characterised by an opaque, yellow/orange coloration, milky-white haemolymph and low haemolymph pressure. Field *et al*. (1992) examined the haemolymph of affected individuals and discovered the presence of a parasitic dinoflagellate resembling *Hematodinium perezi*. A background prevalence of 10–15% appeared to apply over much of the west coast of Scotland, but with incidences up to 70% in the Clyde Sea area.

In view of poor meat quality and the possibility of increased mortality in economically important stocks of *Nephrops*, a considerable amount of research into the aetiology, diagnosis, pathology and incidence of *Hematodinium* infections in *Nephrops* has been undertaken over the last decade. A key element in this research has been the development of diagnostic tools. External assessment of colouration and opacity has been found to underestimate the prevalence (Tärnlund, 2000; Stentiford *et al*., 2001b), and the most commonly-used method is the microscopic examination of pleopods where the parasite is visible in the haemolymph. Field and Appleton (1995) developed a four-point scale for the pleopod method, which allows the progression of the disease to be monitored. Sophisticated immunoassay methods have been developed to allow detection of low-level (sub-patent) and tissue-based (latent) infections that cannot be identified by the pleopod method (Field & Appleton, 1996; Stentiford *et al*., 2001d; Small *et al*., 2002). Nevertheless, the pleopod method remains a useful technique for the detection and monitoring of advanced infections of the haemolymph (patent infections). Both the body colour and pleopod methods have been used to identify *Hematodinium* infections in *Nephrops* populations from east and west Scottish coasts, the southern North Sea and the Skagerrak and Kattegat (Field *et al*. 1992; Field & Appleton, 1995; ICES, 1996; Tärnlund, 2000; Stentiford *et al*., 2001b; Briggs & McAliskey, 2002).

The prevalence of *Hematodinium* infections in *Nephrops* stocks shows marked seasonal patterns. The most common pattern is for peak prevalence in spring and lowest prevalence in autumn. This pattern is evident in stocks on the west coast of Scotland (Field *et al*., 1998; Stentiford *et al*., 2001b) and in the Irish Sea (Briggs & McAliskey, 2002). Studies in Swedish waters using the body colour method indicated the highest prevalence in autumn during the early 1990s (ICES, 1996), but Tärnlund (2000) found no difference between spring and autumn 2000 using the same method, and using the pleopod method found higher prevalence in autumn. Various other patterns of prevalence have been described in relation to size, sex, moult stage and ovary stage, and prevalence within individual stocks is also quite variable between years (Field *et al*., 1998; Stentiford *et al*., 2001b; Briggs & McAliskey, 2002).

Conclusions about *Hematodinium* prevalence based on trawl-caught samples are complicated by the effect of the parasite on burrow emergence and swimming behaviour, both of which affect catchability. Laboratory studies have shown infected *Nephrops* to remain outside the burrow for 19.4% of the day compared with 1.7% in uninfected *Nephrops* – a more than ten-fold increase (Stentiford *et al*., 2001c). Infected animals also show a progressive decline in swimming performance as the infection severity increases (Stentiford *et al*., 2000b). Both responses will increase the exposure of infected animals to trawling and predators, and reduce the ability to escape.

Reduced muscle performance in the earlier stages of the infection appears to be due to the parasite drawing on carbohydrate reserves, perhaps compounded by increased oxygen demand, whilst in the final stages of infection the structure of the muscle is damaged as the parasite depletes amino acids and proteins (Stentiford *et al*., 2000a, 2001a). The culmination of infection is inevitably death, either through exposure to predators and fishing, or through sporulation (Appleton & Vickerman, 1998). The consequences of this mortality for *Nephrops* population dynamics are unknown. It is possible that at least part of the mortality replaces rather than adds to other sources of mortality such as fishing and predation. Further research on this topic is needed, together with an improved understanding of the modes of transmission of the parasite, since there may be important implications for fishery management.

13.3.7 Population regulation

Stock–recruitment relationships

Surprisingly little is known about how the recruitment of juvenile *Nephrops* to a stock depends on the population of adults. Estimates of recruitment and stock biomass are regularly obtained by analytical assessment of fishery data, but for reasons connected with the use of length data to infer ages, these estimates are considered not to represent the true ranges of variation (see Section 13.5.2). Bell (1999) attempted to estimate the form of stock–recruitment relationships for *Nephrops* in the North Sea by combining data from several stocks, thus widening the range of contrast in relative stock biomass and recruitment. A stock–recruitment function fitted to the data showed a negative relationship between stock size and recruitment over the range of 'observed' stock sizes, i.e. a compensatory, density-dependent relationship (Shepherd, 1982).

Stock–recruitment relationships were examined for a wider range of Atlantic stocks by ICES (2000). Recruitment and stock indices were constructed from commercial catch rate data for ranges of length classes corresponding to recruits and sexually mature adults in the fished stocks. No relationship at all was apparent for some stocks (western Irish Sea, Firth of Clyde), possibly because the range of observed variation was too narrow. For one stock (south-east Iceland), the relationship appeared to be linear and positive, a result hard to explain on biological grounds for a sustainably-exploited stock. Negative relationships were apparent for several North Sea stocks and possibly for the south and south-west Portugal stock.

Further exploration using catch rate indices has failed to corroborate these patterns (ICES, 2002), but there are theoretical grounds for supposing that stock–recruitment relationships in *Nephrops* might indeed be density-dependent, with reductions in the numbers of juveniles recruiting to the stock at high adult densities. These are set out by ICES (2000) and include: (1) physical constraints on the distribution of a stock defined by the extent of available muddy habitat (see Section 13.2.3); (2) the probable dependence of newly-settled pre-recruits on the presence of adult burrows (see Section 13.3.3); (3) the territorial behaviour of adults, which constrains the number of burrows per unit area; (4) the likely density-dependence of predation and cannibalism, which may increase the mortality of juveniles at high stock densities (see

Section 13.3.4); (5) the possibility of density-dependent constraints on growth rates at high densities, which might prolong the exposure to heavy predation.

More research is needed into the form of stock–recruitment relationships in *Nephrops*, particularly since this is potentially an extremely important factor for fishery management. More information is also needed on the role of climate and other environmental factors in determining recruitment (see Section 13.5.4 on recruitment declines in Iberian stocks). Hydrodynamic factors appear to constrain the dispersion of larvae to the area of the parental stock in many cases (Brown *et al.*, 1995; and see Section 13.3.2), and it is precautionary to suppose that most if not all stocks are self-recruiting, without significant influx of larvae from neighbouring areas.

Natural mortality

The rate of natural mortality, commonly couched in terms of the instantaneous rate coefficient *M*, is another feature of *Nephrops* populations about which there is remarkably little information. Sources of natural mortality include predation (Section 13.3.5) and parasites and diseases (Section 13.3.6), each of which may be supposed to be density-dependent and to vary from year to year. Nevertheless, for the purposes of stock assessment (Section 13.5.2), *M* is almost always considered to be a constant. Despite attempts at joint modelling of *Nephrops* stocks together with those of major predators (Brander & Bennett, 1986, 1989), there is no real evidence of significant changes in natural mortality levels, for example, as a result of stock declines of North Sea or Irish Sea cod. It may be supposed that this is at least partly because *M* is extremely difficult to measure.

The value of *M* is sometimes estimated from generalisations about the relationships between natural mortality, growth parameters and environmental temperature (Pauly, 1980). This method was used by Sardà and Lleonart (1993) to arrive at estimates for annual *M* of about 0.4 (33%) for both males and females in the Catalan Sea, and by de Figueiredo (1984) to obtain annual *M* of 0.5 to 0.6 (39–45%) for females and 0.3 to 0.4 (26–33%) for males in Portuguese waters. Maynou *et al.* (2003) report various other estimates for Mediterranean stocks, varying from 0.25 to 0.82 (22–56%) for females and from 0.25 to 0.65 (22–52%) for males.

Many of these estimates are rather higher than is plausible, particularly for stocks which also support exploitation. Morizur (1982) used length distributions from 'quasi-unexploited' stocks to obtain estimates for annual *M* of 0.2 to 0.3 (18–26%). The values most commonly assumed for assessment of *Nephrops* stocks in the Atlantic is 0.3 for males and immature females, and 0.2 for mature females (assumed to be less vulnerable to predation during the ovigerous period – see Section 13.3.3). Based on the lower limit of overwinter depletion of burrow densities in the Farn Deeps stock, at locations inferred to be unvisited by fishing vessels, Bell *et al.* (2005) considered that these values of *M* were plausible. Similar values of *M* were assumed for Mediterranean stocks by Sardà *et al.* (1998).

13.4 Harvest of wild populations

13.4.1 Fishing methods

Nephrops is commercially exploited throughout its geographical range, and is subject to a variety of different fishing practices. *Nephrops* habitat is readily accessible to trawling, and this method of fishing dominates the landings in most areas. Static gears are, however, important locally in some inshore areas around Scotland and Sweden, and is the only method of fishing currently used in the Faeroese *Nephrops* fishery.

The types of gear generally vary on a regional basis, and in relation to the nature of the *Nephrops* fishery. On the northern European continental shelf, the fisheries tend to be specifically targeted at *Nephrops*, or are mixed fisheries with cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) or plaice (*Pleuronectes platessa*) as the other target species. In the deeper water to the west of Scotland and south and west of Ireland, megrim (*Lepidorhombus whiffiagonis*) and monkfish (*Lophius* spp.) are the dominant fish in the mixed fisheries, with hake (*Merluccius merluccius*) becoming more important further south. Off the Atlantic coast of the Iberian peninsula, the fisheries target hake, with *Nephrops* as a small but economically important by-catch, while in the Mediterranean, *Nephrops* is the target species in fisheries operating at depths of around 400 m, within the framework of more general multi-species fisheries in this area. A range of the issues relating to trawl fisheries for *Nephrops* are reviewed by Graham and Ferro (2004).

Nephrops *trawl fishery*

Prior to the 1950s, *Nephrops* were largely landed as by-catch in a number of European trawl and seine fisheries, but were also discarded as unwanted by-catch in others. The majority of landings at this time were made by France, principally from the Irish Sea, Celtic Sea and Bay of Biscay, with about 80% of all landings coming from the north-east Atlantic, and 20% from the Mediterranean. Targeted trawling for *Nephrops* on a wider commercial scale is considered to have begun in the late 1950s, as markets developed further. Trawls used to target *Nephrops* were generally wide, with a low headline height, reflecting the lack of both herding and prolonged swimming ability of the species. These were initially adaptations of existing gear, but dedicated *Nephrops* trawls were rapidly developed, particularly for the waters around the UK and Ireland. The traditional *Nephrops* trawl has a low headline, typically less than 2 m, with short wings, constructed from single polyethylene, 70 or 80 mm mesh throughout, although some trawls are constructed with a larger mesh size in the upper sections. Although fish are taken using this type of trawl, they are predominantly designed for the capture of *Nephrops*. The initial trawl fisheries for *Nephrops* were conducted in fine, muddy areas, and trawl ground-gear was light, often made of natural fibre (grass rope). The introduction of rubber discs threaded onto the footropes, and ultimately larger heavier discs (up to 250 mm in diameter) allowed fisheries to develop close to increasingly 'hard' or rocky ground. This design was the precursor to what is known as a 'scraper' trawl, which has extended wings and a heavier construction. The extended wings increase the herding efficiency of groundfish species such as plaice and monkfish. These trawls are often preferred for more mixed fisheries and typically have a larger codend mesh size (>100 mm), to comply with catch regulations. The dual-purpose trawls are similar in design to the scraper trawl but have an increased headline height to enhance the capture of finfish such as haddock and whiting.

The introduction of multiple trawl rigs in the mid-1980s led to further development in *Nephrops* fisheries. This method of trawling was introduced to *Nephrops* fisheries by Danish vessels, towing two conventional long-winged, low headline trawls, and has expanded since the late-1980s to become commonplace throughout the European *Nephrops* fleet in the Atlantic. The use of twin or multiple rig trawls means that the effective spread of a single large trawl can be obtained with multiple smaller trawls (with less hydrodynamic drag), and up to 20–30% greater overall trawl width can be achieved for the same vessel power when compared to a single trawl. When fishing for species such as *Nephrops*, monkfish and flatfish, the increased spread associated with multiple rig trawls can increase the catching efficiency considerably.

According to Sardà (1998), three types of otter trawl gear are used to exploit *Nephrops* in the Mediterranean, used mainly by Spain (western areas), Italy (central areas) and Greece (eastern areas). The types differ in net size and proportions, width of mouth opening and size of otter doors, reflecting local conditions and vessel types and the multispecies nature of the fisheries. The Italian trawl is the smallest type, considered best adapted to *Nephrops* fishing (Sardà, 1998; Maynou *et al.*, 2003). Mesh size in the codend is 40 mm in most areas, but smaller meshes (28–32 mm) may be used by Greek trawlers (Sardà, 1998; Maynou *et al.*, 2003).

Baited traps

Crabs and lobsters have traditionally been fished with baited traps (creels). As already noted, all landings of *Nephrops* from Faeroe Islands waters are now taken by creels. With the development of the UK *Nephrops* trawl fishery, fishermen also used creels to target *Nephrops* in more inshore areas on the west coast of Scotland, either where trawling was banned through legislation or impractical owing to the patchiness of suitable seabed. With the recent development of markets for live *Nephrops* in southern Europe with high market prices, the Scottish *Nephrops* creel fishery has attracted extra effort, and contributes 15–20% of the total landings from some stocks. Aside from the west coast of Scotland, there is creel fishing for *Nephrops* at various other locations around the coasts of the UK, but significant quantities are rarely taken. In Sweden, a creel fishery for *Nephrops* has developed since the mid-1980s in inshore areas where trawling is prohibited. Up to 20% of Swedish *Nephrops* landings from the Skagerrak are taken in creels, and there is also a small Swedish creel fishery in the Kattegat. Historically, there has been some trap fishing of *Nephrops* by Portugal, but catches by this method have been insignificant in recent years.

Although not specifically targeting *Nephrops*, incidental by-catch is made in some gill net fisheries in the Aegean Sea, where *Nephrops* is attracted by the fish catch, and then entangled in the netting (Smith & Papadopoulou, 2003). Traps and trammel nets may also be used by small-scale fishermen in areas of the northern Aegean and Adriatic Sea where trawling is prohibited (Maynou *et al.*, 2003).

13.4.2 Patterns of catchability

The catchability of *Nephrops* in trawls and creels is strongly influenced by the behaviour of the animal, through either availability on the seabed for trawling (related to burrow emergence) or factors affecting entry into creels (related to feeding patterns and agonistic behaviour). These factors vary considerably over time, and also between sex and individual size, which means that the two fisheries exploit different components of the stock, and show different seasonal patterns (see Section 13.3.3).

Since *Nephrops* spend the majority of their time in their burrows (Chapman, 1980), emergence rates are the main factor influencing catchability in trawl fisheries. The burrows extend 20–30 cm below the mud surface, and animals within burrows are unlikely to be caught by a passing trawl. Emergence varies on a daily basis with ambient light level, in relation to the lunar tidal cycle, and also on a seasonal basis in relation to moulting (both sexes, although at different times – see Section 13.3.1) and reproductive state (females). Catch rates are known to vary in relation to all of these factors.

On a daily basis, emergence rates (and hence catch rates) are generally considered highest at dawn and dusk in northern European populations, although this varies with depth and peak emergence timing ranging from midday in deep water to during the night in very shallow populations (Table 13.5). Seasonal patterns of light level also influence this, and fisheries have responded accordingly, with activity in some Scottish inshore fisheries starting operations much earlier in the morning or even concentrated over night in the summer, but only fishing during the day in winter. Over the lunar cycle, emergence appears to be higher on neap tides, when tidal strengths are lower, and it has long been recognised that catch rates are highest at these times (Storrow, 1912).

Ovigerous female *Nephrops* are thought to emerge only rarely from burrows, since they are poorly represented in trawl catches during the egg incubation period (Table 13.3). This is assumed to be related to reduced foraging outside the burrow during this time. However, a noteworthy feature of creel catches is that they include much larger proportions of ovigerous females than trawl catches, indicating that they are attracted at least to immediately available food items. In the Scottish creel fisheries, ovigerous females may comprise 20–30% of the catch during the latter half of the year, while they are largely absent from the trawl catches. Males dominate in trawl catches during the ovigerous period, with the result that fishing mortality on mature males is far higher than on mature females, particularly in winter fisheries (e.g. ICES, 2003).

Catchability in the creel fishery is related to bait attraction, and interactions between animals. Behavioural interactions may mean that smaller individuals tend not to enter creels (cf. Miller, 1990; Addison, 1995; Miller & Addison, 1995, for *Homarus* spp.). Escape of smaller individuals may also be greater in creels than in trawls, owing to

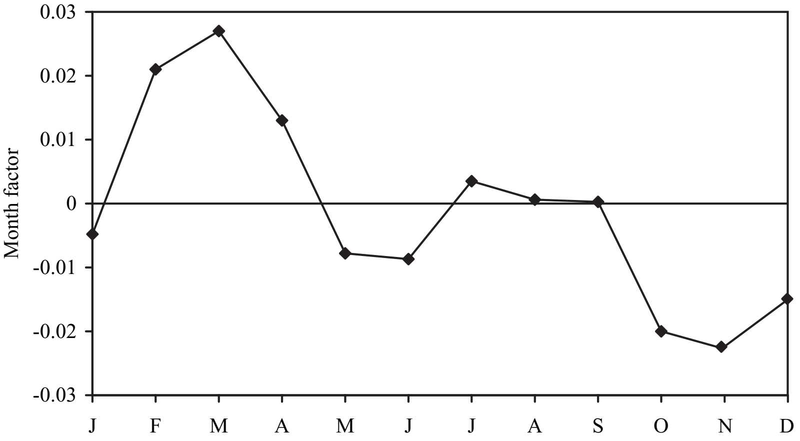


Fig. 13.10 Contribution of month to month variations in *Nephrops norvegicus* landing rate (kg/creel^{-1}) in a Scottish west coast creel fishery (Tuck & Bailey, 2000).

the open nature of the mesh. *Nephrops* selectivity in trawls is generally poor below mesh sizes of 100 mm (Anon, 2002).

Studies investigating the seasonal and longer-term patterns in the creel fisheries on the west coast of Scotland have consistently observed a bimodal pattern in monthly landing rates (Tuck & Bailey, 2000; Figure 13.10). Although this pattern may be influenced by discarding practices, the data appear to reflect availability to creels. A peak landing rate in March is associated with large catches of males, and is followed by a reduction in May and June which may be linked to moulting. The smaller peak in July–August is associated with increased catches of females, which appear to become more available to fishing between egg hatching and the spawning of the next brood. The subsequent decline in landing rates is associated with sharply decreased availability of females after spawning, but masks increases in landing rates of small males, possibly entering the fishery after an autumn moult.

13.4.3 Economic importance

The high unit value of *Nephrops* means that although total landings are relatively low (around 50 to 60 thousand tonnes total annual landings – see Table 13.1) compared to many fish species, they have been the most valuable species landed into the UK and Ireland since the late 1990s, and are also important in a number of other European countries.

Although they have their own fisheries for *Nephrops*, the main importers for both frozen and fresh product are Italy, Spain and France, with net *Nephrops* imports of US$88 million, US$63 million and US$53 million, respectively (FAO, 2002). The main exporters of *Nephrops* are the UK, Denmark and Ireland (US$103 million, US$52 million and US$24 million, respectively), and the Netherlands, Sweden, Morocco and Portugal also export significant amounts.

13.4.4 Species caught alongside Nephrops

Nephrops is taken in fisheries both as the target species and as a valuable by-catch. The species caught alongside *Nephrops* vary considerably in relation to the fishery being exploited and the gear used. In northern Europe, concern over by-catch of whitefish, and cod in particular, in *Nephrops* fisheries has lead to cuts in total allowable catch (TAC) levels for *Nephrops*, independent of management advice given on the basis of *Nephrops* advice. However, by-catch levels appear to vary considerably over space and time, and may not be as high as for fishing activities genuinely targeted at *Nephrops* as might appear from aggregated fishery statistics (Kunzlik *et al*., 2003).

Around the UK, *Nephrops* trawl fisheries can be divided into two main groups on the basis of landings, a very clean *Nephrops* fishery, often on inshore grounds, and a more mixed fishery usually taking place on more offshore grounds where commercial fish are more prevalent (Kunzlik *et al.*, 2003). Further south in the North Sea, the fishery is mixed with plaice as the main fish by-catch. In the Irish Sea, cod, whiting and plaice are taken in *Nephrops* fisheries, while to the south and west of Ireland and in the Bay of Biscay, hake, monkfish and megrim are more important as by-catch. Off the Iberian peninsula, *Nephrops* is itself a minor (although valuable) by-catch in fisheries targeting horse mackerel (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*) (ICES, 2003). There is also a crustacean trawl fishery in Portuguese waters, where *Nephrops* is taken alongside species such as deep-water pink shrimp (*Parapenaeus longirostris*) and rose shrimp (*Aristeus antennatus*) (Monteiro *et al.*, 2001).

In *Nephrops* fisheries, the legal minimum mesh sizes required are often smaller than for most finfish species (with the exception of the Mediterranean), and by-catches and discarding rates of undersize fish and invertebrates can be high (Stratoudakis *et al.*, 2001; Catchpole *et al.*, 2005). Detailed studies of the composition of by-catch in *Nephrops* trawl fisheries have been undertaken in stocks within English (Evans *et al.*, 1994; Catchpole *et al.*, 2005), Scottish (Wieczorek *et al.*, 1999; Bergmann *et al.*, 2002) and Italian waters (Wieczorek *et al.*, 1999). Levels and composition of discards vary considerably with location, even over short distances (Bergmann *et al.*, 2002).

A variety of fish species are taken alongside *Nephrops* in the Mediterranean trawl fisheries, including blue whiting, Mediterranean poor-cod (*Trisopterus minutus capelanus*), megrim (*Lepidorhombus boscii*) and grey gurnard (*Eutrigla gurnardus*) (Mytilineou *et al.*, 1998a). Discards of undersized fish and non-commercial fish and crustaceans have been estimated at 20% of the catch in the northern Tyrrhenian Sea and 40% of the catch in Greek waters (Maynou *et al.*, 2003).

Investigations into *Nephrops* creel fisheries are limited to the Scottish west coast, where fish by-catch varies seasonally and includes poor-cod (*Trisopterus minutus*), the lesser spotted dogfish (*Scyliorhinus canicula*) and more occasionally, cod, haddock, whiting, conger eel (*Conger conger*) and ling (*Molva molva*). Other crustaceans (small edible crab (*Cancer pagurus*), swimming crabs (*Liocarcinus* spp.), squat lobsters, shrimps, hermit crabs (*Pagurus* spp.), starfish and gastropods also feature in catches. This by-catch is largely discarded, and survival in the invertebrates is generally considered to be high, although high levels of seabird predation have been observed in some areas (J.M. Adey, personal communication). Teleost fish often suffer swim bladder damage when creels are lifted, and mortality can be high.

13.4.5 Impacts of fishing

Effects of fishing on seabed and benthic communities

Muddy sediments suitable for *Nephrops* accumulate in high depositional areas where disturbance from currents and storms are uncommon. The effects of trawling disturbance on a muddy sea-loch habitat was investigated by Tuck *et al.* (1998), and wider effects on other *Nephrops* habitats were considered by Ball *et al.* (2000). The most obvious effects were the tracks left by the trawl doors, which may last up to 18 months in some areas. Effects on infauna included a reduction in the abundance of large-bodied fragile organisms, and an increase in the abundance of opportunists, which would ultimately lead to a community with reduced species abundance and faunal diversity (Ball *et al.*, 2000). Recovery from experimental disturbance was observed, but is thought to take longer than in other habitats (Tuck *et al.*, 1998), where communities in more dynamic environments may be more adapted to natural disturbance. With the exception of seapens, epifauna are generally scarce in muddy habitats, and direct effects are likely to be limited, and less than for harder sediment habitat types.

The effects of creeling on what are considered to be the more fragile components of muddy habitat seabed communities have also been examined. Kinnear *et al.* (1996) investigated the effects of creel fishing for *Nephrops* on seapen communities in a Scottish sea loch. The seapen species present (*Pennatula phosphorea*, *Virgularia mirabilis* and *Furniculina quadrangularis*) were found to be resilient to smothering, dragging and uprooting by creels, and each of the species was able to recover in terms of orientation in the sediment and feeding activity following disturbance. Seapen mortality throughout the investigations was very low.

Nephrops *discarding*

Discarding of undersize or poor quality (soft post-moult) *Nephrops* occurs in most northern European *Nephrops* fisheries, and discarding rates can be high in some areas (Evans *et al.*, 1994; Redant & Polet, 1994; Bergmann *et al.*, 2002). Mortality rates of discarded individuals have been estimated at 75% under typical commercial trawl fishery conditions (Sangster *et al.*, 1997), although recent simulation experiments suggest that mortality rates may be higher in the Kattegat and Skagerrak, where the discarded animals are exposed to low salinity surface waters (Harris & Ulmestrand, 2004). In some cases, discards are left on deck for considerable periods before being thrown overboard, and probably suffer 100% mortality. Evans *et al.* (1994) considered that very little of the catch of *Nephrops* and by-catch species from the Farn Deeps fishery was returned to the seabed, most of it being removed for human consumption or eaten by seabirds at the surface of the sea.

As already noted, behavioural and selectivity factors result in very low catches of undersize *Nephrops* in creel fisheries, and any discarding is related to marketing (or local agreements) rather than minimum landing size. Creeling maintains captured animals in good condition and discard survival is high (Sangster *et al.*, 1997).

13.5 Monitoring and management

13.5.1 Data collection programmes

Regular biological monitoring programmes (mostly length sampling of the landings and occasionally the discards) have been in operation on most *Nephrops* stocks in the ICES area (see Table 13.1) since the early or mid-1980s (ICES, 2003), the main incentive being national interests and the increasing economic importance of the *Nephrops* fisheries in the 1970s and 1980s. The introduction of a management system based on total allowable catches (TACs) for the *Nephrops* fisheries in the northern and western EU waters in 1992, and the associated need for catch predictions and management advice, was a further stimulus for EU member states to set up new or to extend existing data collection programmes on their *Nephrops* fisheries. Initially, these programmes remained mostly focused on the landings, but with the growing need for better quality data on the removals (which also include dead discards), many sampling programmes were extended to also cover the discards. Sampling routines have been reviewed by the ICES Study Group on Life Histories of *Nephrops* (ICES, 1996), and it can be seen that there are considerable differences in design, depending on local fishing and auctioning practices. Sampling levels also differ substantially, from 1 to >50 length measurements per tonne of *Nephrops* landed (figures based on ICES, 2003). In the early 1990s, underwater television surveys were introduced to obtain fishery-independent estimates of *Nephrops* stock sizes (Bailey *et al.*, 1993) and since then, they have become a critical element in the assessment of *Nephrops* stocks, particularly around Scotland.

In the Mediterranean, the focus of data collection programmes for assessment purposes has, from the very beginning, primarily been on sea surveys with research vessels and/or commercial trawlers. The main reason for this is that port and market sampling are logistically difficult in most Mediterranean countries, where commercial landings are taking place in a great number of often-small ports. Many of these surveys however, were carried out within the framework of research projects of limited duration and therefore lack the continuity that is required for longer-term fisheries management systems based on regular stock evaluations and catch forecasts. Outstanding exceptions are the GRUND survey (with >700 sampling stations, mostly in the Italian waters) and the MEDITS survey (with >1000 stations on the entire continental shelf of the western, northern and eastern Mediterranean). Both surveys target demersal stocks in general (*Nephrops* amongst them) and have now been pursued for many consecutive years (since the early 1980s for GRUND and the mid-1990s for MEDITS) (Relini, 2000; Bertrand *et al.*, 2002). The potential of underwater television surveys for stock assessment purposes has also been explored in the Mediterranean (Smith, *et al.*, 2003; Smith & Papadopoulou, 2003; and see Section 13.5.2), but so far such surveys have not been performed on a regular basis.

Since 2002, the collection of fishery-related technical, biological and economic data in the European Union (which comprises all major *Nephrops* fishing countries except Iceland, Norway and Croatia) has been subject to Council Regulation 1534/2000 and Commission Regulation 1639/2001 (meanwhile modified and amended by Commission Regulation 1581/2004). The three regulations combined are commonly known as the 'Data Collection Regulation' or DCR. With respect to *Nephrops*, the DCR requires regular sampling of the landings and discards by stock unit, and six-yearly updates of biological parameters such as sexual maturity and growth, also by stock unit. The implementation of the DCR has contributed to the consolidation of many existing *Nephrops* sampling programmes, and to the initiation of several new ones, particularly on discards. In its present version, the DCR is effective until 2006, but it is expected that it will be prolonged for another period of at least six years thereafter.

13.5.2 Assessment methods

The term 'stock assessment' is often used in its narrowest sense to mean the application of mathematical methods to estimate the abundance or biomass of an exploited stock, its rate of exploitation and often other statistics such as levels of recruitment of juveniles to the fishable stock (e.g. Hilborn & Walters, 1992). Such assessments are generally based on combinations of commercial fishery, survey and biological sampling data (e.g. ICES, 2004). The outcomes are usually compared against criteria for over-exploitation and used to determine likely prospects for future stocks and fisheries. Assessments of this type are currently carried out on many exploited *Nephrops* stocks (e.g. Eiríksson, 1992; Sardà *et al.*, 1998; ICES, 2003).

A wide range of increasingly sophisticated 'analytical' assessment methods have been developed for application to exploited marine stocks (e.g. Hilborn & Walters, 1992). These deal not just with estimation but also with the description of uncertainty around assessment outcomes and placing results in the context of precautionary frameworks for fishery management. We consider below how some of these methods have been applied to *Nephrops*, but before doing so it is worth examining stock assessment in the much wider sense of any approach to obtaining information on stock and fishery status and trends.

Trends in fishery statistics

At its simplest, stock assessment can involve straightforward examination of trends in commercial catches or catch rates. *Nephrops* stock assessments of this type have been performed for a century or more. For example, Storrow (1912) examined trends in landings data for the *Nephrops* fishery off the north-east coast of England (Farn Deeps ground) for 1895 onwards, and used monthly catch rate data to separate the effects of fishing effort and changes in the availability of *Nephrops* in determining seasonal patterns of landings. Basic summaries of trends in landings, catch rates, sex ratio, mean size in the catch and other fishery statistics continue to form an important part of the regular assessments of exploited *Nephrops* stocks in the north-east Atlantic, and for some stocks this is the only source of information on stock status (ICES, 2003, 2004).

Mean size in catch samples can be informative about changes in some population processes. Increases in mean size could reflect either declines in recruitment, i.e. decreased numbers of small individuals in the population, or decreased mortality, i.e. increased numbers surviving to attain the larger size classes, and the opposite interpretations could apply to decreases in mean size. Clearly, changes in mean size can only be interpreted alongside other sources of information. Mean size can also be affected by changes in discarding practices and the size-selective properties of the fishing gear, e.g. brought about by an increase in the minimum legal mesh size. Mean size is often calculated for just the size classes unaffected by discarding (typically 35 mm carapace length and larger) (ICES, 2003, 2004).

Catch and landings per unit effort (CPUE and LPUE) are often treated as indices of stock abundance. This requires the assumption that catchability (proportion of the population captured by a unit of fishing effort) remains constant over time. Quarterly and sex-specific CPUE and LPUE data are often used to account for seasonal and sex-related differences in *Nephrops* catchability (ICES 2003, 2004). Typical units would be kg per hour of trawling, but adjustments for vessel power are sometimes used. CPUE and LPUE are most reliably measured from catch returns supplied by a standard 'reference' fleet of commercial vessels. Fariña and González Herraiz (2003) used CPUE data from several fleets to show declining trends in *Nephrops* stocks around northern Spain and Portugal. Eiríksson (1999) examined spatial correlations in CPUE trends to determine geographical stock units for *Nephrops* around the southern coast of Iceland. Changes in the efficiency of fishing operations can cause problems for interpretation of CPUE and LPUE. For example, the introduction of 'rock-hopper' trawl gear and more precise global positioning systems (GPS) during the 1990s allowed *Nephrops* fishers in the Bay of Biscay to exploit previously inaccessible grounds and to locate their operations more precisely. The result was that LPUE statistics for *Nephrops* vessels remained stable at relatively high values whilst the stock biomass in the Bay of Biscay declined by almost a third between the late 1980s and the late 1990s (ICES, 2003). Bell *et al.* (2005) showed that spatial targeting of fishing effort at a sedentary *Nephrops* stock also creates the potential for CPUE and LPUE to be maintained at misleadingly high levels during a stock decline. There is no information about whether this has actually occurred in practice, but there has been some evidence of concentration of fishing effort on the remaining centres of concentration in a heavily depleted Portuguese *Nephrops* stock.

Some of the problems in interpreting commercial LPUE and CPUE data can be addressed using statistical methods such as generalised linear modelling to account for sources of variation in catch rates such as vessel size, gear type and seasonal factors (e.g. Hilborn & Walters, 1992). Sbrana *et al.* (2003) used cluster analysis of commercial trawl catch data from the Tyrrhenian Sea (western Mediterranean) to identify 'metiers', or fishing tactics, corresponding to different assemblages of species in the catch, vessel characteristics and fishing areas, and applied generalised linear modelling to isolate an annual *Nephrops* abundance signal adjusted for vessels and months.

Trawl surveys

Besides being used to infer stock trends from commercial fishery data, CPUE is also commonly used as an index of abundance from trawl surveys directed at various species. Scientific surveys have the advantage over commercial statistics in that they are directed fully at a target species and undertaken in controlled circumstances. However, limits on time and resources mean that the host of factors which affect catch rates (e.g. Maynou & Sardà, 2001; and see Sections 13.3.3 and 13.4.2), cannot be expected to be averaged out as they might be in the multiple trawl tows underlying commercial data. Short-term variation in *Nephrops* catch rates, such as the greater catches on neap than on spring tides, have long been recognised (Storrow, 1912), and factors such as weather conditions and sea state are also known to be important (Maynou & Sardà, 2001). For this reason, and particularly considering the strong diurnal patterns in catch rates (Chapman, 1980), trawl surveys are generally considered to be an unsatisfactory method of measuring *Nephrops* stock trends (e.g. Bailey *et al.*, 1993; Briggs, 2000). Nevertheless, Tuck *et al.* (1997b) showed that under carefully controlled circumstances, trawl catch rates could provide a useful index of local abundance. Catch rates in trawls timed to coincide with times of peak burrow emergence were strongly correlated with underwater television estimates of burrow densities (see below) at the same locations (see also Smith & Papadopoulou, 2003). Trawl surveys have also successfully been used to describe spatial patterns in *Nephrops* stocks and to provide point estimates of stock biomass (Fariña *et al.*, 1994; Maynou *et al.*,

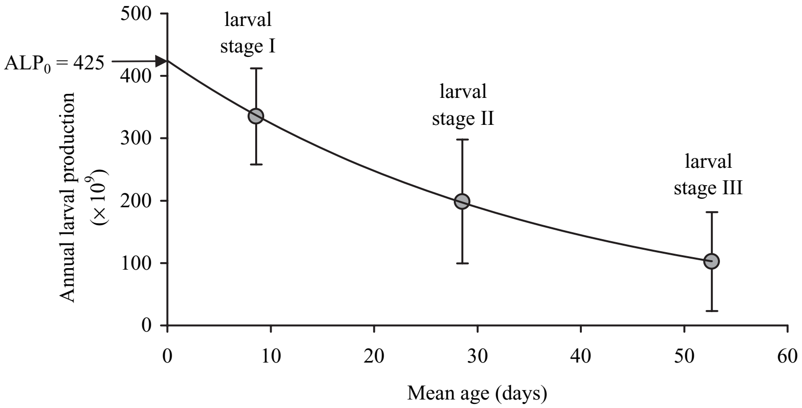


Fig. 13.11 Calculation of annual larval production for *Nephrops norvegicus* in the Irish Sea from estimates of abundance at three larval stages. A mortality curve through the estimates is extrapolated to age zero to obtain an estimate of ALP_0. Error bars represent two standard errors (adapted from Briggs *et al.* 2002).

1998), but the narrow set of conditions for satisfactory standardisation of trawl sampling are likely to restrict trawl surveys to use as a research tool rather than a routine stock assessment method. Statistical methods such as generalised linear and additive modelling may offer some scope for development in this area.

Despite their dependence on factors affecting catchability, trawl surveys have one very desirable property – they are independent of a fishery. The quality and ease of interpretation of fishery statistics depends on many factors, including fishers' reporting behaviour, the spatial- and species-specific nature of targeting of fishing effort, management and market-driven changes in fishing practices, discarding practices, gear modifications and changes in fishing power and efficiency. All of these factors are under experimenter control in a scientific survey. Besides trawl surveys, two other types of fishery-independent stock assessment methods have been applied to *Nephrops*, and these are described below.

Annual larval production method

The annual larval production (ALP) method for estimating the spawning stock biomass (*SSB*) of females involves taking estimates of larvae abundance from larvae surveys, back-calculating the total number of larvae produced at egg-hatching time (ALP_0) by applying mortality estimates, and dividing the result by an estimate of the effective fecundity per unit weight of females (E_r) (Briggs *et al.*, 2002):

$$SSB = \frac{ALP_0}{E_r}$$

The main uncertainties in the method are in the estimates of larvae mortality and effective fecundity. In the most rigorous application of the ALP method to *Nephrops* so far, Briggs *et al.* (2002) used a combination of field and laboratory studies to obtain robust estimates of these quantities for the Irish Sea stock. A mortality curve fitted to estimates of the total abundance of three larval stages was extrapolated to age zero to obtain an estimate of $ALP_0 = 425 \cdot 10^9$ larvae produced at hatching (Figure 13.11). Fecundity was measured at 104 eggs per g of female, of which 35% was estimated to be lost during the incubation period, giving an effective fecundity of 68 eggs per g of female. This results in an estimate of female *SSB* in the Irish Sea of 6288 t, which compares well with a contemporary estimate of 7750 t from analytical assessment of commercial fishery data (ICES, 2001). The ALP method has previously been applied in the Irish Sea by Thompson *et al.* (1986) and Nichols *et al.* (1987), giving female *SSB* estimates in the range 8000 to 12 000 t, and in the Firth of Clyde by Tuck *et al.* (1997b), who also noted a reasonable correspondence between ALP and analytical assessment estimates.

The ALP method appears to work well in providing fishery-independent estimates of *Nephrops* stock biomass, but its heavy demands on labour and resources means that it is unlikely ever to be used as a routine monitoring tool. Opportunities to apply the method are most likely to arise as a result of plankton surveys directed at other or additional aims, as was the case for Briggs *et al.* (2002) who used *Nephrops* larvae data from cruises directed at sampling fish eggs and larvae in the Irish Sea (Fox *et al.*, 1997; Dickey-Collas *et al.*, 2000b).

Underwater television surveys

The underwater television (UWTV) survey method has seen widespread use for fishery-independent stock assessments, and is now a routine monitoring tool for a number of stocks. Work by Chapman (1985a, b) has shown that it is possible to measure *Nephrops* burrow densities by underwater photographic and television surveys of the grounds. The underwater television approach has been developed into a full stock assessment method (Bailey *et al.*, 1993; Marrs *et al.*, 1996), and has been applied to various stocks in the north-east Atlantic and Mediterranean (Table 13.4).

The method typically involves slowly towing a sledge-mounted television camera over the ground, and counting the number of burrow systems over a measured distance. Identification of *Nephrops* burrows, and determining which burrow entrances correspond to the same burrow system is a skilled task, which inevitably involves some degree of subjectivity, but there is generally good agreement between counters, both between and within laboratories (Marrs *et al.*, 1996; Addison *et al.*, 2000). Application of UWTV in the eastern Irish Sea has proved particularly difficult because of the abundance of burrowing species other than *Nephrops* (J.M. Elson, personal communication), especially the angular crab *Goneplax rhomboids*, the burrows of which can be confused for *Nephrops* (Marrs *et al.*, 1996). Marrs *et al.* (1996) provides a key for identifying burrows of *Nephrops* and other species, which may occur on the same grounds.

Other issues relating to the interpretation of television images include burrow occupancy and 'edge' effects relating to the width of the field of view in relation to the diameter of burrow systems (ICES, 2000; Smith *et al.*, 2003), but there is general agreement that one intact burrow system equates with one adult *Nephrops* (although more than one juvenile may also occur in the burrow complex) and that the density of burrow systems is a good index of population abundance (Addison *et al.*, 2000).

Conversion of density to biomass requires a good estimate of the size composition of the population, which owing to the selectivity and biases of trawls is generally not available. Nevertheless, Tuck *et al.* (1997b) used UWTV to obtain stock biomass estimates for the Firth of Clyde that were of a similar order to comparable analytical and ALP estimates.

Regular UWTV surveys are now undertaken for *Nephrops* stocks in Scottish waters and in the North Sea, with time series extending back to the early 1990s in some cases (ICES, 2003, 2004). The method provides robust corroboration of stock trends identified by analytical assessments and other stock indices, and for the Fladen Ground, a large offshore stock in the northern North Sea, UWTV now provides the main basis for catch advice (ICES, 2003). The method is likely to see increasing use as the basis for management advice in the future, particularly given some difficulties in the interpretation of commercial fishery data (ICES, 2004), and there is considerable interest in applying UWTV to stocks of *Nephrops* in other parts of its geographical range. Marrs *et al.* (1996) noted a significant correlation between the diameter of burrows and the size of the occupants, and it has been suggested that UWTV surveys could potentially use measurement of burrow sizes to obtain indices of recruitment as well as stock size (Addison *et al.*, 2000).

Aside from stock monitoring, UWTV is also used as a research tool. Bell *et al.* (2005) applied the method to examine spatial patterns in the depletion of *Nephrops* on the Farn Deeps grounds (North Sea) over the course of a winter fishing season. Smith and Papadopoulou (2003) used the method to describe seasonal fluctuations in stock density in Pagasitikos Bay (Aegean Sea).

Analytical assessment methods

The foregoing account demonstrates that there are a number of fishery-independent techniques and simple fishery statistics that are used to provide information on the status and trends of *Nephrops* stocks. Nevertheless, formal analytical assessments based on commercial fishery data are still the main basis for management advice for many exploited *Nephrops* stocks.

A major problem for analytical assessments is that there is no routine method of age determination of *Nephrops*, so that inferences about the age structures of stocks and catches are drawn from size-frequency distributions. Some of the first analytical assessments for *Nephrops* stocks were performed by Jones (1979) using length cohort analysis (LCA), a length-based analogue of Pope's (1972) cohort analysis. The method uses data on the length composition of the catch, together with values for natural mortality and von Bertalanffy growth parameters, to estimate stock size and fishing mortality at size, and using weight-at-age data can generate information on the state of exploitation in relation to growth overfishing. (Growth overfishing relates to the trade-off between gains from growth and losses from natural mortality, and is said to occur when animals are harvested at too small a size for yield to be maximised.) The relatively modest data demands have led to the method being widely used to assess *Nephrops* stocks in the north-east Atlantic (e.g. ICES, 2001) and in the Mediterranean (Sardà *et al*., 1998). A major drawback of the method is that it is applicable only to steady-state (equilibrium) stocks, i.e. to stocks showing no overall trend in abundance or level of exploitation. LCA allows no conclusions to be drawn about the effects of fishing on the capacity of the stock to replace itself (recruitment overfishing), and in the case of declining stocks can give a misleadingly optimistic view of stock status with respect to growth overfishing (ICES, 2001). Increasingly, LCA is being abandoned in favour of methods applicable to dynamic stocks.

Abella *et al.* (1999) considered that a steady-state assumption was justified for *Nephrops* stocks in the Ligurian and Tyrrhenian Seas (western Mediterranean), but nevertheless failed to fit equilibrium surplus production models to time series of mortality estimates. Attempts to fit similar models, but in a dynamic context (biomass dynamic models; Hilborn & Walters, 1992), have also not been successful for *Nephrops* stocks, probably because of the lack of 'contrast' in the data (ICES, 2000).

The most successful application of dynamic stock assessment methods to *Nephrops* have used age-based virtual population analysis (VPA). The main input to VPA is a time series of catch-at-age data. The problem of age determination has been overcome by deterministic 'slicing' of length compositions into age classes using von Bertalanffy growth parameters (ICES, 2004). This has been criticised on the grounds that it ignores variations in growth between individuals and between year classes, thus 'smearing' the year-class signal in the data (ICES, 2004). The apparent stability of *Nephrops* stock trends from VPA is probably at least partly spurious, but the method has nevertheless proved very successful when combined with other sources of information on stock trends, such as CPUE and LPUE trends and fishery-independent methods (ICES, 2003, 2004).

Explicitly length-based dynamic methods have also been applied with some success (Dobby, 2004; ICES, 2004), and there has also been some use of methods which make fewer demands on the necessity to determine age (ICES, 2002; Mesnil, 2003). The results have provided rather similar results to comparable VPA assessments, although rather more variability in stock trends was apparent from the length-based methods (Dobby, 2004).

13.5.3 Management measures and management structures

Various technical measures are in place for the management of *Nephrops* fisheries. Minimum legal sizes (MLS) are 20 mm carapace length (CL), 70 mm total length (TL) in the Mediterranean, Irish Sea, west of Scotland, Bay of Biscay, Portugal and Spain, 40 mm CL, 130 mm TL in the Kattegat and Skagerrak and 25 mm CL, 85 mm TL in most other areas. Relatively high mortality of discards (Symonds & Simpson, 1971; Guégen & Chareau, 1975), however, means that the selective properties of the fishing gear are the primary determinant of mortality at size.

The regulations on gear and mesh size specifications are too complex and extensive to summarise here, but in most areas of the north-east Atlantic

70–80 mm diameter meshes are specified for the codends of trawl gear, often with square-mesh panels to allow the escapement of young fish. Traditional trawlers in the Mediterranean use a relatively unselective 40 mm mesh. Most of the gear regulations are aimed at limiting by-catch and mortality of fish rather than improving the size-selectivity of the gear for *Nephrops*. Graham and Ferro (2004) provide an extensive account of gear design and regulations for *Nephrops* fisheries in the north-east Atlantic and the Mediterranean.

The primary tool used to manage *Nephrops* fisheries in the north-east Atlantic is the total allowable catch (TAC). Many of the fisheries in this area are shared between different nations, and advice on appropriate levels for annual TACs is given by the International Council for the Exploration of the Sea (ICES). ICES assessments and advice for *Nephrops* are based on small Management Areas comprising one or more stock units. Current management within the EU is based on aggregating these Management Areas into TAC areas, which often are much larger. Except in the case of some declining stocks, advice on *Nephrops* TACs is based on historical landings that have been seen to be sustainable. Analytical and other assessments are used as indicators of relative stock trends rather than as a quantitative basis for setting catch limits (ICES, 2003). However, fishery-independent UWTV surveys (see Section 13.5.2, Underwater television surveys) have recently been used as the basis for TAC advice for the Fladen Ground, a large offshore stock in the northern North Sea where the surveys indicated scope for increases in landings beyond historical levels. In the case of the depleted Bay of Biscay and Atlantic Iberian *Nephrops* stocks, recent TAC advice has been informed by stock projections, indicating levels of landings under which stock re-building targets might be achieved (ICES, 2004).

Nephrops TACs within the EU are agreed internationally at ministerial level, with a proportional allocation key used to determine the quotas for individual nations. Agreed TACs tend to be higher than advised, particularly when restrictive management is proposed. The fact that TAC areas are larger than the notional Management Areas can lead to difficulties in specific areas. For example, uptake of the North Sea TAC on the expanding Fladen Ground fishery can lead to problems in quota availability off the north-east coast of England, where the fishery starts later in the year. Interactions with fisheries for other species can be an important factor in discussions about appropriate TAC levels, although in practice the levels are set in relation to single species advice for *Nephrops*. Some reductions in *Nephrops* TACs have been specified in the Irish Sea and North Sea, where there has been concern about levels of by-catch from heavily depleted cod stocks. It is doubtful, however, that these cuts have contributed significantly to any reduction in overall fishing mortality for cod or other fish species taken alongside *Nephrops*.

No biological reference points or formal management objectives are set for the *Nephrops* fisheries managed within the EU. The only formal use of biological reference points is by Iceland in setting its own national TACs for September–August fishing seasons. Stock projections based on VPA are used to determine levels of landings corresponding to $F_{0.1}$ – the level of fishing mortality at which the slope of a yield per recruit curve falls to 10% of its value at the origin (zero fishing mortality). This reference point is close to, but precautionarily less than, the fishing mortality at maximum yield per recruit, $F_{\max}$, which is itself a proxy for the fishing mortality at maximum sustainable yield (see Section 13.5.4). Although this reference point relates to maximising yield rather than protection of spawners, it has often been pointed out that growth overfishing is likely to set in at a lower level of fishing mortality than recruitment overfishing.

Aside from the MLS specifications mentioned above, there is no specific management of *Nephrops* fisheries in the Mediterranean (Maynou *et al.*, 2003). The 40 mm minimum mesh size applies to all trawlers. There are also some controls on the total capacity of the trawling fleets and limitations on the engine size of new trawlers. Local management measures applying to all trawl fisheries of a given area include seasonal closures in Italy and Greece and limits of daily working time to 12 hours for many ports on the Catalan coast of Spain. According to Maynou *et al.* (2003), technical measures and effort control regulations in the

Mediterranean are not reviewed regularly. Caddy (1993) provides information on general fishery management in the Mediterranean. There are various current initiatives relating to the monitoring and management of Mediterranean fishery resources, including the MEDITS bottom trawl survey (Abella *et al.*, 1999; Fiorentini *et al.*, 1999) and the Adriamed Working Groups in the Adriatic Sea (Adriamed, 2000).

13.5.4 Status of stocks

Many *Nephrops* fisheries are considered to be at least ‘fully’ exploited, in the sense that yield per recruit (a proxy for yield, in the absence of information on recruitment) is often close to its maximum value in males. Figure 13.12 shows yield-per-recruit curves for the North Minch *Nephrops* fishery off the west coast of Scotland. Yield per recruit (hereafter referred to as ‘yield’) is calculated using data on weight, natural mortality and fishing mortality at age or size at a given level of fishing intensity, and measures the trade-off between foregoing gains in biomass from growth and pre-empting losses in biomass from natural mortality (Gabriel *et al.*, 1989). In this example, the fishing mortality at which yield would be maximised ($F_{\max}$) is about 30% lower than the level of current fishing mortality (F) in males, therefore technically there is growth overfishing. However, the potential gains in yield from a reduction in F is negligible. Females in this stock are more lightly exploited than males, owing to their lower vulnerability to trawling during the ovigerous period (see Section 13.3.3). Technically, they are ‘under’-exploited, in the sense that greater yields could be achieved at higher fishing

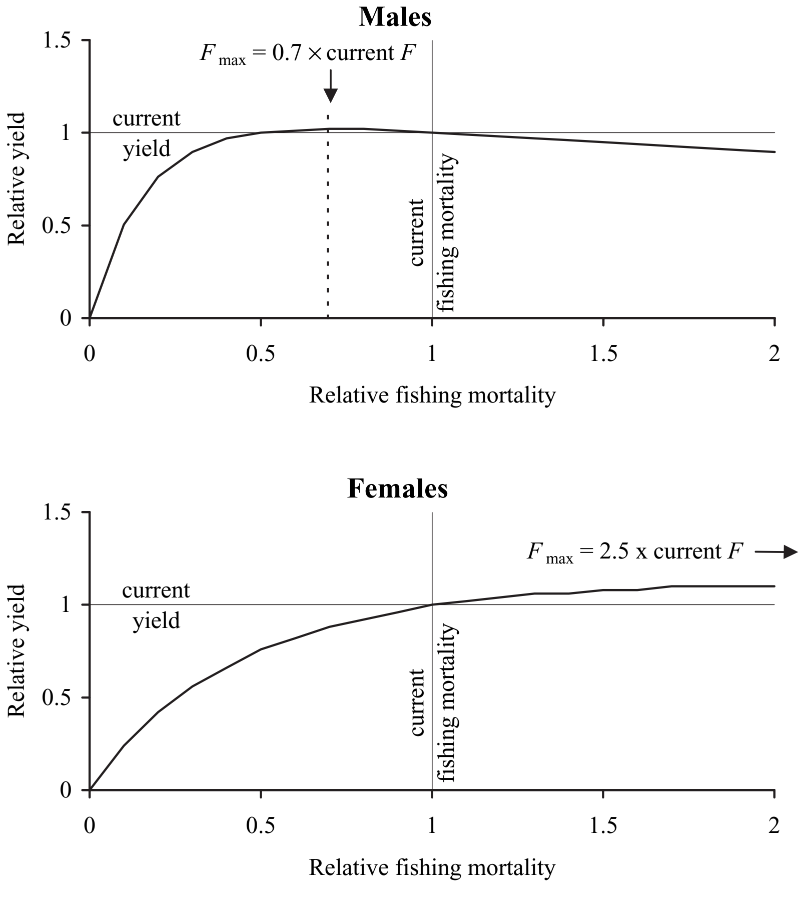


Fig. 13.12 Yield-per-recruit curves for the North Minch *Nephrops norvegicus* fishery, from ICES (2003). Maximum yield per recruit of males would be obtained with a 30% reduction in fishing mortality, whereas maximum yield per recruit of females would be obtained with a 150% increase in fishing mortality.

mortality (i.e. F is below F_{max}). However, the slope of the yield curve is very shallow, so that potential gains in yield are very small. Taking the two sexes together, the total fishery yield is probably close to its theoretical maximum given the pattern of selection at age (or size).

The pattern shown in Fig. 13.12 is fairly typical for *Nephrops* fisheries north of the English Channel, particularly when a significant proportion of the annual fishing effort occurs during the winter period when females are less available to trawl gear. In the Irish Sea, where there is a strong summer fishery, similar quantities of males and females are taken in the landings, and the two sexes are exploited at about the same level.

Recent fishing mortality values for various Atlantic and Mediterranean stocks are summarised in Table 13.6, in most cases for males and females

Table 13.6 Fishing mortality of *Nephrops* stocks in the north-east Atlantic and Mediterranean. Mean F, arithmetic mean annual instantaneous rate of fishing mortality for a reference group of ages or lengths; ϕ_{max}, proportion of current fishing mortality at which yield per recruit is maximised; —, data not available. Values for Kattegat & Skagerrak and Bay of Biscay stocks are based on assessments for males and females combined.

		Males		Females		
Area	Stock	Mean F	ϕ_{max}	Mean F	ϕ_{max}	Reference
Denmark/Sweden	Kattegat & Skagerrak	0.25	2.80	sexes combined		ICES (2003)
North Sea	Fladen Ground	0.31	1.43	0.25	1.33	ICES (2003)
	Moray Firth	0.47	0.76	0.17	1.84	ICES (2003)
	Firth of Forth	0.95	0.39	0.25	0.93	ICES (2003)
	Farn Deeps	0.49	0.51	0.12	1.12	ICES (2003)
	Botney Gut	0.47	0.89	0.34	0.85	ICES (2003)
West of Scotland	North Minch (trawl)	0.58	0.70	0.20	2.53	ICES (2003)
	North Minch (creel)	0.33	2.09	0.08	4.00	ICES (2003)
	South Minch (trawl)	0.52	0.73	0.13	2.40	ICES (2003)
	South Minch (creel)	0.17	3.24	0.01	3.99	ICES (2003)
	Firth of Clyde	0.77	0.53	0.18	1.62	ICES (2003)
Irish Sea	Western Irish Sea	0.57	0.82	0.75	0.69	ICES (2003)
	Eastern Irish Sea	0.60	0.55	0.48	0.79	ICES (2003)
South & West of Ireland	Porcupine Bank	0.27	1.78	0.13	3.90	ICES (2003)
	Aran Grounds	0.91	0.92	—	—	ICES (2003)
	Celtic Sea	0.54	0.64	—	—	ICES (2003)
France	Bay of Biscay	0.48	0.62	sexes combined		ICES (2004)
Iberian Peninsula	North Galicia	0.50	0.77	0.13	5.25	ICES (2004)
	Cantabrian Sea	0.18	—	0.07	—	ICES (2002)
	West Galicia & North Portugal	0.70	0.33	0.31	0.87	ICES (2004)
	South & Southwest Portugal	0.53	0.24	0.72	5.67	ICES (2004)
	Algarve	0.51	0.64	0.52	0.70	Sardà *et al.* (1998)
	Gulf of Cadíz	0.61	0.54	0.13	3.51	ICES (2004)
Western Mediterranean	Alboran Sea	0.32	0.35	0.51	0.30	Sardà *et al.* (1998)
	Catalan Sea	0.82	0.32	1.03	0.35	Sardà *et al.* (1998)
	Ligurian Sea	0.45	0.53	0.32	0.70	Sardà *et al.* (1998)
	Tyrrhenian Sea	0.52	0.51	0.78	0.42	Sardà *et al.* (1998)
Eastern Mediterranean	Adriatic Sea	0.42	0.77	0.76	0.42	Sardà *et al.* (1998)
	Gulf of Euboikos	0.29	0.93	0.47	0.81	Sardà *et al.* (1998)

assessed separately. Also given are values for $_{\max}$, the proportion of current fishing mortality at which yield would be maximised (i.e. $F_{\max}/F$). A $_{\max}$ value of 2 indicates that yield would be maximised at twice the current level of F, whereas a value of 0.5 indicates maximum yield at half the current F. It can be seen that for most Atlantic stocks $_{\max}$ is less than 1 for males and greater than 1 for females. For the west of Scotland creel fisheries, which are assessed separately from the trawl fisheries since they are spatially discrete, $_{\max}$ for males is greater than 1, reflecting the relatively low levels of exploitation by this method.

In terms of $_{\max}$ (though not in terms of mean F), the Mediterranean stocks appear to be more heavily exploited (low $_{\max}$), and there is not a strong distinction between male and female exploitation levels. Based on considerations of yield per recruit, Sardà *et al.* (1998) classified the fisheries as 'fully exploited' in the Catalan Sea, Adriatic Sea and Tyrrhenian Sea, 'moderately exploited' in the Ligurian Sea and Gulf of Euboikos and 'lightly exploited' in the Alboran Sea.

Yield-per-recruit analysis offers some information on the status of stocks with respect to growth overfishing, but provides no perspective on the likelihood of adverse recruitment trends. Sardà *et al.* (1998) used estimates of stock biomass as a proportion of the biomass that would be expected for a virgin (unexploited) stock to infer that fishing may be damaging future recruitment prospects in several Mediterranean stocks, irrespective of yield considerations: the percentage of virgin stock biomass was below 30% for females in the Alboran, Catalan, Tyrrhenian and Adriatic Seas.

The distinction between considerations of growth and recruitment overfishing is even more marked in the Atlantic stocks. Based on the $_{\max}$ values in Table 13.6, it could be concluded that there is little cause for concern about most stocks. Fishing mortality is above the optimum for many stocks, particularly in males, but the potential gains in yield upon reductions in fishing mortality are mostly very small (ICES, 2003, 2004; Figure 13.12). Estimated trends in recruitment and stock biomass tell a very different story for some stocks. Broadly, the Atlantic stocks can be divided into three categories: stocks to the north of the English Channel, where recruitment levels are stable, or at least fluctuating without adverse long-term trend; stocks in the Bay of Biscay, where stock biomass and recruitment are at relatively low levels compared with historical estimates; and stocks around the Iberian peninsula, where there have been drastic declines in recruitment and stock biomass, often for the entire history of stock monitoring (ICES, 2003, 2004). These three patterns are exemplified in Figure 13.13. The declines in the Bay of Biscay were for some years masked by increases in efficiency of the fleet (see Section 13.5.2). In the case of some of the Iberian stocks, the quality of data and length of time series precluded dynamic 'age'-based analyses (see Section 13.5.2), and hence a full appreciation of the nature of stock trends, until relatively recently.

Prospect for these declining stocks are mixed. It appears possible for adverse stock trends to be halted or reversed in the Bay of Biscay through the introduction of more selective gear (greater escapement of the younger age classes) and relatively modest reductions in fishing effort (Graham & Ferro, 2004; ICES, 2004). For the Iberian stocks, there remains the suspicion that recruitment declines are driven by climate rather than fishing mortality, although recent analyses have failed to confirm this (ICES, 2002). Exploitation levels and the implementation of advice on TAC levels are driven by other species taken in the mixed fisheries, principally hake. The main hope for these stocks and fisheries is the implementation of area closures, as proposed under a joint hake/*Nephrops* recovery plan (ICES, 2004).

Naturally, this summary is a gross oversimplification of the status of *Nephrops* stocks across its geographical range. It is worth pointing out that the quality of assessments and of the inferences drawn about state of exploitation are only as good as the data on which they are based. The increasing use of fishery-independent methods for stock assessment offers some hope for improvement in this area.

Finally, a fourth category can be added to the summary of the status of Atlantic stocks – stocks supporting developing fisheries, with scope for expansion. The large Fladen Ground, Norwegian Deep and Horn Reefs stocks in the North Sea all

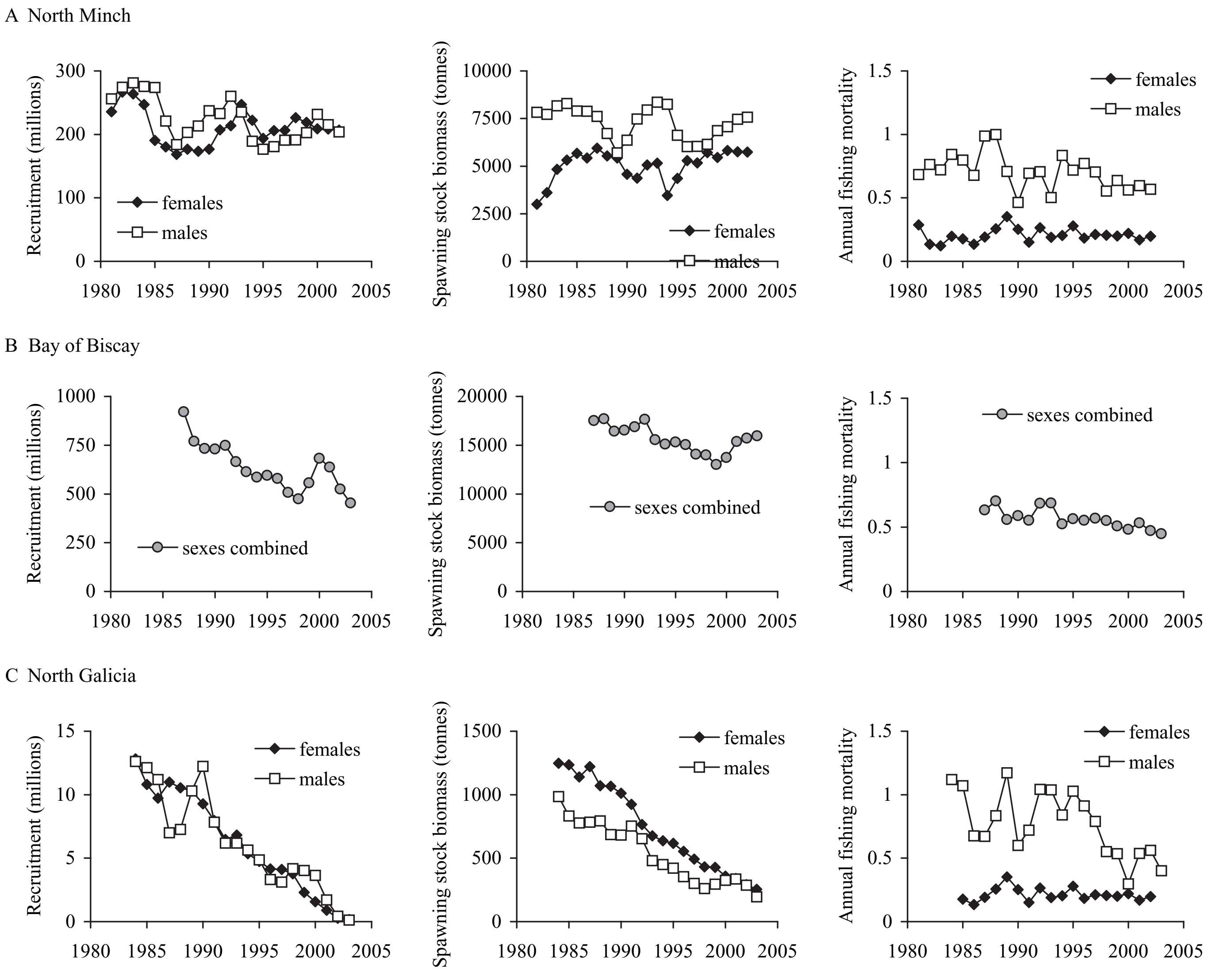


Fig. 13.13 Estimated trends in recruitment, spawning stock biomass and fishing mortality in three *Nephrops norvegicus* stocks (from ICES, 2003, 2004).

fall into this category. There are no analytical assessments for these stocks, but trends in landings, LPUE and, in the case of the Fladen Ground, underwater television surveys of burrow densities, all suggest that they are relatively lightly exploited, and that there is scope for exploitation to increase, particularly by moving into the least exploited areas of the stocks (ICES, 2003). For the future, we might expect to see similar developments for poorly known deep-water stocks towards the edge of the continental shelf to the west of Scotland and Ireland.

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Chapter 14
Scyllarides Species

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14.1 Introduction

Slipper lobsters, family Scyllaridae (Latreille, 1825), is a taxon of lobsters for which limited scientific information is available, compared to that for commercially valuable lobsters in the Nephropidae and Palinuridae families. Nevertheless, they have been known of and described since the late 1700s with numerous species being discovered after 1852 (Holthuis, 2002). They are found within the superfamily Palinuroidea that consists of spiny lobsters (Palinuridae), furry lobsters (Synaxidae), and slipper, shovelnose, or bulldozer lobsters (Scyllaridae) (Holthuis, 1991). The Scyllaridae are organised into four subfamilies comprised of twenty genera (Holthuis, 2002): the Ibacinae, Arctidinae, Scyllarinae and Theninae. Only three genera, *Thenus* (Theninae), *Scyllarides* (Arctidinae), and *Ibacus* (Ibacinae) form significant fisheries because individual species tend to be large in size (Mikami & Kuballa, 2006). Of these, the largest body of knowledge exists for *Scyllarides* (Gill, 1898). This is due, probably, to the large number (14) of species known in this genus (Holthuis, 1991), their wide geographical distribution in tropical and subtropical habitats around the world, the large size they attain as adults (up to 50 cm total length in *S. haanii*, according to Holthuis, 1991), and their economic importance as edible crustaceans. The present review is an attempt to summarise the somewhat patchy information available in the scientific literature on this genus.

14.2 Taxonomy and systematic hierarchy

14.2.1 Features of the genus

The genus *Scyllarides* belongs to the subfamily Arctidinae and is typified by a dorsoventrally compressed body with a highly vaulted carapace that may or may not have a small, shallow, cervical incision. The mandibular palp is typically trisegmented. There are only two genera in this subfamily, *Arctides* and *Scyllarides* (Holthuis, 1991, 2002). The genus *Scyllarides* is characterised by a first abdominal somite that lacks a transverse groove dorsally and a carapace that lacks a postorbital spine. The abdomen shows no dorsal sculpture, apart from a median ridge (Holthuis, 1991).

14.2.2 Species and distribution

All distribution patterns presented here refer to adult specimens only. The English FAO names will be found in Holthuis (1991). *Scyllarides* species are illustrated in Fig. 14.1.

Scyllarides aequinoctialis (Lund, 1793; Fig. 14.1A; English FAO name – Spanish slipper lobster) is also the type species of the genus. In this genus, the carapace is less highly vaulted, the cervical incision is nearly absent, and pregastric and gastric teeth are barely set off from the surface. However, the dorsal surface of the first abdominal somite bears three well-defined and highly distinctive spots: a horseshoe-shaped middle spot, and

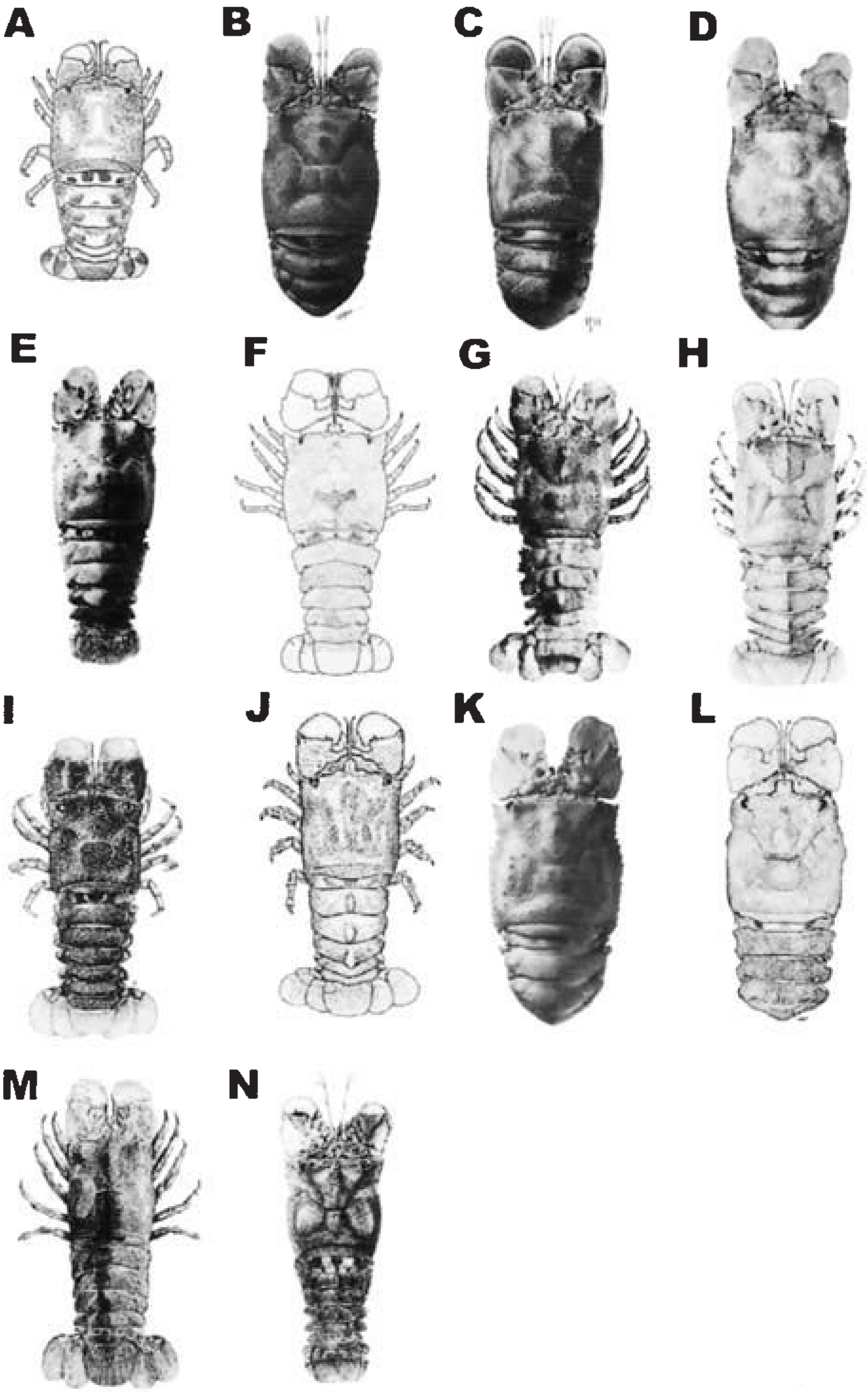


Fig. 14.1 Lobsters within the *Scyllarides* genus. (A) *Scyllarides aequinoctialis*; (B) *S. astori*; (C) *S. brasiliensis*; (D) *S. deceptor*; (E) *S. delfosi*; (F) *S. elisabethae*; (G) *S. haanii*; (H) *S. herklotsii*; (I) *S. latus*; (J) *S. nodifer*; (K) *S. obtusus*; (L) *S. roggeveeni*; (M) *S. squammosus*; (N) *S. tridacnophaga* (modified from Holthuis, 1991, 1993).

two rounded sub-medial spots. These lobsters are found in the Western Atlantic from South Carolina, USA and Bermuda via the West Indies, including the Gulf of Mexico and the Caribbean, to southern Brazil. The maximum total body length (TL) is over 30 cm and carapace length (CL) is about 12 cm. Their depth distribution is from less than 1 m to 180 m, but usually not deeper than 64 m. These lobsters prefer substrates of sand or rocks that are often found on outer reefs (Holthuis, 1991).

Scyllarides astori (Holthuis, 1960; Fig. 14.1B; English FAO name – Galapagos slipper lobster) is found in the Eastern Pacific. The gastric and pregastric teeth forming broad elevations characterise the carapace of this species. The first abdominal somite bears two distinct lateral spots, between which are numerous small spots that may fuse together. However, the geographical range of this species is unclear. It may be endemic to the Galapagos Islands (Holthuis & Loesch, 1967; Hickman & Zimmerman, 2000), with larval presence around the Cocos Islands (Reck, 1983). According to Holthuis (1991) and Gotshall (1998), *S. astori* is also found in the Gulf of California, so its status as an endemic species may require revision. This typically reddish-brown coloured lobster generally reaches a TL of 30 cm, although the maximum recorded size is 37.8 cm (Hearn, 2004). It is found on rocky substrates, preferring vertical walls with caves and crevices (Barr, 1968; Martínez *et al*., 2002), where it shelters during the day. Reck (1983) observed individuals from shallow depths (0–5 m) to at least 40 m, while Gotshall (1998) suggested a depth range up to 90 m. According to Martínez *et al.* (2002) and Hearn *et al.* (2003), it is less abundant in the immediate subtidal zone, the preferred habitat for the red spiny lobster *Panulirus penicillatus* that shares similar habitats with *S. astori* in the Galapagos Islands.

Scyllarides brasiliensis (Rathbun, 1906; Fig. 14.1C; English FAO name – Brazilian slipper lobster) is characterised by the presence of a cervical incision along the lateral margin of the carapace and tubercles on the surface of the carapace near the gastric tooth. The first abdominal somite bears only two red lateral spots dorsally. There is very limited information on the distribution of this species. Its TL is about 20 cm with a CL of up to 12 cm. It is found in 22–38 m of depth in the Western Atlantic, in Brazil, from Maranhão to Bahaia (Holthuis, 1991). There is also a record of this species from Dominica in the West Indies (Holthuis, 1991) on sand, gravel, and rock bottoms (Coelho & Ramos-Porto, 1983/1985, 1998).

Scyllarides deceptor (Holthuis, 1963; Fig. 14.1D; English FAO name – hooded slipper lobster) has distinct grooves on its carapace with well-defined gastric and pregastric teeth, however, the cervical incision while wide, is not very distinct. The dorsal surface of the first abdominal somite bears two very distinct and sharp spots. This species reaches a TL between 13–27 cm and a CL of 5–12 cm. It is found in the Western Atlantic from southern Brazil to northern Argentina in depths from 45 to 200 m (Williams, 1986) and on substrates similar to *S. brasiliensis* (Coelho & Ramos-Porto, 1983/1985, 1998).

Scyllarides delfosi (Holthuis, 1963; Fig. 14.1E; English FAO name – three-spot slipper lobster), like *S. deceptor*, has distinct grooves on its carapace and well-defined gastric and pregastric teeth. Its cervical incision is distinct, but narrow. The first abdominal somite bears one circular central spot and two irregularly shaped lateral spots on its dorsal surface. The TL of this species reaches up to 25 cm and the CL is typically 6–9 cm. It is found in the Western Atlantic along the north coast of South America from Venezuela to Brazil, in depths between 42 and 80 m on muddy substrates (Opresko *et al.*, 1973).

Scyllarides elisabethae (Ortman, 1894; Fig. 14.1F; English FAO name – Cape slipper lobster) has distinct cervical and postcervical incisions along the lateral margin of its carapace. The TL of this species exceeds 25 cm and its CL reaches 9 cm. It is found only in the Indian Ocean along southeast Africa in substrates of fine sand or mud and at depths ranging from 37 to 380 m (usually at less than 100 m) (Williams, 1986).

Scyllarides haanii (De Haan, 1841; Fig. 14.1G; English FAO name – Aesop slipper lobster) has a distinct dorsal groove on the carpus of the first pereiopod, and a large medial hump on the fourth abdominal somite. The first abdominal somite bears two small but distinct lateral spots and a large, irregular median spot (Holthuis, 1991). The TL of this species reaches 50 cm and the maximum CL so far reported is 17 cm. It is found in the Indo-West Pacific from the Red Sea and western Indian Ocean to Japan, Korea, China, Indonesia, Australia and Hawaii in depths ranging from 10 to 135 m on rocky substrates (Holthuis, 1991).

Scyllarides herklotsii (Herklots, 1851; Fig. 14.1H; English FAO name – red slipper lobster), like *S. haanii*, has the dorsal groove on its first pereiopod, but its fourth abdominal somite does not bear a large hump. Its first abdominal somite bears three circular or irregularly-shaped red spots that are widely separated. The maximum TL reported for this species is about 32 cm, but usually they are not more than 25 cm. It is found in West Africa from northern Senegal to southern Angola on sand and rocky substrates, but sometimes on mud, and mostly at depths between 5 and 70 m. There are reports of this lobster in deeper water, beyond 200 m (Holthuis, 1991).

Scyllarides latus (Latreille, 1851; Fig. 14.1I; English FAO name – Mediterranean slipper lobster) is similar to both *S. haanii* and *S. herklotsii*, in that it too bears a dorsal groove on its first pereiopod. Like *S. herklotsii* it lacks a large hump on its fourth abdominal somite. The first abdominal somite bears a large central, circular spot that is separated from the lateral spots by a narrow yellow ring-like zone. The carapace is covered in conspicuous and high tubercles. There is a considerable body of knowledge on this species due to studies done in the Azores Islands, Israel, and Italy. It is found mainly on hard substrates at depths of 4 to 100 m (Holthuis, 1991) in the Mediterranean Sea and Eastern Atlantic from the coast of Portugal to Senegal, Madeira, the Azores, the Selvagens, and Cape Verde Islands (Maigret, 1978; Fischer *et al.*, 1973, 1981; Campbell, 1982; Martins, 1985a; Holthuis, 1991). However, in many areas, and especially along the Mediterranean coasts of Europe, this species is rare due to overfishing (Spanier, 1991). It is also found on artificial reefs (Spanier *et al.*, 1990). Holthuis (1991) reported the maximum TL of this species to be about 45 cm, with a CL of up to 12 cm. However, the studies of Martins (1985a) in the Azores, Bianchini *et al.* (1996) in Italy, and Spanier *et al.* (1988) and Almog-Shtayer (1988) in Israel indicate that the present sizes are smaller due most likely to selective fishing pressure on larger specimens. Spanier and Lavalli (1998) reported that females tended to be larger than males and Atlantic specimens seem to be heavier than those from the southeastern Mediterranean. However, a genetic comparison of *S. latus* from Israel, Italy, and the Azores Islands indicated very little variability between these populations (Bianchini *et al.*, 1998).

Scyllarides nodifer (Stimpson, 1866; Fig. 14.1J; English FAO name – ridged slipper lobster) bears a large swollen hump in the upper basal part of the carpus of the first pereiopod, and three distinct red spots on the first abdominal somite. All pereiopods have conspicuous red bands on the propus, merus, and carpus. The posterior margin of the second abdominal somite bears a prominent tooth. The TL of this species typically reaches about 35 cm and its CL ranges from 11 to 13 cm (Holthuis, 1991). It occurs in depths of up to 42 m and on sandy substrate or sand mixed with mud, shells, coral, coralline algae, or sponges, and is also found on limestone block ridges (Shipp & Hopkins, 1978) and artificial reefs or the undersides of drilling platforms (Moe, 1991). It may bury into sediment. This species' colouration is cryptic on limestone ledges and rocky outcroppings (Lyons, 1970; Ogren, 1977; Fischer, 1978; Hardwick & Cline, 1990; Holthuis, 1991).

Scyllarides obtusus (Holthuis, 1993; Fig. 14.1K; local name – stump) is a recently-described species from the waters off Saint Helena (Holthuis, 1993). Previously, this species was identified with various *Scyllarides* species from the Atlantic Ocean and the waters off East Africa. It is closest in form to the West African *S. herklotssi* and South American *S. delfosi*, but differs from the former in having a swollen base of the carpus of the first pereiopod, more pronounced ridges on all pereiopods, a wider and flatter carapace with more prominent gastric and pregastric teeth, and closer-placed spots on the first abdominal somite. It differs from the latter in having a flatter carapace with a more distinct and rough postcervical groove and larger, more distinct lateral margin teeth, and more closely-spaced and equally-sized spots on the first abdominal somite. The largest specimen reported had a CL of 106 mm

(Holthuis, 1993). This species is endemic to the area surrounding Saint Helena and occurs on hard substrates at depths between 5 and 75 m. It supports a local fishery, and has done so since early times; the earliest reference to this lobster is from 1646 (Holthuis, 1993).

Scyllarides roggeveeni (Holthuis, 1967; Fig. 14.1L; English FAO name – Easter Island slipper lobster) has distinct gastric and pregastric teeth, a deep cervical groove on the carapace, three distinct spots on the first abdominal somite, and distinct humps or medial ridges on the second through fourth abdominal segments. The TL of this species is about 30 cm, with a CL of 11 cm. It is only found off Easter Island but is poorly understood because no regular fishery exists for it (Holthuis, 1991).

Scyllarides squammosus (H. Milne Edwards, 1837; Fig. 14.1M; English FAO name – blunt slipper lobster) bears a cervical incision along the lateral margin of its carapace, and two pointed teeth on the inner orbital margin. The orbit is nearly closed due to the presence of a toothed lobe along the inner orbital angle that nearly touches the outer orbital angle. The first abdominal somite bears three red spots: a poorly defined medial spot and two well-defined lateral spots. The maximum TL of this species is about 40 cm and its CL reaches up to 15 cm. It is found in the Indo-West Pacific from the eastern coast of Africa to Japan, Hawaii, Melanesia, New Caledonia, and Australia on reefs and rocky substrates of a few metres depth to about 80 m (Holthuis, 1991). It is most common at depths between 20 and 50 m (Fischer & Bianchi, 1984).

Scyllarides tridacnophaga (Holthuis, 1967; Fig. 14.1N; English FAO name – clamkiller slipper lobster), like *S. roggeveeni*, has distinct gastric and pregastric teeth, sharp median ridges on the second to fourth abdominal somites, and three distinct spots on the first abdominal somite. It differs from *S. roggeveeni* in that its pregastric tooth is two-topped, its cervical groove is shallow, and the central spot on the first abdominal somite is sharply defined rather than being indistinct. The TL of this species reaches 30 cm and its CL ranges from 6 to 12 cm. It is found in the Indo-West Pacific throughout the Red Sea (up to Eilat, in the northern tip of the Gulf of Aqaba), along the eastern African coast (Somalia, Kenya), in the Gulf of Aden, along Pakistan and the western coast of Thailand. This lobster is found mainly on or close to reefs and other hard substrates at depths between 5 to 112 m (Holthuis, 1991).

14.3 Anatomy

The anatomy of adult slipper lobsters follows the general decapod body plan of having a segmented body divided into three regions: the head (cephalic region), thorax, and abdomen. The cephalic and thoracic regions are fused into a cephalothorax, which is covered dorsally and laterally by the carapace. As with most malacostracans, the cephalic region is comprised of five segments, each of which bears a pair of appendages – in this case, the first and second antennae and the true mouthparts (mandible, first maxillae, and second maxillae). These appendages are primarily sensory in function and are involved in feeding. The thoracic region is comprised of eight segments, each of which bears paired appendages that serve feeding (including sensory) and locomotory functions. Those appendages include the first, second, and third maxillipeds and the first through fifth pereiopods. The abdominal region, often misnamed the ‘tail’, consists of six segments, the first five of which bear a pair of biramous pleopods (aka ‘swimmerets’), and the last of which bears pleopods that are modified into broad flattened appendages called uropods. The telson or true tail is not a segment (Schram, 1986) and forms the central axis of the tail fan, which is then flanked by the uropods.

As in nephropid and palinurid lobsters, the thoracic appendages consist of inner (endopodite) and outer (exopodite) branches that emerge from a basal segment called the protopodite (Phillips *et al.*, 1980). Each of these parts is also segmented to provide flexibility via seven joints, all of which act as a simple hinge flexing in only one plane (Macmillan, 1975). Moving proximally to distally, the protopodite is divided into the coxa and basis; the endopodite is divided into the ischium, the merus, the carpus, the propus, and the dactyl. The exopodite is divided into the proximal basal region and the distal multi-articulate flagellum.

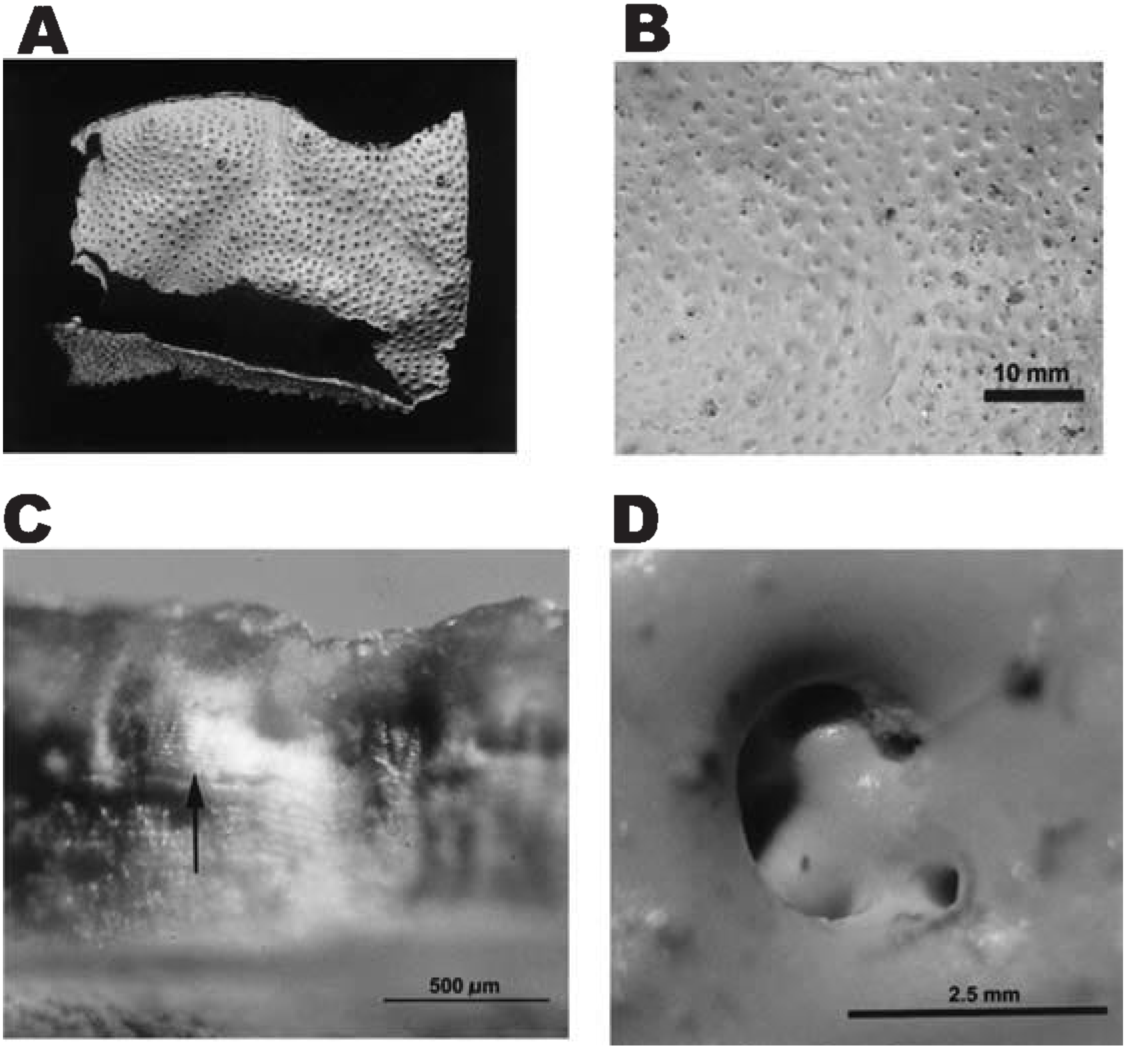


Fig. 14.2 (A) Tuberculate surface of a slipper lobster carapace; (B) inner surface of carapace showing the pits formed by tubercles; (C) histological section of the exoskeleton, showing numerous laminate layers; (D) single tuberculate pit, showing inner strut structure that confers added strength to carapace (modified from Tarsitano *et al*., 2006).

Adult slipper lobsters differ from clawed and spiny lobsters in several important respects. Their carapace is dorsoventrally flattened and bears numerous blunt tubercles on its surface, which contrasts with the spines borne upon less-flattened spiny lobster carapaces and the barrel-like, smooth carapaces of nephropid lobsters. The structure of these tubercles (Fig. 14.2) confers a strength advantage to slipper lobsters – each tubercle acts as a 'blunt-cracking' device that prevents a crack from running the length of the carapace (Barshaw *et al*., 2003; Tarsitano *et al*., 2006). The carapace is also significantly thicker, and thus stronger than either clawed or spiny lobster carapaces (Barshaw *et al*., 2003).

All segments of the legs of spiny lobsters and clawed lobsters are covered in a 'bottlebrush' setal tuft pattern comprised of fine chemo- and mech-

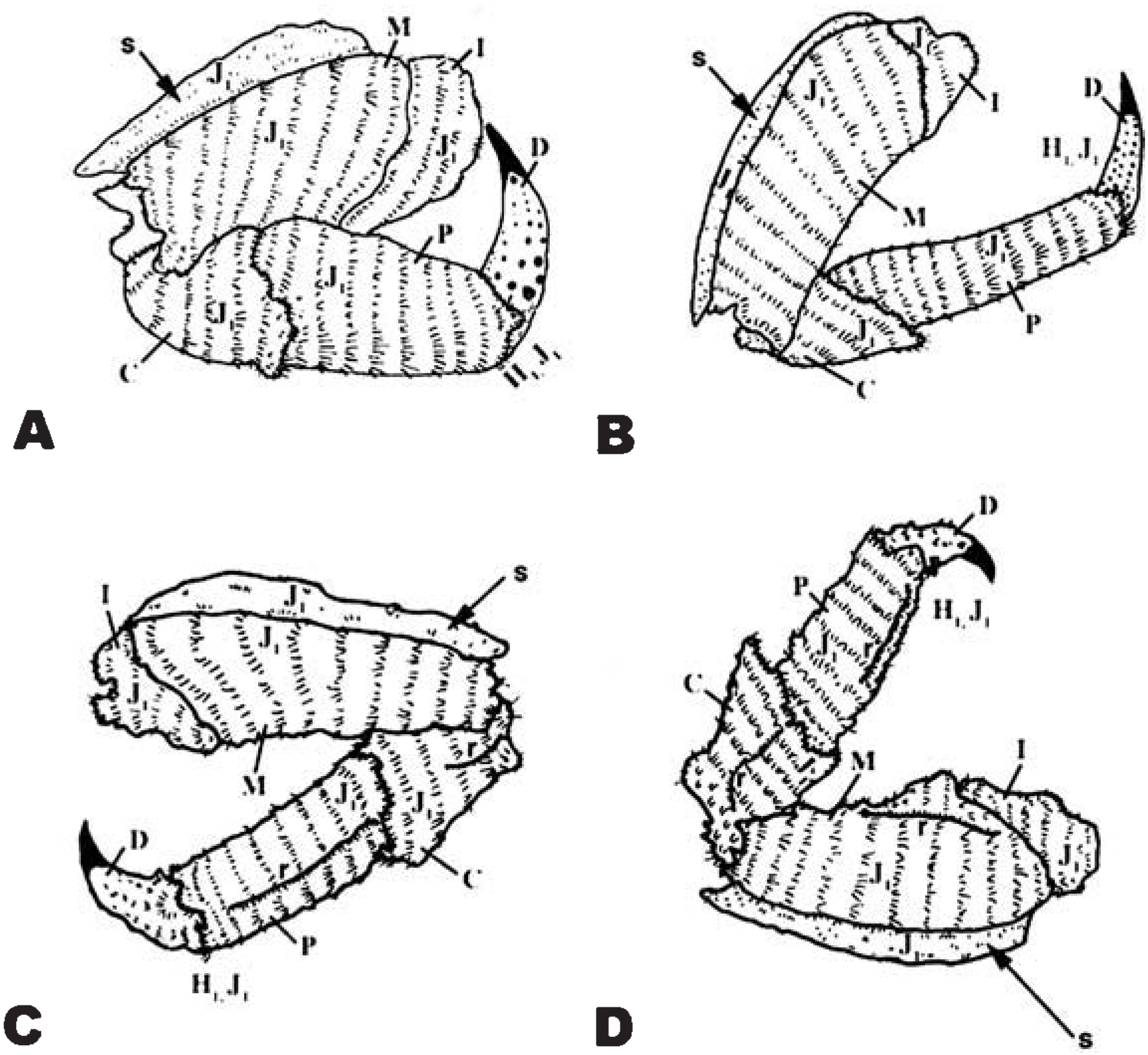


Fig. 14.3 Outer, or aboral views of walking legs of *Scyllarides* spp. (A) left 1st pereiopod; (B) left 2nd pereiopod; (C) right 3rd pereiopod; (D) right 4th pereiopod. D, dactyl; P, propus; C, carpus; M, merus; I, ischium; s, meral shield; J_1, cuspidate setae; H_1, simple setae; •, stripped dactyl setal pit (modified from Malcom, 2003).

anosensory hairs, to support probing and exploratory behaviour. The segments of the pereiopods of slipper lobsters, in contrast with the general arthropod pattern (shared even with insects), are much less setose. Additionally, slipper lobsters lack any chelae on their first or second pereiopods – instead, the first through fourth pereiopods end distally in a distinctly-sharpened dactyl nail, covered in a tough cuticle that lacks setae, which presumably is an adaptation to opening their preferred molluscan prey (Malcom, 2003; Fig. 14.3). The dactyl of the fifth pereiopod is sexually dimorphic: in males it follows the typical pattern of forming a blunt nail, but in females, the dactyl and propus segments articulate to form a small, false chela with which the female grooms and ventilates the eggs attached to her pleopods (Moe, 1991; Malcom, 2003; Fig. 14.4).

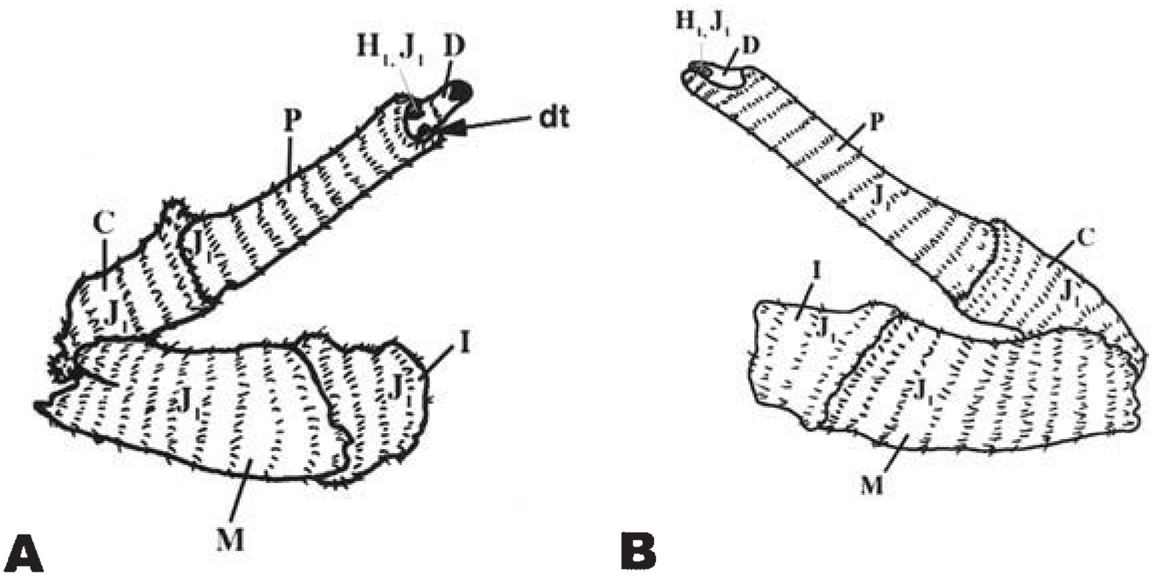


Fig. 14.4 Inner, or oral views of the left 5th pair of walking legs of *Scyllarides* spp. (A) male; (B) female, showing false chelae formed by dactyl and propus segments. D, dactyl; P, propus; C, carpus; M, merus; I, ischium; s, meral shield; J_1, cuspidate setae; H_1, simple setae; dt, dactyl tuft (modified from Malcom, 2003).

Slipper lobster antennules (first antennae) are foreshortened to ~0.05% of their body length – in clawed lobsters, antennules represent 0.1 body lengths, and in spiny lobsters they can reach 1.5 body lengths (F. Grasso, unpublished data). These antennules bear four segments, the most distal of which branches into a lateral and medial flagellum (Fig. 14.5). Each flagellum is composed of smaller segments called annuli. The lateral flagellum bears numerous types of sensory hairs on the annuli that most likely have chemo- and mechanosensory functions (Weisbaum & Lavalli, 2004). The second antennae, which are slender and rod-like in clawed and palinurid lobsters, become shortened and flattened dorsoventrally to the point where they are hard to recognise as antennae. They are comprised of six segments, but these are all severely reduced in length and are flattened into plate-like structures. The sixth segment forms a plate with a wide range of movement in the dorsoventral plane that seems important in controlling the pitch of swimming and is also used in intraspecific aggression (see Sections 14.5.1 and 14.5.5). This appearance of the second antennae is responsible for the names for these lobsters, such as 'shovel-nosed' or 'bulldozer' lobster (Holthuis, 1991).

Internally, the alimentary tract is divided into the foregut, midgut and hindgut. The foregut and hindgut is lined with chitinous cuticle that is shed at each moult, while the endodermal midgut lacks such a cuticular lining (Johnston, 2006). The foregut is comprised of a short oesophagus that leads into the two-chambered proventriculus (anterior cardiac and posterior pyloric stomachs). In clawed and spiny lobsters, the cardiac stomach typically bears a gastric mill with distinct ossicles (teeth) for grinding the food; however, these ossicles are severely reduced or even absent in slipper lobsters, reflective of the soft nature of the animal's diet (Johnston & Alexander, 1999). In phyllosomal larvae, the proventriculus is simply a non-divided tube that lacks ossicles; instead it bears brushworks of setae on its posterior lateral edges and spines and other setae on its dorsal and ventral surfaces that serve to sort fine particles (Mikami & Takashima, 1993; Mikami *et al*., 1994; Johnston, 2006). The midgut is comprised of a small dorsal caecum and large bi-lobed digestive gland (hepato-

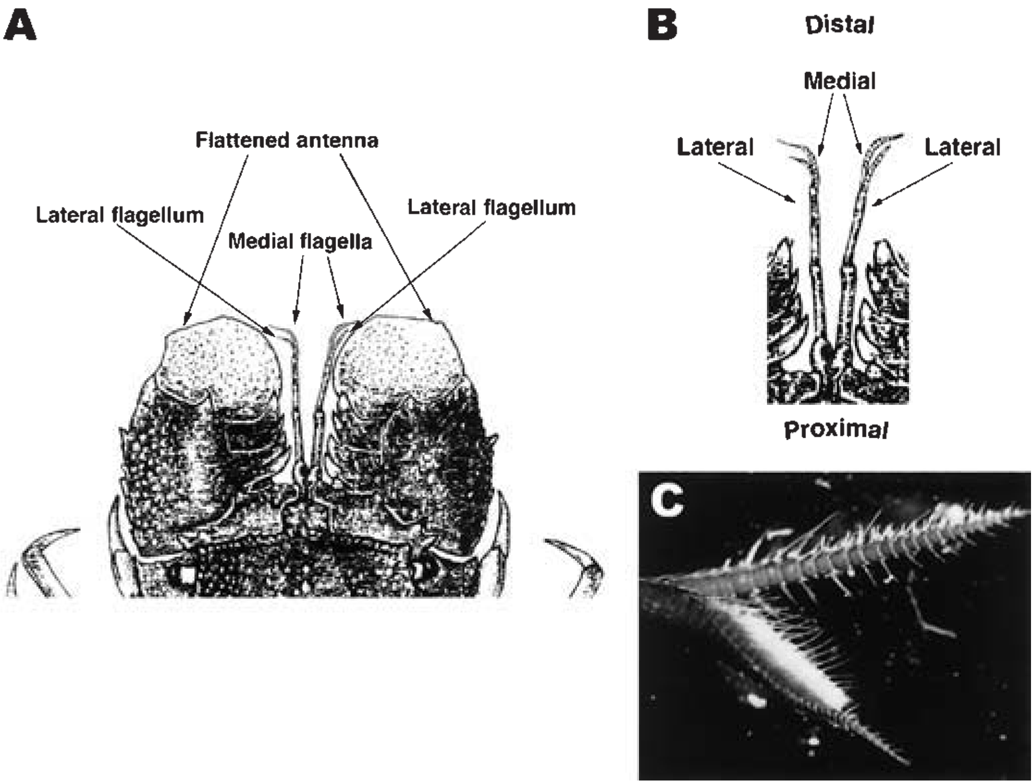


Fig. 14.5 Anterior aspect of a slipper lobster (*Scyllarides* spp.). (A) paired second antennae, erroneously dubbed 'shovels' or 'flippers', have six segments, and are shortened and flattened dorsoventrally; (B) paired first antennae, or antennules, have four segments, the most distal of which branches into a lateral and medial flagellum; (C) flagella are composed of smaller segments (annuli) upon which setae are borne (modified from Holthuis, 1991 and Weisbaum & Lavalli, 2004).

pancreas). The hindgut is a simple tube terminating at the anus on the telson (Johnston, 2006).

As in other decapods, the circulatory system is open. While open circulatory systems have been considered to be low-pressure and sluggish, higher malacostracans have highly regulated and efficient systems with flow patterns that rival vertebrate closed systems (McMahon & Burnett, 1990). In contrast to nephropids, no work has been done on scyllarid circulatory systems.

14.4 Life history

The life history of scyllarids parallels that of palinurids and can be divided into a series of developmental phases. These lobsters typically begin their pelagic lives as phyllosomal larvae, i.e., flattened, leaf-like, transparent planktonic forms with long appendages and cephalic shields that are very long and wider than the thorax (Phillips *et al.*, 1983). However, some scyllarids hatch as a naupliosoma (prelarva; Fig. 14.6A), which is a short-lived form (a few hours) that bears only the first three pairs of cephalic appendages (Booth *et al.*, 2005; Sekiguchi *et al.*, 2006). In such primitive forms, the antennae bear natatory setae, and the total length of the animal reaches 1–2 mm (Booth *et al.*, 2005). Three species of *Scyllarides* apparently hatch as this early form: *S. aequinoctialis* (Robertson 1968, 1969), *S. herklotsi* (Crosnier, 1972), and *S. latus* (Martins, 1985a). Others hatch as a phyllosoma (Fig. 14.6B–D) with the full suite of cephalic and thoracic appendages; abdominal appendages are typically

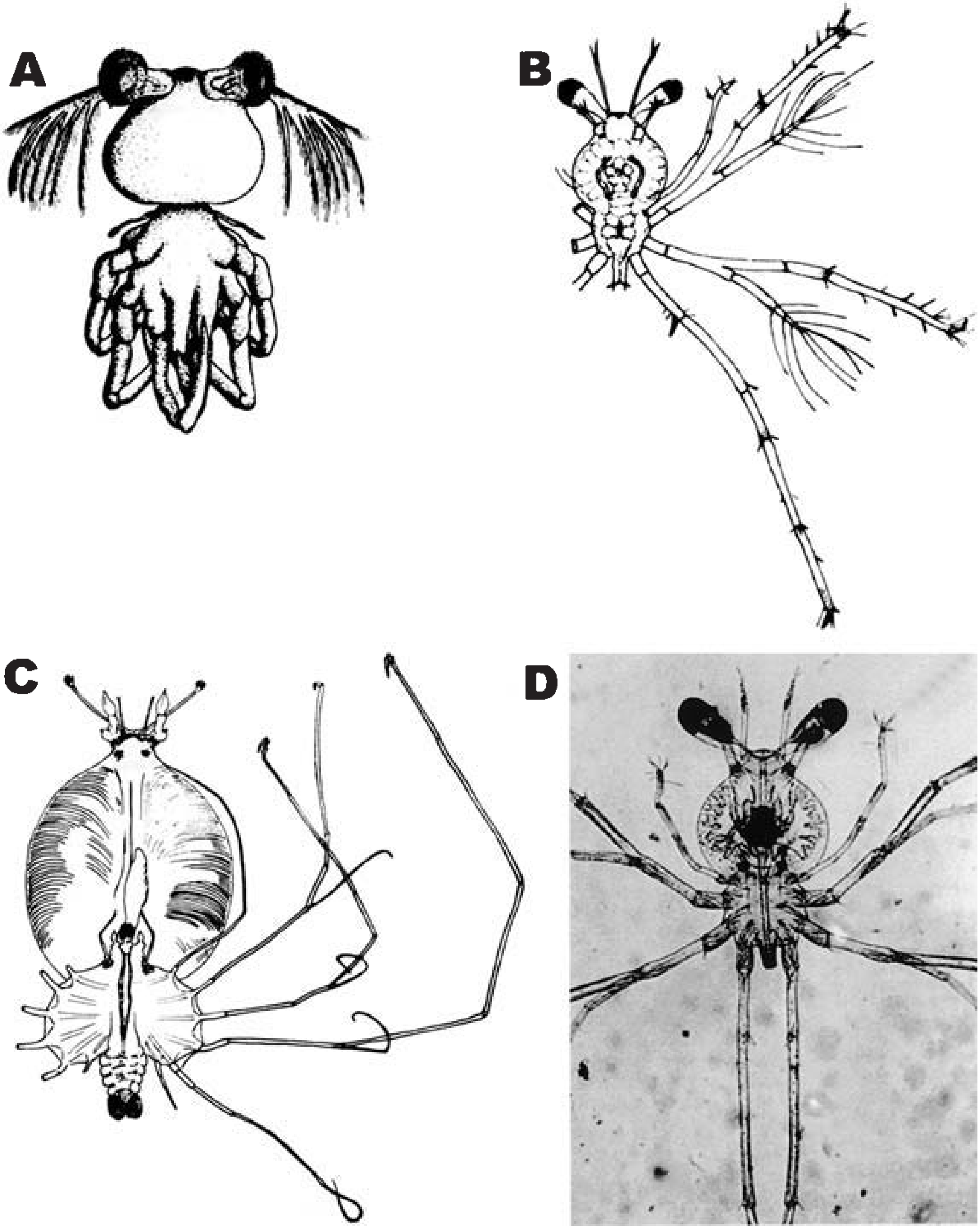


Fig. 14.6 Larvae of *Scyllarides latus*. (A) naupliosoma (· 50); (B) phyllosoma stage I (· 20); (C) phyllosoma stage IX (· 2.2); (D) phyllosoma stage I, hatched in the laboratory on 19 June 1994 (from Martins, 1985a (A–C) and Bianchini & Raisa, 1997 (D)).

absent or rudimentary in early phyllosomas, but appear in later stages (Booth *et al*., 2005; Sekiguchi *et al*., 2006).

All thoracic appendages bear an exopodite until the larvae undergo their metamorphic moult into postlarvae. At that time, exopodites are lost from all thoracic appendages except the maxillipeds, where they are retained and used for generating currents around the mouth region (Lavalli & Factor, 1992, 1995). However, scyllarid phyllosomas deviate from other decapod larvae in that they are missing an exopod on the third maxilliped (but see Phillips *et al*., 1983 who assert that the third maxillipeds bear a conspicuous exopod bud in *S. haani* and/or *S. squammosus*). Whether this indicates a phylogenetic separation of feeding strategy or swimming requirements is unknown (Booth *et al*., 2005).

The developmental period for scyllarid phyllosomas is far more variable than that for palinurids, and can last from a few weeks to at least 9 months (Booth *et al*., 2005). Depending on the species, scyllarids metamorphose into a nisto phase (= to the pueruli in spiny lobsters). This nisto phase is responsible for making the transition from a planktonic to a benthic life. The nisto settles, moults, and the lobster then begins its benthic life as a young juvenile and eventually matures into the adult, reproductive phase.

14.4.1 Phyllosomas

Dispersal of phyllosomas varies among species and depends largely on whether the parental stock is found within lagoons formed by coral island barrier reefs or in deeper waters (Johnson, 1971a, b; Yeung & McGowan, 1991; Baisre, 1994; Coutures, 2000). Those hatched in coastal lagoons tend to remain there, while those hatched in deeper water gradually move shoreward, such that final-stage phyllosoma of some scyllarids are found much closer to shore than is typical of palinurid phyllosomas (Sekiguchi *et al*., 2006). *Scyllarides aequinoctialis*, *S. astori*, *S. herklotsii*, *S. nodifer*, and *S. squammosus* all have oceanic distributions of their phyllosomas and are presumed to be dispersed in a manner similar to that for palinurids, since few mid- to late-stage larvae are found in inshore regions (Robertson, 1969; Johnson, 1971b; McWilliam & Phillips, 1983; Phillips *et al*., 1983; Yeung & McGowan, 1991; Coutures, 2000; see Table 1 in Booth *et al*., 2005). The larvae undertake diel vertical migrations, but data are limited as to the extent of these migrations and the species-specific preferences for various depths (Minami *et al*., 2001; Sekiguchi *et al*., 2006), as well as the efficacy of their swimming behaviour. It is likely that smaller instars vertically migrate less than later, larger instars (Yeung & McGowan, 1991). Those species or instars that do exploit this strategy may use passive transport by occupying vertical strata that move them in specific directions (Sekiguchi *et al*., 2006). Some *Scyllarides* spp. phyllosomas even travel attached to the aboral surface of jellyfish medusae (Shojima, 1963), which may affect larval dispersal or allow them to remain relatively near shore (Booth *et al*., 2005; Sekiguchi *et al*., 2006).

Duration of the planktonic larval period varies from several weeks to months. In the genus *Scyllarides*, only a few species have been studied, and for these, the planktonic larval development period appears to last between 6–10 months, with the number of instars ranging from 11–13 (Robertson, 1969; Crosnier, 1972). Total length reached during the phyllosoma phase ranged from 25–48 mm (Michel, 1968; Robertson, 1969; Johnson, 1971a; Crosnier, 1972; see Table 1 in Booth *et al*., 2005).

Phyllosomas are feeding larvae and appear to be predatory, using their pereiopods to hold onto food items, which are then shredded by the maxillipeds and masticated by molar processes of the mandibles (Mikami & Takashima, 1993). Mostly fleshy foods are ingested; such food types are more readily available in coastal waters than in offshore, oligotrophic waters (Mikami *et al*., 1994; Booth *et al*., 2005; Sekiguchi *et al*., 2006). Some *Scyllarus* larvae have been observed holding hydromedusae, but it is not known if these were subsequently ingested (Shojima, 1963).

14.4.2 Nistos

The final-stage phyllosoma moults into the nisto, or postlarval stage, which, like spiny lobster pueruli and clawed lobster postlarvae, recruit into the benthic environment. The nistos are neither completely planktonic nor completely benthic – they are caught in plankton tows demonstrating that they are pelagic at least part of the time (Booth *et al.*, 2005). In many species of scyllarids, the nisto appears to bury into soft substrates during the day and swim actively at night; some species even change colouration daily between these two habitats to remain cryptically coloured in both (Booth *et al.*, 2005). Some scyllarid nistos are excellent swimmers (using their abdominal pleopods), while other species are poor swimmers; some are also capable of executing tail flips (backward swimming) as a means of escape (Lyons, 1970). Webber and Booth (2001) suggest that these swimming differences exist due to marked differences in the size of pleopods among different species. However, this suggestion has not been adequately tested.

Like the phyllosoma, the nisto is completely transparent, which makes it cryptic in the water column and, no doubt, helps it to avoid predation. It has a large, flattened, disc-shaped carapace and a small abdomen, and may more closely resemble adult *Ibacus* and *Paribacus* forms than adult *Scyllarides* forms. As such, it has in the past been referred to as a 'pseudibacus' (Chace, 1966; Crosnier, 1972; Holthuis, 1993). No information is currently available on the duration of the nisto stage for *Scyllarides* species. However, in other scyllarid lobsters, the phase lasts from 7 to 24 days (see for review, Table 1 in Booth *et al.*, 2005). The nisto is typically 9–13 mm in carapace length (Michel, 1968; Lyons, 1970; Crosnier, 1972; Holthuis, 1993).

As with spiny lobster pueruli, the nisto appears to rely on energy reserves, rather than to actively feed (Sekiguchi *et al.*, 2006). However, its proventriculus has features that are transitional between the phyllosoma and the juvenile (Johnston, 2006) and suggest that the ability to process and sort ingested food particles is more advanced than it is in phyllosomas. While the phyllosoma lacks a cardio-pyloric valve that divides the anterior cardiac chamber from the posterior chamber, the nisto has this feature. But, like the phyllosoma, the nisto lacks a gastric mill, suggesting that food, if consumed, is similar in softness to that of the phyllosoma, and is primarily masticated by the mouthparts prior to ingestion (Johnston, 2006).

Nistos are morphologically similar to juveniles and, like juveniles and adults, have flattened second antennae. The structure of the abdominal pleopods is the main morphological difference between the nisto and the juvenile, with nisto pleopods bearing swimming (natatory) setae (Williamson, 1969). The colouration pattern also differs: transparent for the nisto and reddish-brown coloured for the juveniles.

14.4.3 Juveniles

In contrast to an ever-increasing body of knowledge of the juvenile life of clawed and spiny lobsters, almost nothing is known about the juvenile habits of slipper lobsters. In *S. latus* no live juvenile has ever been sampled (Spanier & Lavalli, 1998). The smallest individual commercially fished off the Israeli coast weighed 100 g. Almog-Shtayer (1988) reported that the smallest male in her sample was 64 mm CL (200 g) and the smallest female was 69 mm CL (252 g). The smallest animals caught by Bianchini *et al.* (1996) weighed 100 and 103 g. Two small exuviae were recorded in the coast of Israel – one of 38 mm CL at 15 m depth and the other of 47.5 mm found washed ashore. A small preserved male of 34.3 mm CL was recorded in the Museum of Zoology of the University of Florence, 'La Specola'. It had been collected by a scientific trawl in Italian waters, possibly at a depth greater than 400 m. This record may suggest that, at least in this species, the nisto settles on the substrate in deep water and the juveniles develop there. Similar suggestions have been made for other scyllarids. For example, *Ibacus* juveniles appear to migrate shoreward from offshore waters to recruit into adult grounds (Stewart & Kennelly, 1997).

Juveniles of both *S. latus* and *S. nodifer* were also rare in other studies carried out in the Mediterranean and Atlantic (Lyons, 1970; Hardwick & Cline, 1990; Bianchini *et al.*, 1996). Hearn *et al.* (2006; personal communication) and Hearn (2004), following earlier studies by Reck (1983) and Murillo *et al.* (2003), noted that *S. astori* displays a narrow size range, with almost complete absence of juveniles (few individuals smaller than 20 cm total length). He suggested that the juveniles occupy a different spatial niche from adults and are far more cryptic than adults. It is clear that in order to obtain sufficient numbers of small individuals, specific sampling techniques must be developed which target the juveniles, which may prove difficult if many of the species have juvenile development in deep, oceanic waters.

Rudloe (1983) reared juveniles of *S. nodifer* from CL of 23 mm to 73 mm and predicted that approximately 18 months and 9–10 moults were required to reach the adult size (for details see Section 14.8). In contrast, Hearn (2004) suggested that 7–8 years are necessary for juvenile *S. astori* to recruit fully into the adult population – this species, in particular, seems to have very slow growth rates.

14.4.4 Adults

Arctidinid adults are typically large. Sex ratios are close to unity in those species that have been adequately sampled (*S. latus*, Martins, 1985a; Spanier & Lavalli, 1998; *S. astori*, Hearn, 2004). Females generally exceed 90–100 mm CL, although sexual maturity can be reached at smaller sizes for some species (e.g. *S. squammosus*, 65–81 mm CL, DeMartini & Kleiber, 1998). Shortly after mating, they extrude a large number of eggs (conservative numbers range from 140 000 to 356 000), based on total length of the individual, with those eggs ranging from 0.6 to 0.7 mm in diameter (Martins, 1985a; DeMartini & Williams, 2001; Hearn *et al*., 2006). Such high fecundity rates may be an adaptation to oceanic loss of larvae and variable recruitment of nistos due to cyclic changes in oceanic climate (Booth *et al*., 2005). The eggs are brooded for 4–8 weeks before release over a number of days (*S. latus*, Bianchini & Ragonese, 2003), although Almog-Shtayer (1988) reported that *S. latus* females carried eggs for only an average of 16.5 days. Ovigerous females are more commonly sampled in colder to warm, but not hot months (Hearn *et al*., 2006). There is some evidence that they may return to inshore reefs earlier than males in the autumn and leave sooner after shedding eggs in the midsummer, possibly to maximise thermal regimes for developing embryos (Spanier *et al*., 1988). Most species appear to move to colder, deeper waters when inshore water temperatures rise steeply in the summer or, for those species that remain in lagoons, have higher abundances at locations where thermal regimes are less than 25°C (Hearn, 2004).

Growth has not been well studied for most *Scyllarides* spp. and is primarily inferred from recapture studies and/or laboratory experiments. In some species, mean CL is larger for females than for males (*S. latus*, Martins, 1985a; Almog-Shtayer, 1988), while in others, males exceed females in size (*S. astori*, Hearn *et al*., 2006). Tag–release studies suggest that lobsters moult annually (*S. latus*, Bianchini *et al*., 2001), although data from *S. astori* populations suggest that moults occur every 18 to 24 months (Hearn, 2004; Hearn *et al*., 2006). In laboratory settings, slipper lobster growth increments can be regressive, a circumstance due possibly to holding conditions (Almog-Shtayer, 1988; Bianchini *et al*., 2001). Moulting typically occurs at night and in cooler to warmer months (Chessa *et al*., 1996; Spanier & Lavalli, 1998; Bianchini *et al*., in press). Death at moult is generally infrequent, ranging from 8–22% (Spanier & Barshaw, 1993; Chessa *et al*., 1996). The old exoskeleton starts softening some 10–22 days premoult, while the new shell is fully hardened three weeks post-moult. The entire process takes approximately seven hours, with lobsters remaining shelter-bound for 5–9 days post-moult (Almog-Shtayer, 1988). Exuviae are left outside shelters, and there is no evidence that slipper lobsters consume them, as do clawed lobsters (Spanier & Lavalli, 1998).

The adult digestive system of scyllarids has been studied and described fully, but only for *Thenus orientalis* (Johnston & Alexander, 1999) and *Ibacus peronii* (Suthers & Anderson, 1981). Thus, the information provided here is not for *Scyllarides* species *per se*, but is presumed to be similar to that for *Thenus* and *Ibacus*. As in clawed and spiny lobsters, the oesophagus of slipper lobsters is short, presumably to allow for rapid ingestion (Johnston, 2006). It leads into the proventriculus, which is divided into the anterior cardiac stomach and the posterior pyloric stomach. In clawed and spiny lobsters, the cardiac stomach has three large ossicles that comprise the gastric mill (one medial and two lateral 'teeth'); however, in slipper lobsters, these teeth are reduced in size and are less calcified

(Johnston & Alexander, 1999). This difference is likely to be due to the diet specialisation that has occurred in slipper lobsters – that of primarily consuming bivalve flesh, or other fleshy items, compared to clawed and slipper lobsters that consume both flesh and shell fragments. The overall effect of the reduction in ossicular size and additional folding of the proventricular wall is to expand the volume capacity of the cardiac stomach (Suthers & Anderson, 1981; Johnson & Alexander, 1999). Food proceeds from the cardiac stomach to the pyloric stomach through a cardio-pyloric valve, which lacks the spines and accessory teeth seen in other decapods (Johnston & Alexander, 1999). The pyloric stomach possesses dense mats of setae that provide filtering of the semi-digested, masticated food particles entering from the cardiac stomach, such that only the smallest particles pass into the digestive gland while larger particles pass into the midgut caecum and then into the hindgut (Johnston & Alexander, 1999). Little is understood about the digestive enzymes involved in food breakdown (Johnston, 2006). Other aspects of adult physiology are completely unknown at this time.

14.5 Behaviour

Slipper lobster behaviour, like so many other aspects of their biology, has also not been well studied. Those studies that exist focus mainly on one species, *Scyllarides latus*, with occasional others being examined. Because these animals are held readily in laboratory settings, there is potential for understanding many behaviours, as has been done for nephropid lobsters, *Homarus americanus* and *H. gammarus*, and for several spiny lobster species.

14.5.1 Feeding behaviour

Slipper lobsters have become specialised for feeding on bivalves or clams, mussels, and oysters. Bivalves have existed since the pre-Cambrian era and have colonised much of the world's marine and aquatic environments. Given their specialisation for feeding on bivalves, it seems almost certain that the radiation of slipper lobsters followed the beds of bivalves around the world. Where clawed lobsters crush small bivalves with their claws and spiny lobsters use their mandibles to crack and chip away at small bivalve shells to access the meat, slipper lobsters have evolved an elegant feeding mechanism that involves using the physics of the bivalve shell to their advantage, while, at the same time, overcoming the disadvantage of the extremely effective adductor muscles that keep molluscan valves closed. To get around this energetic cost, slipper lobsters have evolved a bivalve opening mechanism that employs delicate manipulation and mechanical advantage for prying. In essence, they 'shuck' bivalves (Lau, 1987; Spanier, 1987), using tactile and olfactory senses, as well as a guided mechanical advantage, to avoid the cost that a 'brute force' mechanism would require. In contrast, clawed lobsters use repetitive loading via their crusher claw to cause fracture lines in the rigid shell of bivalves (Moody & Steneck, 1993). This works because there is little organic matrix that would blunt the cracks created by repetitive loading. Spiny lobsters lack claws but have, in their place, strong mandibles, which they use to bite cracks into the valve edges of bivalves (K. Lavalli, personal observations). Once a sufficiently large hole is bitten into the edge, the lobster can dig molluscan flesh out of the shells. In the case of both claw-loading and biting of bivalves, the process to crack the shell takes some time; this time probably exceeds that needed by slipper lobsters to shuck shells. Slipper lobsters, like spiny lobsters, lack claws, and apparently also lack strong mandibles; thus, they resort to using their legs – and specifically their dactyl tips – to open bivalves (Lau, 1987; Spanier, 1987).

During the feeding sequence, slipper lobsters typically approach a bivalve with their antennules down near the substrate. Upon encountering the mollusc, the lobster picks up the shell with the first two to three pairs of walking legs and repetitively probes the outer valves with its antennules, as though 'smelling' and assessing the shell for its possible value (Malcom, 2003). This behaviour contrasts with that of clawed and spiny lobsters that do not use their antennules for such probing activities, but instead use them to distantly 'chemo-orient' to the food source (Devine & Atema, 1982;

Zimmer-Faust & Spanier, 1987; Moore & Atema, 1991; Moore *et al*., 1991a, b; Beglane *et al*., 1997; Nevitt *et al*., 2000; Derby *et al*., 2001). In clawed and spiny lobsters, the setose walking legs are used for initial assessment of the penetrability of the shell (Derby & Atema, 1982). After an initial assessment of the shell by the antennules, the slipper lobster then holds it firmly with either the first, third, and fourth pairs of walking legs, or the second, third, and fourth pairs of walking legs, and uses dactyl tips of either the second or first pair of walking leg to repetitively probe the edges of the valves (Malcom, 2003). By such repetitive probing, they eventually wedge the dactyl tips into the shell edge and then insert the tips further and further into the shell – a process known as 'wedging' (Lau, 1987). Once one pair of pereiopod dactyls is inserted, another pair – usually those of the second and/or the third pereiopods – is used to cut the mantle tissue along the pallial line (line of attachment to the valve). Then the lobster uses a 'scissoring' motion of the first two pairs of walking legs to increase the opening angle and to provide access to the adductor muscles (Fig. 14.7A, B; Malcom, 2003). The second walking legs cut the adductor muscles, so that the valves open freely. With the valves open, the meat is repetitively scraped out of the valves and passed directly to the third maxillipeds (Fig. 14.7C, D; Lau, 1987; Malcom, 2003). These appendages are used to stretch the flesh and pass the strands back to the subsequent five pairs of mouthparts for ingestion. Until the molluscan flesh is actually passed back to the third maxillipeds, the antennules make repeated downward motions to probe inside the valves, to touch the flesh, and to touch the shell as the legs scrape the flesh from it (Malcom, 2003).

The sensory-motor mechanisms that slipper lobsters use in shucking are unknown at this time. Visual cues can be excluded because the shucking process takes place beneath the animal and is outside the field of view of its dorsally-placed eyes. Touch, proprioceptive, and chemosensory modalities are candidates and there is evidence to suggest that each is involved. The touch and proprioceptive senses that could control this task are located in the legs. For manipulation, the positions of each leg segment, as well as each leg in its entirety, informed by proprioception, are likely to signal the size, orientation, and location of the bivalve shell through signalling of joint angles. Points of contact for application of manipulative forces may be sensed through tactile sensors on the dactyl tips or through the tension in muscle organs. The legs do bear numerous tufts of setae (Malcom, 2003), but most are placed on the more proximal segments of the propus, carpus, merus, and ischium, rather than the distal dactyl (see Fig. 14.3A–D; Fig. 14.8A). Those that are present on the proximal edge of the dactyl segment are usually damaged, most likely due to the abrasive action they suffer while shucking. However, the setae may pick up information from the surrounding water as the flesh of the bivalve is exposed to that water after valve opening. Setal types present consist mostly of simple, cuspidate, teasel-like, connate, and miniature simple (Fig. 14.8B–F) (Malcom, 2003). Simple setae have been demonstrated to have both chemo- and mechanoreceptive functions in clawed (Derby, 1982) and spiny lobsters (Cate & Derby, 2001).

Perhaps the most interesting aspect of the feeding process is the role of the chemosensors. It is unclear how slipper lobsters detect buried food items, as they lack setal tufts on the tips of their pereiopod dactyl segments. Nonetheless, they are capable of digging bivalves out from 3.5 cm of sediment (Almog-Shtayer, 1988), and increase flicking rates of the antennules while doing so, or when bivalves are deposited in their holding tanks (K. Lavalli, personal observations). Obviously, the antennules, acting as distance chemoreceptors, play some role in the detection process, but that role is not understood. Once a bivalve is located and the lobster engages in shucking behaviour, leg motions are suspended several times while the lobster brings its distance chemoreceptor organs (antennules) beneath the carapace and into contact with the bivalve (Malcom, 2003). This is surprising for two reasons. First, the chemosensory maxillipeds are better positioned to reach the shell. Second, as mentioned above, the tactile and proprioceptive sense from the legs should be sufficient to provide feedback information during opening. But, because slipper lobsters are unique in lacking distally placed dactyl setal tufts, they may not be able to obtain sufficient sensory feedback without using

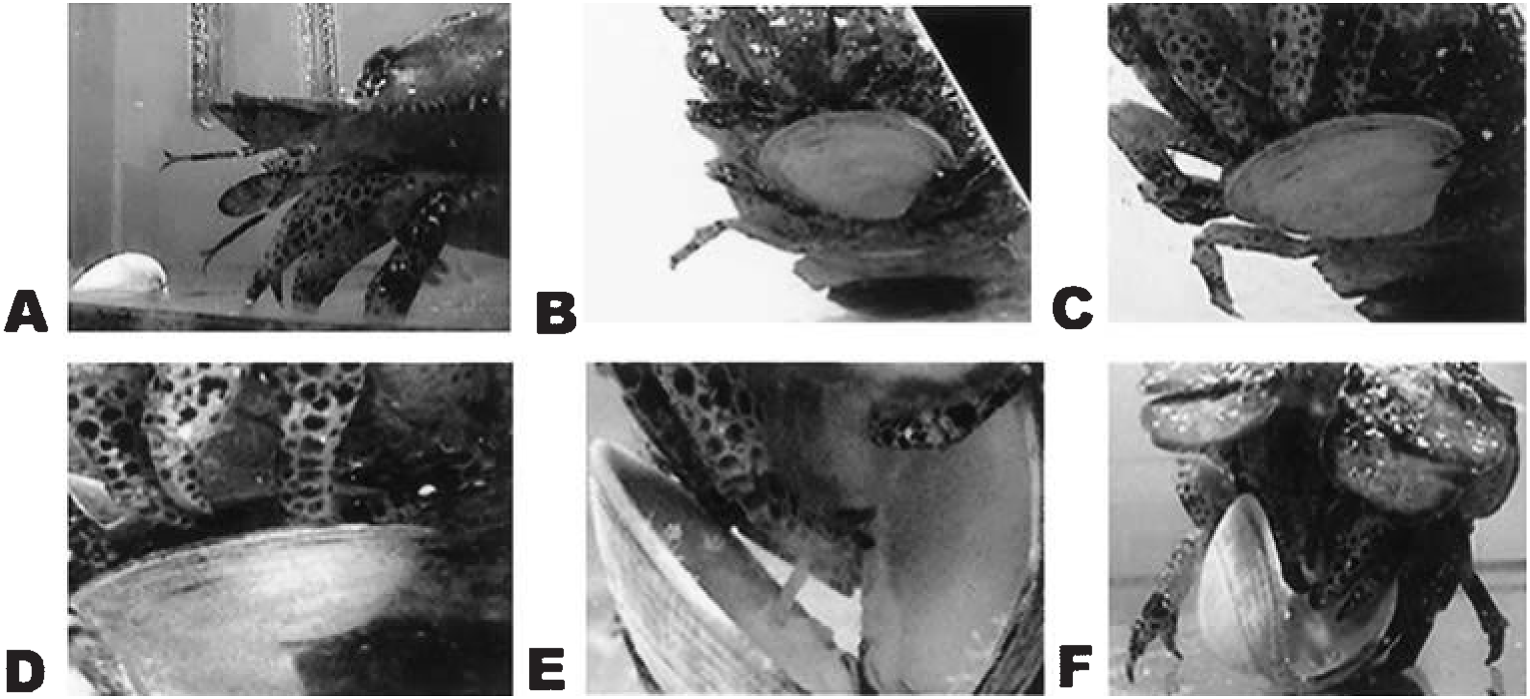
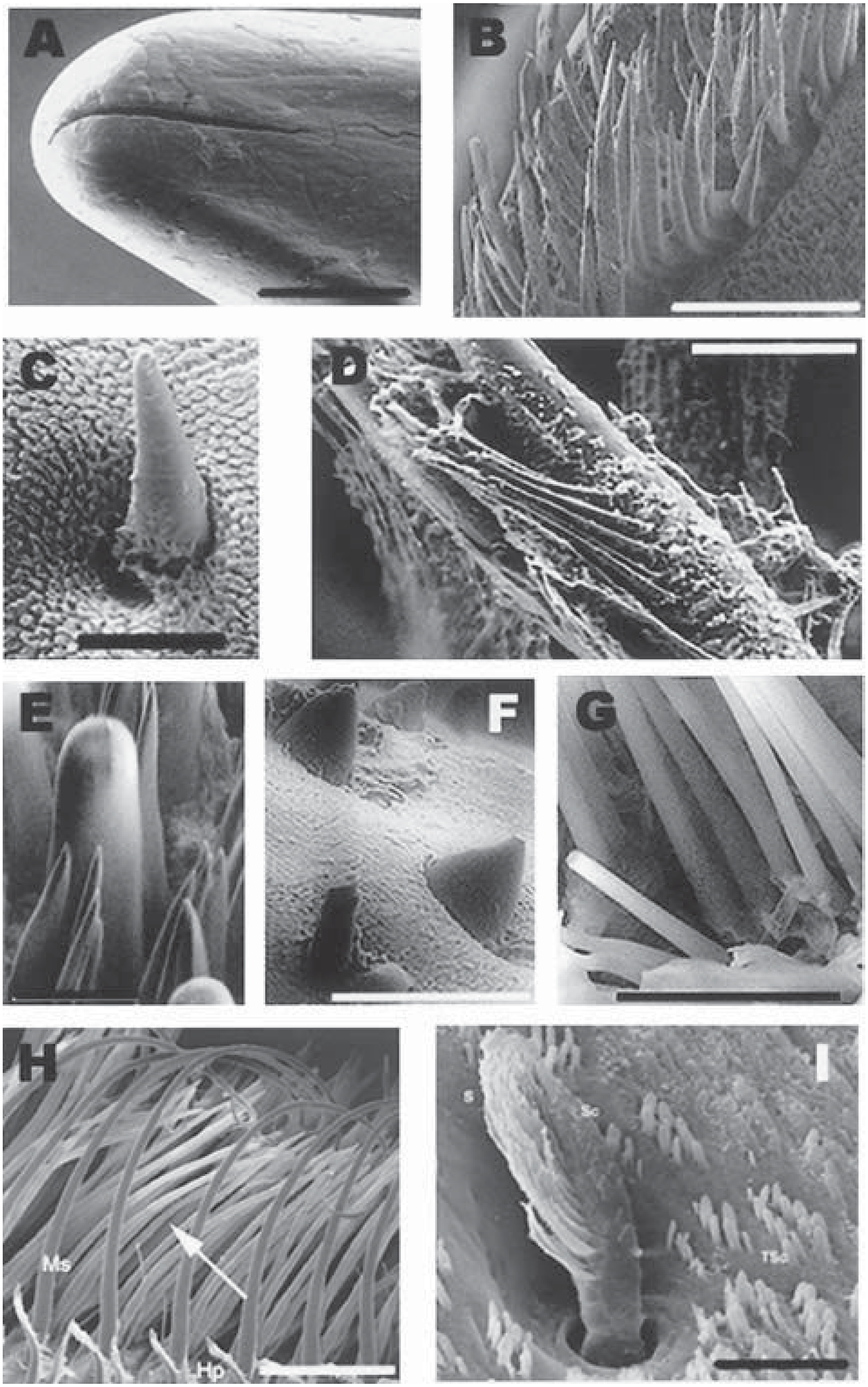


Fig. 14.7 The feeding process of scyllarid lobsters. (A) investigative behaviour, using the antennules; (B) probing of the shell by the first two sets of pereiopods; (C) insertion of the pereiopods into the shell; (D) wedging and subsequent cutting of the adductor muscles; (E) opening of the shell and removal of the bivalve flesh; (F) scraping of the empty shell.


A
B
C
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the antennules. Thus, the antennules may be used as both a contact and distance chemoreceptive mechanism. The annuli of the lateral flagella are covered with a variety of different types of setae (Weisbaum & Lavalli, 2004; Fig. 14.8G, H); many of these have already been identified as chemoreceptors and/or mechanoreceptors in clawed and spiny lobsters. The positioning of the setae places them in a position where stimuli carried by currents, possibly generated by the exopodites of the mouthparts, can reach them and provides an assessment of the shell and flesh within.

While the preferred food is molluscan bivalves, slipper lobsters are also known to take sea urchins, crustaceans, sponges, gastropods, barnacles, sea squirts, algae (*Ulva* spp.) and fish flesh. Different species may well prefer different food items; for example, *S. latus* prefers bivalves to all other food items, and *S. astori* prefers white sea urchins, *Tripneustes depressus* (Martínez, 2000), yet both display a varied diet as seen by stomach content analyses (Martínez, 2000). Very few studies have been made of the gut contents of wild slipper lobsters (e.g. Martínez, 2000 and Lau, 1988 are two of the few), so individual species preferences remain largely unknown. Laboratory preference tests with *S. latus* show a preference of soft flesh to crabs, and bivalves to soft flesh or snails, while no preference was shown between choices of oysters, clams, and limpets (Almog-Shtayer, 1988).

From observations on species that are gregarious (e.g. *S. latus*, Barshaw & Spanier, 1994a), there is intraspecific competition over food items. The least aggressive of such encounters is the 'approach/retreat' sequence common to all lobsters (Atema & Cobb, 1980) – one lobster walks towards the other which responds by walking away or otherwise avoiding the approaching lobster. A more aggressive encounter involves use of the flattened second antennae and is called a 'flip'. Here the lobster jerks up its flattened second antennae under the opponent's carapace, attempting to dislodge it. In the most intense aggressive behaviour, the attacking lobster grabs the anterior portion of the opponent and holds on with the dactyl nails of the walking legs. The opponent usually tail flips, as does the attacking lobster, which causes the opponent to end up on its back. Often after this 'face grab' manoeuvre, both lobsters are holding onto the same food item, ventral side to ventral side, and they continue in this fashion until one lobster finally relinquishes its hold on the food item (Barshaw & Spanier, 1994a).

14.5.2 Sheltering behaviour and substrate preferences

Adult specimens of *Scyllarides* spp. are camouflaged to a certain extent due to their flattened morphology and colouration that blends into hard substrates (e.g. Ogren, 1977; Spanier & Lavalli, 1998). However, in the brightly illuminated water of their shallow habitats, this camouflage provides only limited concealment against diurnal predators. *Scyllarides* spp. therefore, like most other lobsters, are nocturnal. They forage during the night and shelter during the day on the ceilings of caves, in crevices in vertical rocky walls (e.g. Barr, 1968; Martínez *et al.*, 2002 for *S. astori*; Spanier & Lavalli, 1998 for *S. latus*), and in other natural dens, as well in artificial reefs in the field (includ-

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Fig. 14.8 Setal types found on scyllarid pereiopods and antennules. (A) dactyl tip of left 2nd pereiopod of *S. aequinoctialis*; (B) simple setae set in groove on oral surface of left 5th pereiopod propus of *S. nodifer*; (C) cuspidate seta of right oral surface of 3rd pereiopod propus of *S. aequinoctialis*; (D) teasel-like seta with setules from left 1st pereiopod, aboral surface of *S. aequinoctialis*; (E) cuspidate and simple setae of female's right 5th pereiopod dactyl, oral surface of *S. aequinoctialis*; (F) conate setae on merus shield of 3rd right pereiopod, oral surface of *S. nodifer*; (G) miniature simple setae covering the cuticular surface of the aboral surface of propus of *S. aequinoctialis*; (H) aesthetasc (arrow), modified simple setae (Ms), and hemi-plumose setae (Hp) found on the ventral surface of the antennular flagellum; (I) toothbrush setae found on the dorsal surface of the antennular flagellum showing scale (Sc), setules (S), and textured scaling on flagellar surface (TSc). Scale bars: (A) = 200 m; (B) = 200 m; (C) = 200 m; (D) = 20 m; (E) = 50 m; (F) = 250 m; (G) = 350 m; (H) = 273 m; (I) = 20 m (modified from Malcom, 2003 (A–F); Weisbaum & Lavalli, 2004 (G, H)).

ing shipwrecks), or in man-made shelters in the laboratory. However, in laboratory holding tanks, where predators are not encountered for a long time, they tend to shift to diurnal activity (Spanier *et al.*, 1988, 1990; Spanier & Almog-Shtayer, 1992). Microhabitat preferences have been determined for S. *latus* by providing lobsters with a variety of shelter designs in artificial reefs made of used car tyres (for a review of such studies, see Spanier & Lavalli, 1998). *Scyllarides latus* significantly preferred horizontally-oriented dens to vertically-oriented dens where light levels were higher. They also preferred shelters with small, multiple openings, like those between tyres, to those with larger entrances (in the tyres themselves). When additional 'back doors' were experimentally blocked, they stopped using these manipulated dens.

A tendency for gregarious sheltering among *S. latus* was observed in a survey of natural dens where 95% of lobsters cohabited with one or more conspecifics (Spanier & Almog-Shtayer, 1992). This gregarious behaviour was also observed in the laboratory and for very large lobsters (>100 mm CL), which differs from gregarious spiny lobster species where the tendency for cohabitation is greater in smaller and medium-sized animals (Spanier & Zimmer-Faust, 1988). Similar clustering behaviour was observed among *S. latus* in naturalistic habitats and with artificial shelters in laboratory tanks. In the absence of a predator, freshly caught laboratory-held lobsters significantly preferred and formed clusters under an opaque artificial shelter compared to a transparent shelter of the same shape and size. When they were supplied with no shelter but with shade, the lobsters concentrated under the shade (Spanier & Almog-Shtayer, 1992). When neither shelter nor shade was supplied, they showed distinct gregarious behaviour similar to the defensive 'rosette' observed in migrating Caribbean spiny lobsters under attack by a triggerfish (Herrnkind, 1980; Kanciruk, 1980; Herrnkind *et al.*, 2001). Gregarious sheltering of more than 50 *S. latus* individuals was observed by Spanier (personal observation) in a single, large, open cave at a depth of 30 m. However, field predation studies indicate that gregarious behaviour does not confer any advantage on individuals within the group who are under attack by fish predators. They suffer an equal amount of predation as do lone animals exposed to the same fish predators and gain only a small advantage of time, as predatory attack patterns are less focused when lobsters are grouped (Lavalli & Spanier, 2001). Reports of gregarious behaviour also exist for *S. nodifer* (Moe, 1991), but nothing is known about the function of such behaviour.

There have been some observations (both in natural habitats and laboratory settings) of specimens of *S. latus* sharing dens with the Mediterranean moray eel, *Muraena helena*, with no apparent predator–prey interactions between the fish and the lobsters (Spanier & Almog-Shtayer, 1992; H. Martins, personal communication). Sharing shelters with the moray eel may have mutual benefits: the octopus, *Octopus vulgaris*, is a prey of the moray eel and may be a predator of the lobster. Thus, by cohabiting, the lobster may be protected by a moray, which preys on octopus, and the moray eel may take advantage of any octopus attracted to the shared den by the presence of its prey – the lobster. However, this association needs to be further studied to elucidate any such mutualistic interaction.

The adults of most species are found on hard substrates (see Section 14.2.2). It is likely that *Scyllarides* spp. sampled both on hard and soft substrates derive from circumstances where lobsters that usually shelter in hard substrates were collected in soft substrates during their short- and long-term movements. Nevertheless, a few species have been reported only on soft substrates (e.g. *S. elisabethae*). Holthuis (1991) states that *S. elisabethae* seems to dig into the mud; he also mentions that *S. aequinoctialis* buries in the sand, although others report that this species is a reef dweller that shelters within coral rock caves and under coral heads (Moe, 1991). It is assumed that such digging into soft substrates is an anti-predator adaptation, similar to that seen in other lobster genera living long-term or temporarily on soft substrates. However, as Spanier and Weihs (1992) point out, the extremely flattened antennae of *Scyllarides* spp. have not been observed as a means by which to move soft sediments, but instead seem to play a hydrodynamic role in controlling swimming (see

Section 14.5.5) and in fighting conspecifics (see Section 14.5.1).

When held in captivity, even in large, naturalistic aquaria, *S. latus* ceased to show substrate preferences within two months, after initially spending significantly more time on rocky substrates (Barshaw & Spanier, 1994b). In contrast, Chessa *et al.* (1996) reported that in laboratory experiments, lobsters preferred rough artificial substrates (plastic carpet) over smooth ones only after having experience with each for some time. The rougher substrates allowed the lobsters to cling with their nail-like dactyls, which protects their vulnerable ventral surface from predators (see Section 14.5.3). Other than these two reports – one using natural structures and one using artificial structures, substrate preferences have not been well studied in other *Scyllarides* spp. and can only be inferred from areas where they are caught.

14.5.3 Predators and anti-predator behaviour

The response of slipper lobsters to predator attack has been well studied (Spanier *et al.*, 1988, 1991; Spanier & Almog-Shtayer, 1992; Spanier *et al.*, 1993; Barshaw & Spanier, 1994a, b; Lavalli & Spanier, 2001; Barshaw *et al.*, 2003) and consists of three strategies, two of which are typically executed in sequence: (1) the 'fortress strategy' in which the animal grasps the bottom and attempts to outlast its attacker's motivation to penetrate its hard shell (described in Barshaw *et al.*, 2003); (2) the 'swimming escape' response (described in Barshaw & Spanier, 1994a, b; Barshaw *et al.*, 2003; see also Section 14.5.5); and (3) remaining sheltered in dens (Spanier *et al.*, 1988; Spanier & Almog-Shtayer, 1992; see also Section 14.5.2). Lacking claws (like *Homarus* spp.) or long spinose antennae (like spiny lobsters; see Zimmer-Faust & Spanier, 1987; Spanier and Zimmer-Faust, 1988; Lozano-Álvarez & Spanier, 1997; Herrnkind *et al.*, 2001) with which to fend off swimming predators, slipper lobsters have developed a shell that is twice as thick and more durable to mechanical insult than clawed or spiny lobsters (Barshaw *et al.*, 2003). They use their short, strong legs to grasp the substrate and resist being dislodged (Barshaw & Spanier, 1994a, b). When this 'fortress defence' fails, they are exceptionally deft swimmers capable of evasive manoeuvres like barrel rolls (presumably using their flat, broad antennae like reciprocal aileron stabilisers on an airplane wing) en route to a shelter (Spanier *et al.*, 1991; see Section 14.5.5). Also they may suddenly change the direction of their swimming, presumably to confuse the chasing predator. This is an energetically costly response to a threat and is generally used as a last resort. It has been argued that slipper lobsters have matched the energy invested by clawed lobsters in claws, and spiny lobsters in antennae, by increasing only moderately the thickness of their shells and bettering their swimming escape behaviour (Barshaw *et al.*, 2003). This strategy appears to support a highly successful lifestyle, as slipper lobsters are the most diverse group of lobsters with nearly 80 species distributed worldwide (Booth *et al.*, 2005).

As demonstrated with *S. latus*, slipper lobsters also display a variety of shelter-related behaviours that provide a third highly effective survival strategy (Barshaw & Spanier, 1994a). By combining nocturnal foraging with diurnal sheltering, as well as carrying food to their shelters for later consumption, slipper lobsters may fully minimise their exposure to diurnal predators. Horizontally-oriented shelters supply shade and reduce visual detection by diurnal predators. Small shelter openings also supply shade and in addition, increase physical protection against large diurnal predators, especially fish with high body profiles, such as the grey triggerfish. Clinging may enable the lobsters to survive an attack inside a den and even in open areas. Multiple shelter openings enable escape through a 'back door' if a predator is successful in penetrating the den. They can then escape by using their fast tail-flip swimming capability (see Section 14.5.5). The tendency for cohabitation with conspecifics may be adaptive because of collective 'prey vigilance' and defence or concealment among cohorts ('selfish herd' response or the 'dilution effect' *sensu* Hamilton, 1971). If all else fails, their thick carapace, designed to effectively blunt cracks, may serve them in times of exposure to attacking predators.

The function of sheltering, as a predator-avoidance mechanism against diurnal fish was tested in a series of field-tethering experiments on *S. latus*, by Barshaw & Spanier (1994b). Tagged lobsters were tethered with monofilament line inside and outside an artificial reef. All predation events occurred only during the day. Predation by the grey triggerfish, *Balistes carolinensis*, a high-body-profile, large, diurnal fish, was significantly less on lobsters tethered in the reefs compared to those tethered in open areas. The lobsters tried to cling to the substrate relying on their armature and lack of movement to protect them. Because the lobster could not tail-flip to some shelter, the fish was eventually able to turn the lobster over and consume it by biting through its thinner, vulnerable ventral surface.

Besides the triggerfish, sharks (e.g. the spotted gully shark, *Triakis megalopterus*) have been reported to feed on *S. elisabethae* in South Africa (Smale & Goosen, 1999), dusky groupers (*Epinephelus guaza*) have been reported as predators of adult and juvenile *S. latus* (Martins, 1985a), and red (*Epinephelus morio*) and gag grouper (*Mycteroperca microlepis*) have been reported as predators of *S. aequinoctialis* and *S. nodifer* (Lyons, 1970). Combers (*Serranus* spp.) and rainbow wrasse (*Coris julis*) apparently prey on juvenile *S. latus* (Martins, 1985a).

Fig. 14.9 External sperm mass on *S. latus* female (arrows) (from Bianchini & Raisa, 1997).

14.5.4 Mating behaviour

Because scyllarids copulate, spawn and brood readily in the laboratory, some aspects of their reproductive biology are known; however, less is known of the actual mating behaviour or the rituals involved during the mating process. Males produce white, gelatinous spermatophores, which they carry around on the base of their fourth and fifth pereiopods (Almog-Shtayer, 1988; E. Spanier, personal observations). These are transferred externally to females. It is not clear whether females retain the spermatophores externally and fertilise their eggs externally, or whether they somehow manipulate the spermatophore and store it internally. In some species, females have been observed carrying spermatophores externally for 6–10 days or less prior to egg extrusion (*S. latus*, Martins, 1985a; Almog-Shtayer, 1988; Fig. 14.9), while in others, the lack of observable spermatophores prior to egg extrusion has led to a belief that the spermatophore is stored internally and fertilisation is internal (*S. nodifer*, Lyons, 1970; *S. squammosus*, DeMartini *et al*., 2005). Females of most species can spawn multiple broods in a season due to short brooding periods (but see Hearn *et al*., 2006 for a contrasting view, in which *S. astori* broods once annually), and these broods are usually carried during spring and summer months. Only in *S. latus* have both eggs and spermatophores been observed simultaneously (Almog-Shtayer, 1988). It is possible, but so far not known, that different species of *Scyllarides* employ different strategies for fertilisation.

14.5.5 Movement patterns

Slipper lobsters demonstrate two modes of movement: (1) slow, benthic walking movements that may be nomadic within a small home range, or migratory from inshore, shallower waters to offshore, deep waters and (2) swimming movements that can be used for rapid escape or, as some have suggested, for vertical movements in the water column.

Daily and seasonal horizontal patterns

Tagging studies of *S. latus* off the coast of Israel indicate that they also may demonstrate two annual patterns of movement: local nomadic movements made while inshore and migratory offshore movements. Three hundred and fourteen lobsters caught at an artificial tyre-reef complex were tagged between the carapace and the abdomen, using numbered spaghetti tags (Spanier *et al.*, 1988). Lobsters were also marked by puncturing small holes in the telson and were released at their site of capture. In a later phase of this study, they were also tagged between the third and fourth abdominal segments. Thirty-two percent were recaptured at least once, 9% were recaptured twice and 2.6% were recaptured three times. All but 3% of the recaptured tagged lobsters retained their spaghetti tags. These remaining 3% were identified by the holes punctured in their telsons or the scars left by these holes after moulting. However, a later laboratory study of tag retention in these lobsters (Spanier & Barshaw, 1993) found that only 40% of the animals retained tags, positioned between the carapace and abdomen, after moulting. Since most of the field lobsters in the first study were tagged in this anterior position and the scars of the holes disappeared after 2–3 moults, many individuals may not have been properly re-identified. During the inshore lobster season (February to June in the south-eastern Mediterranean), lobsters left their shelters at night to make short-term movements to forage and bring back food (mostly bivalves). More than 71% of tagged lobsters were repeatedly recaptured in the artificial reef site during the season. Time between repeat captures was 1–17 weeks (mean 29 days) and this rate probably represents short-term movements for foraging or local nomadism (Spanier *et al.*, 1988).

In contrast, only 7.2% of the tagged lobsters were recaptured in the same man-made shelter site after more than half a year. Time between these captures ranged between 10–37 months (mean 338 days) and may represent long-term movements or migration. Returning lobsters have to orient and locate the small artificial reef site in the widespread continental shelf. Due to limited cooperation with local fishermen, only 11 tagged lobsters were reported outside the artificial shelter site. Divers caught six about 300–800 m off the reef site. Fishermen caught the rest in the late part of the summer, 2–3 months after tagging, 20–35 km north of the site and at depths greater than 50 m (Spanier *et al.*, 1988).

For several years, a seasonal survey of all lobsters was conducted in the above-mentioned artificial tyre-reef complex (Spanier *et al.*, 1988). Lobsters appeared in the reefs in early winter (December–early February), with their numbers peaking in the spring (March–May). From June onward, their numbers decreased in the shallow part of the continental shelf and they disappeared from shallow water in August–September to the beginning of the following winter. This seasonality correlates with water temperature. They appear in the shallow part of the continental shelf (15–30 m depth) when water temperatures are the lowest for the south-eastern Mediterranean region (15–16°C) and their numbers decrease when water temperatures increase to 26–27°C (Spanier *et al.*, 1988). A similar trend is seen in the yield of the commercial fisheries off the Mediterranean coast of Israel.

Several traps set offshore, off-season and at a depth of 48 m, caught lobsters in October. Water temperature at these trap sites, was 23.6°C while in the much shallower artificial reef site at 18.5 m, where no lobsters were detected, it was 27.7°C. Also, lobsters were caught during the fall at depths greater than 50 m by a rough bottom trawl (Spanier *et al.*, 1988). This limited information suggests that slipper lobsters off the coast of Israel seasonally move to deeper and more northerly waters (i.e. colder water). By migrating, the colder-water lobsters may avoid the high, and perhaps unfavourable, summer and autumn temperatures in the shallow waters of the Levant basin of the Mediterranean. Today these temperatures may rise as high as 31°C, which may cause moulting difficulties or abnormalities (also reported by Spanò *et al.*, 2003). Some lobsters kept in the laboratory with ambient water supply in the fall died while moulting or only incompletely moulted. This happened after they were exposed for over two months to water temperatures of 26°C and higher (E. Spanier, personal observations). Thus, one possible function of the seasonal shallow-to-deep migration may be to meet physiological and behavioural requirements for moulting. Moulting in deeper habitats may also be a predator avoidance strategy during this vulnerable period. Berry (1971) pointed out that while most spiny lobsters are associated with hard substrates that supply shelters, some deep-water species appear to exhibit behavioural adaptations for soft substrates, perhaps because of fewer predators in greater depths. Slipper lobsters could switch to soft bottoms at greater depths for the same purpose.

Of 115 *S. latus* tagged by Bianchini *et al.* (2001) in 1995–1997, 29 individuals were later recovered up to 70 weeks after tagging. One tagged female was caught by a trammel net, after being 1575 days at large, at ~5 km from the place of release. Contrary to the findings of Spanier *et al.* (1988), the recurrence of tagged specimens during every period of the year, at least in Sicily, reduces the possibility of widespread seasonal horizontal migrations, although some specimens might displace vertically. In a mark–recapture programme in the Galapagos Islands, Hearn *et al.* (2006) reported that of a total of 1926 *S. astori* tagged and released back into the wild, 116 (6%) were recaptured and reported by the local fishers. No information was reported on distances between release and capture locations; thus, it is unknown whether *S. astori* migrates to deeper water to moult, or simply behaves in a more cryptic fashion during this vulnerable period (as reported for *S. latus* by Spanier *et al.*, 1988).

Returning slipper lobsters seem to be capable of shoreward homing movements to return to the artificial reef site. The advantage of this homing ability is obvious. Most of the continental shelf off the Mediterranean coast of Israel is flat. Natural rocky outcrops that supply shelters with the physical parameters preferred by lobsters constitute a very small portion of the shallow shelf. Thus, it may be advantageous for lobsters to 'recall' these preferred natural or artificial sites and to return to them after short- as well as long-term movements. It seems that they just walk, or walk and swim relatively long distances. The mechanism by which the Mediterranean slipper lobster orients and locates these preferred habitats is completely unknown. They may use some geomagnetic cues or magnetic maps, as has been reported for spiny lobsters (Lohman, 1984, 1985; Boles & Lohman, 2003). Lohman (1984, 1985) found magnetic remenance in the Western Atlantic spiny lobster, *Panulirus argus*, along with the ability to detect geomagnetic fields, while Boles and Lohman (2003) demonstrated that spiny lobsters could orient homeward and navigate without any cues from their outbound, displacement trips.

Swimming behaviour (vertical movements)

In mechanical terms, tail-flip swimming in crustaceans constitutes locomotion in which a single 'appendage' – the abdomen – produces thrust by a combination of a rowing action and a final 'squeeze' force when the abdomen presses against the cephalothorax (Neil & Ansell, 1995). Although the tail-flip response is known in adults and juveniles of all three major taxonomic groups of lobsters (e.g. Jacklyn & Ritz, 1986; Newland & Neil, 1990; Newland *et al.*, 1992; Jeffs & Holland, 2000), as well as in other crustaceans, it is best developed in slipper lobsters. Tail flipping is first developed in the nisto phase, where it can vary among species in strength (Robertson, 1968; Lyons, 1970; Higa & Saisho, 1983; Barnett *et al.*, 1986).

The hydrodynamics of swimming in slipper lobsters has been well studied in *Ibacus peroni*, *Thenus orientalis* (Ritz & Jacklyn, 1985; Jacklyn & Ritz, 1986), and *Scyllarides latus* (Spanier *et al.*, 1991). Although there is information for other types of slipper lobsters, this discussion will focus solely on what is known about *Scyllarides* swimming. *Scyllarides latus* uses a 'burst-and-coast' type of swimming (see Weihs, 1974) in response to a predator (triggerfish) or harassment from divers. Large amplitude movements of the tail propel the lobster quickly backwards, with periods of acceleration reaching top velocities of three body lengths per second; these movements are followed by periods of powerless gliding, decelerating to velocities of less than one body length per second. The force per tail beat ranges between 1.25 to more than 3.00

newtons and correlates with body length because additional force is needed to move the greater mass of larger animals, rather than to increase speed and acceleration. The intermittent fast-escape swimming is only of short duration and does not appear to be used for foraging or long-range movements; instead it is an emergency response, whereby the animal invests considerable energy resources to reduce its exposure time in the open area until it can reach safety. Spanier and Weihs (1992) suggested that the flattened second antennae of *S. latus* (mistakenly called ‘shovels’ or ‘flippers’), with their movable joints, play an important hydrodynamic role in controlling the swimming movement. Essentially, they serve as stabilisers and rudders in ‘take-off’, acceleration, gliding, turning, and landing. Significant lift is created during backward tail flips and articulation of the flattened first antennae (aka ‘rudders’) alters the distributions of this lift so that pitching and rolling movements are possible. In contrast, spiny lobsters found in similar habitats and ranges (e.g. *Jasus edwardsii*), produce a negligible amount of lift during each tail flip and do not possess antennae that were shaped or positioned properly to control any created lift. As a result, spiny lobster tail flips are not efficient for continuous swimming or manoeuvring (Ritz & Jacklyn, 1985; Jacklyn & Ritz, 1986). Neil and Ansell (1995) compared data of swimming performance for a number of decapod, mysid, and euphausid crustaceans. Maximum velocity of body movement achieved during the tail flip is similar across the adults in each group, and ranges from 10 mm to 300 mm body lengths, although this represents a 30-fold difference in the velocities expressed as body lengths per second. *S. latus* is ranked as the fastest of those tested, with a maximum velocity of close to 1 m per second compared to 0.6 m per second in the clawed lobster *Nephrops norvegicus* (Newland *et al*., 1988).

In a more recent analysis, Spanier and Weihs (2004) identified the contribution of the tail as propulsor, legs as landing gear, and second antennae as control surfaces. They also examined secondary hydrodynamic effects of carapace curvature and the longitudinal ridge associated with vortex production and control. A possible function has been postulated for this ventrolateral curvature (keel) of the lobster carapace. It may be similar to the scale armature of rigid-body boxfishes. In a detailed study of these fish, Bartol *et al.* (2002) found that the ventral keels produce vortices that serve to stabilise motion, resulting in a smooth swimming trajectory. Is this the case for slipper lobsters too?

The carapace and abdomen of slipper lobsters, like those of other decapod crustaceans, are covered with stiff, presumably mechanosensory hairs (Fig. 14.10). In slipper lobsters, this basic pattern shows two distinct elaborations. First, the hairs are arranged in groups of 7–12 on small islands of hard, protruding cuticle (about 500 islands are present on the carapace, depending on the species). Second, this pattern continues out onto the surfaces of the flattened antennae to the extent that the antennae, when extended, appear to form a continuous surface with the carapace. These structures are likely to serve a hydrodynamic sensing role during the swimming escape response and may provide important sensory feedback for the lobster while swimming. However, the sensory modalities involved in swimming remain largely unknown.

14.6 Diseases

Scyllarides specimens become ill occasionally and die in the laboratory from as yet unknown causes. Lobsters caught in the field that have not moulted recently, are covered by barnacles, vermetid worms, and other bio-fouling agents. Yet there are only a few reports on diseases or parasites of slipper lobsters in general, and of *Scyllarides*, in particular (eg. Bianchini & Raisa, 1997). This limited information is covered in Chapter 5.

14.7 Harvest of wild populations

While *Scyllarides* spp. are large, and thus preferable for human consumption, only a few species support fisheries (Williams, 1986; Holthuis, 1991). *Scyllarides astori* (Holthuis & Loesch, 1967), *S. deceptor* (Ramos, 1951), *S. delfosi* (Opresko *et al*., 1973), *S. elisabethae* (Fischer & Bianchi, 1984), *S. roggeveeni* (Holthuis, 1972), and *S. tridacnophaga* are usually consumed if caught, but

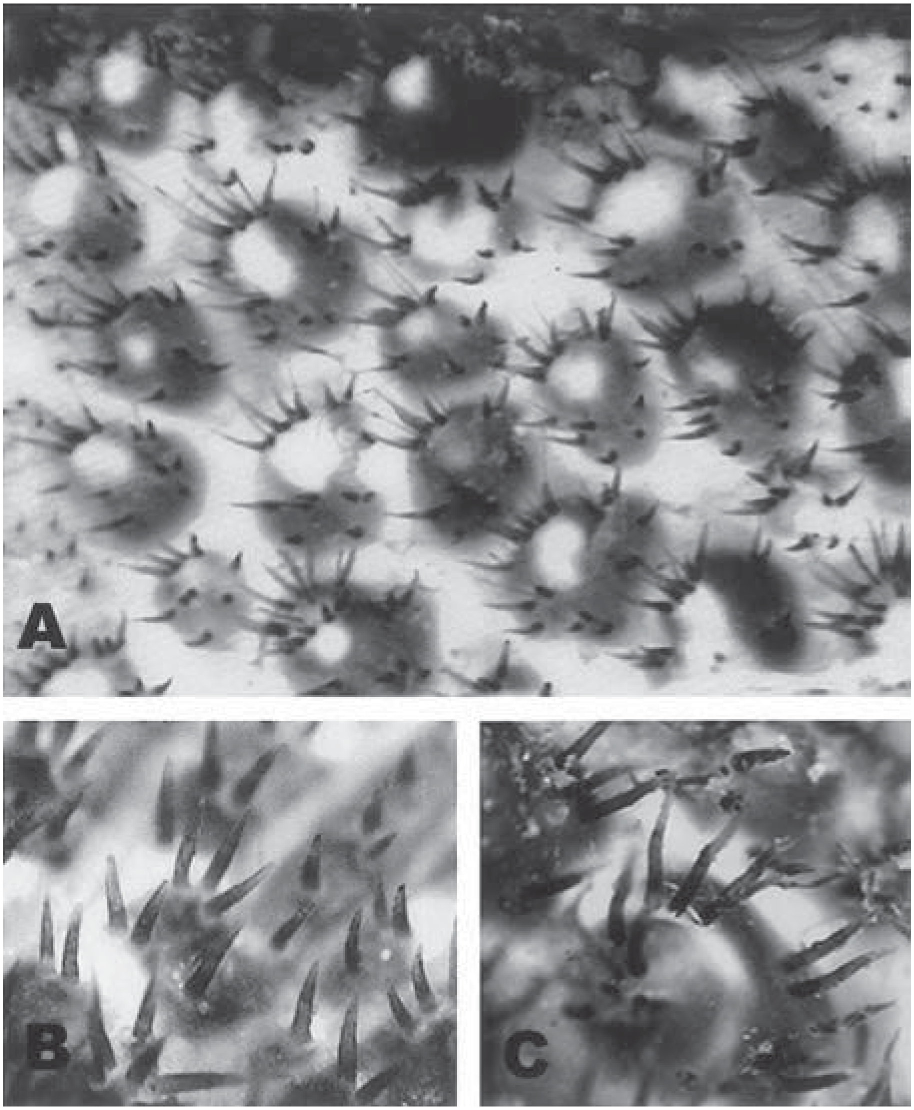

Fig. 14.10 Setal tufts found covering the surface of the scyllarid (*S. latus*) carapace. (A) setal tufts of tubercles; (B) arrangement of setae (likely cuspidate or simple setae) within carapace tufts; (C) single tuft, showing distribution of setae around tubercle.

they are fairly rare and support no commercial fisheries. Those that are captured are typically taken as by-catch of trawling operations (Rudloe, 1983) or in trammel nets (Holthuis, 1991). The more common or more highly esteemed species may or may not support commercial fisheries. For example, Holthuis (1991) reported that while *S. aequinoctialis* is eaten throughout its range, its meat is not considered of high quality, particularly when compared with the more popular sympatric palinurid species, *Palinurus argus*. However, Moe (1991) reported that due to the large size of *S. aequinoctialis* and its sweet meat, it is highly valued by fishermen and supports a small pot fishery in Puerto Rico; it is also taken elsewhere in the recreational fishery for spiny lobsters. In contrast, *S. brasiliensis* (Fausto Filho *et al.*, 1966; Freitas & Santos, 2002), *S. haanii* (Holthuis, 1991), *S. herklotsii* (Fischer *et al.*, 1981), and *S squammosus* (Fischer & Bianchi, 1984) are fished and highly regarded as food, but they do not necessarily support a target fishery – instead they are caught incidentally in other pot fisheries (particularly spiny lobster pot fisheries) or by hand (by divers) and sold fresh in markets. Part of the problem in fishing these less commonly-taken species lies in understanding the effects of various trap configurations (shape/design, weight, presence of floats, movability in stormy weather, etc.) on the trapability of the lobsters, particularly if they regularly engage in both horizontal and vertical movements (O'Malley, 2004). In some species, traditional spiny lobster traps are ineffective, due to the specific sheltering preferences of many species (see Section 14.5.2). For example, *S. nodifer* is typically not caught in spiny lobster traps and is taken by trawl; however, a modified den type trap, covered in durable black polyurethane successfully captures this species (Anon., 1983; Moe, 1991). *Scyllarides squammosus* seems to be easily trapped in 'Fathom Plus' round pots in both the Hawaiian Islands and in Queensland, Australia (Sumpton *et al.*, 2004). Many of these other, less exploited species may prefer a trap that mimics their natural den configurations, but this has not been adequately tested for any species other than *S. nodifer.*

Hearn *et al.* (2006) report that as spiny lobster and sea cucumber populations have declined due to overfishing around the Galapagos Islands, pressure is now increasing to specifically target *S. astori* populations, with the result that landings have increased (Martínez *et al.*, 2002; Molina *et al.*, 2004) and a fishery may develop in the near future. *S. astori* are currently caught as by-catch in the spiny lobster fishery or by divers with surface-supplied air (hookah system) at times when the sea cucumber fishery is non-active (Hearn *et al.*, 2006). There is also an effort underway to develop a fishery in Queensland, Australia targeting both *S. squammosus* and *S. haanii.* A trial fishery comprised of only a few licensed boats has been operating since 1998, has landed less than five tonnes annually, and has been collecting fishery-dependent data which is not currently available to the public due to agreements between the government and the fishing industry (Sumpton *et al.*, 2004). Whether it develops more fully or, if developed, remains sustainable, is not predictable as little biological data is available for these species. For example, in Hawaii, the lobster fishery for *Panulirus marginatus* captured *S. squammosus* in equal numbers (Polovina *et al.*, 1991). As a result, minimum harvestable sizes were established for *S. squammosus* (based on spiny lobster parameters) and several studies were conducted on the shape of trap vents to reduce the capture of sublegal adults (Everson *et al.*, 1992; Parrish & Kazama, 1992). Even with these measures in place, the fishery for *S. squammosus* in Hawaii was closed in 2000 because it was not sustainable (DeMartini *et al.*, 2005). Currently, only three species appear to support targeted seasonal fisheries: *S. nodifer* (Hardwick, 1987), *S. latus* (Holthuis, 1991), and *S. obtusus* (Holthuis, 1993).

14.7.1 **Scyllarides nodifer** ***fishery***

The fishery for *S. nodifer* began in the 1980s and is basically a trawl fishery in the Gulf of Mexico in 'hang-free' corridors where trawls are less likely to be caught on rocks and damaged (Hardwick, 1987). Most of the fishers involved in this fishery are shrimpers (B. Sharp, personal communication). In the 1980s, approximately 500 lobsters could be taken each night during spring and summer months, which corresponded to this species' spawning season (Moe, 1991). These 'hang free' corridors support repetitive trawling, leading Hardwick (1987) to estimate the population of these lobsters as 6.14 million individuals. Additional fisheries for this species have opened in the Florida Keys, conducted by divers for the aquarium trade (B. Sharp, personal communication). *Scyllarides nodifer* is also taken as by-catch in *P. argus* pots in the Florida Keys, but not in great numbers. Because *S. aequinoctialis* is sympatric with *S. nodifer*, it is often taken as by-catch of the ridge slipper trawl lobster fishery, but is not nearly as numerous (Moe, 1991).

14.7.2 Scyllarides latus *fishery*

Scyllarides latus has been exploited throughout its range in both the Mediterranean and Atlantic for some time (Spanier & Lavalli, 1998), with negative repercussions for the size structure of the population and the population sizes (Maigret, 1978; Martins, 1985a; Lewinsohn & Holthuis, 1986; Spanier, 1991; Bianchini *et al*., 1996). Atlantic populations have suffered the greatest decline in both population numbers and size structure – at one time, lobsters captured typically weighed 1–3 kg (Saldanha, 1979; Bianchini *et al*., 1996), now they range in weight from 200 g to 1.5 kg (Bianchini *et al*., 1996). Pots baited with bivalves and diving (with hand collection or spearing) are both used as capture methods (Spanier & Lavalli, 1998).

14.7.3 Scyllarides obtusus *fishery*

Scyllarides obtusus has been misidentified and confused with *S. latus*, *S. elisabethae*, and *S. herklotsii* (Holthuis, 1993), but it is a species endemic to Saint Helena where it has sustained a fishery for over 400 years. The fishery is mostly active between November and March and is accomplished with traps baited formerly with albacore (*Thunnus alalunga*) and currently with other fish species (typically tuna, *Thunnus* spp., or skipjack, *Katsuwonus pelamis*) set at about 27 m depth (Edwards, 1990). Catches average about 1.3–2.2 kg per pot, with an average live weight of 1.15 kg (Edwards, 1990).

14.7.4 Fishery concerns

Unfortunately, and because of the limited numbers of slipper lobsters taken around the world compared with spiny lobsters, almost no regulations exist for exploited *Scyllarides* populations. Where they do exist, they protect berried females and may impose minimum legal sizes (e.g. Florida for *S. nodifer*; Hawaii for *S. squammosus*; Galapagos Islands for *S. astori*; Queensland, Australia for *S. squammosus* and *S. haanii*). However, imposition of these minimum legal sizes is often based on no data, or as in the Hawaiian fishery for *S. squammosus*, is based on spiny lobster size parameters rather than slipper lobster size parameters (DeMartini & Kleiber, 1998). Little work has been done thus far on trying to determine size at sexual maturity, taking into account the difference between physiological maturity (where a lobster might be capable of reproduction, but does not reproduce) and functional maturity (where the lobster is reproductively active) (DeMartini *et al*., 2005). Because unberried but mature slipper lobster females may be indistinguishable from immature females on the basis of gross morphological features, such as those used for assessing spiny lobster maturity (changes in the number of pleopod setal number, relative length of abdominal and thoracic segments, or proportional lengths of pereiopod segments at the pubertal moult), a tool needs to be developed to assess maturity in the field. Thus far, only in *S. squammosus* has such a tool been developed (DeMartini *et al*., 2005) – a relative pleopod (exopod) length to tail (abdomen) width relation that is verified as highly accurate with histological examination of ovary condition. Without knowledge of the population's size structure and the size at maturity, any population targeted for a fishery is at risk of over-exploitation. Such over-exploitation has occurred with *S. latus*, such that fishing bans are now in effect for populations in the Azores and Italy, and marine parks/reserves have been declared in specific areas off Israeli waters (Spanier & Lavalli, 1998). Similar overfishing could occur in species that have limited ranges and spawning grounds (e.g. *S. nodifer*, *S. astori*, and *S. obtusus*). Recognising these problems, developing fisheries for other *Scyllarides* species are attempting to address issues of seasonal closures and minimum landing sizes before problems arise (e.g. *S. astori* fishery, Hearn *et al*., 2006; *S. squammosus* and *S. haanii* fisheries in Queensland, Sumpton *et al*., 2004).

14.8 Aquaculture and restocking

Few scyllarid species have been cultured from larvae to nisto (Sekiguchi *et al*., 2006), but no *Scyllarides* species has been among those so cultured. Although specimens of *Scyllarides* spp. readily reproduce and carry eggs in the laboratory (e.g.

Martins, 1985a, b; Almog-Shtayer, 1988; Bianchini *et al.*, 1998; Spanier *et al.*, 1988), the long duration of the larval stages along with a lack of understanding of their dietary requirements, proper thermal, salinity and light–dark regimes, and hydrodynamic design of rearing tanks has curtailed aquaculture attempts (Sekiguchi *et al.*, 2006). In addition, aquaculture of juveniles has also been difficult because they are not readily collected in the wild. Only Rudloe (1983) attempted to raise *S. nodifer* from trawl-collected juveniles. She maintained the animals, with mean CL of 45 mm, in a large circular tank supplied with filtered, natural seawater. Live bivalves were, as in other *Scyllarides* spp., the preferred food. No problems of diseases, malnutrition or water quality were encountered. Growth increments per moult ranged between ~20% of CL for animals of 20–40 mm CL to ~3% in animals of 80–100 mm CL. Intermoult intervals ranged between three weeks and three months. On the basis of these data, growth from postlarvae to 300 g was hypothesised to require 9–10 moults over an 18 month period.

A small restocking experiment of *S. latus* was initiated in Sicily (Bianchini *et al.*, 1998, 2001). Since juveniles were not available, only a few hundred adults were tagged and released to the benthos one by one by scuba divers. Many of these animals were recaptured, suggesting that predation upon adult *S. latus* was minimal. Because genetic comparisons of this species from different areas in Sicily (Bianchini *et al.*, 2003) show little variability among individuals, non-local breeders might be used for restocking without harming biodiversity. The current decline of the *S. latus* resources seems to be due to a shortage in recruitment rather than to environmental degradation, thus Bianchini *et al.* (1998) suggest that proper habitats, now depleted of *S. latus* in Sicily, could be recolonised with great success by restocking adults.

14.9 Summary

Although the body of knowledge on lobsters of the genus *Scyllarides* has increased considerably in the recent few decades, a considerable gap still exists for this taxon compared to taxa within the clawed and spiny lobster genera. Most information focuses on a single species of the *Scyllarides* – *S. latus*, but even so, there is no information on the biology and ecology of larvae or juveniles and very little information on the adults. Although many of the *Scyllarides* species are increasing in commercial importance, fisheries statistics are incomplete or altogether absent. Many of the species have been exploited for decades and may even be overexploited. Increasing fishing pressure occasionally accelerates research on species, as is the case of *S. astori* in the Galapagos Islands; however, it endangers the existence of the populations in many habitats. There is an urgent need for more research on all aspects of the biology of this genus, particularly that concerning moult and growth, reproduction, and incidence of disease. Better knowledge concerning distribution of larval stages, settlement areas of nistos, and ecology of juveniles would be helpful for gaining an understanding of factors influencing recruitment into adult populations. The results of such future studies may enable the development of proper management tools for sustainable utilisation of this potential marine resource.

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Chapter 15

Conclusions

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In editing this volume I have read each of the chapters at least twice. The thing that astounds me is the level of research activity being conducted around the world on this group of animals. Some of this research is due to the animals being the subject of studies by students at university level for their postgraduate degrees, but the majority of research is being undertaken because of the commercial importance of lobsters. I recently published a review of this subject entitled 'Lobsters: the search for knowledge continues (and why we need to know)' (Phillips, 2005) but the demand for knowledge does not abate and the range of information that is needed becomes wider every year.

This book provides a comprehensive review of marine lobsters. All of the chapters are as up to the moment as possible, but there is new material published every day. A special feature of lobster researchers all over the world is that they meet approximately every four years for in-depth presentations and discussions and the venue moves from country to country. Such meetings include biologists, economists, managers and government and industry representatives. While we were preparing this book, a two-volume work was published in New Zealand by the New Zealand Journal of Marine and Freshwater Research (2005), presenting the papers selected for publication from the Proceedings of the 7th International Conference and Workshop on Lobster Biology and Management, held in Hobart, Tasmania, Australia in 2004.

We have attempted to capture the major outlines of this material in this book (and naturally almost all the authors of the chapters of this book attend these meetings), but it indicates the level of worldwide interest in this group of animals. This interest is not just among scientists. There is a wide range of publications which publish research, economic and other information on lobsters, ranging from that of Griffiths *et al*. (2004), to the July 2005 issue of the respected magazine 'Seafood International' which featured the global lobster industry.

The biological sustainability of the lobster populations which are the basis of the commercial fisheries, has been the principal area of interest of scientists, managers, governments and fishers for a very long time. Today, new ideas aimed at increasing the product value of the landed catch by adding range diversification and reducing the costs of its capture are developing. The recent rapid escalation of the cost of fuel for the vessels used in the capture of lobsters has been a major stimulus for these ideas. Bio-economic models are being developed and these are becoming increasingly complicated as more social and environmental issues are included.

Perhaps the greatest challenge which has developed in recent years, which both scientists and managers are now facing, is the demand for management not only of the populations of lobsters, but also of the ecosystems supporting them. At this time it has been more a case of endorsement of the acceptance of the idea of ecosystem management, rather than a serious tackling of the allocation of resources, the collection of the data needed for this purpose, and the development of the new models needed to analyse the information. However, some progress is being made and a model to examine recruitment in degraded habitats of the Florida spiny lobster *Panulirus argus* has been developed (Butler *et al*., 2005).

The Western Rock Lobster Fishery in Western Australia is claimed to be an example of a successfully-managed lobster fishery (Phillips & Melville-Smith, 2005). It is well positioned through the efforts of many years of collaborative management, supported by well-directed research and monitoring programmes, such that it will be able to enjoy future prosperity. Currently, the sustainability of the stock is not in doubt as the 2003/04 catch is predicted, based on the level of puerulus settlement four years ago, to be at least 13 000 metric tonnes, near to the highest recorded catch (Phillips & Melville-Smith, 2005). In recent years the fishery has had to weather global issues such as the terrorist attacks of 11 September in the USA, a slow economic recovery in major far eastern markets, and most recently the SARS virus. This has raised economic concerns and stimulated attempts to develop new markets (Department of Fisheries, 2001). However, while some future questions in the rock lobster fisheries have been identified, it is inevitable that other unforeseen issues will arise, as fisheries sustainability is a dynamic process. The challenge for fisheries researchers, managers and industry, is to have the foresight to identify these potential problems and to have the means and ability to address them.

One of the most interesting occurrences in the lobster world has been the near doubling of the catch of the clawed lobster, *Homarus americanus*, between 1992 and 1999 (ASMFC, 2000). There are many theories about the reason for this increase and it has generated extensive review of the data on the fishery (Steneck & Wilson, 2001), but as pointed out by Fogarty (1995), 'long term monitoring of critical life history phases must be undertaken if we are to understand the regulatory mechanisms controlling these populations'. An example of an unforeseen circumstance in the *H. americanus* fishery is a recent disease outbreak. A wasting disease, shell disease, is affecting lobsters in Long Island Sound (New York and Connecticut) and fishers are concerned that it is due to the effects of insecticides (Phillips, 2005). It occurs at a significant incidence as it is affecting population dynamics by changing natural mortality rates (S. Cobb, personal communication).

Two areas of new significance reported in this book, which can affect lobster fisheries, are aquaculture and the establishment of marine protected areas. Lobster aquaculture has been a dream of many people for a long time. Studies on *H. americanus* have resulted in the production of a detailed CD of data needed for the process (Goldstein & Bartko, 1999). Spiny lobster aquaculture is in the developmental stage and is a fertile area for research activity (see Chapters 10–12). The number of lobster species being examined for suitability for culture or enhancement is large. They include *Jasus edwardsii*, *Sagmariasus verreauxi*, *Panulirus ornatus*, *Homarus gammarus*, *P. argus*, *P. japonicus*, *P. cygnus*, *P. interruptus*, *Palinurus elephas* and *P. homarus* among others (Phillips & Liddy, 2003). A new development in lobster research is that only a little of the research on aquaculture of spiny lobsters is being published as it is considered 'commercial in confidence'.

Marine protected areas are definitely a popular topic and there are numerous discussions taking place as to their suitable size, location, purpose, monitoring of effectiveness, etc. This includes areas which have lobsters and therefore by definition generally excludes fishing, either commercial, recreational, or both. Lobster fisheries have therefore a direct interest in marine protected areas. Before a decision in support or rejection of a particular area for a reserve is made, a lot of information is required. An excellent study by Lipcius *et al.* (2001) sheds interesting light on the degree of success in selection of these areas for *Panulirus argus* that would yield a 50% chance of increasing recruitment of this species.

Ehrhardt (2005) has pointed out that *P. argus*, the most prolific spiny lobster in the Caribbean region, is typical of spiny lobster species and is highly resistant to fishing pressure. This is because of its high population fecundity, the long persistence of the larval stages in the open ocean currents, and their resilience to predation. *P. argus* in the Caribbean has yielded an average catch of about 38 000 metric tonnes over the last 20 years, worth an estimated US$456 million annually. This has occurred despite most local fisheries reaching full or over-exploitation levels. The current levels of exploitation are not sustainable and a change in both minimum size of capture and its enforcement are recommended to achieve sustainability. Unfortunately, based on past history this seems unlikely to be achieved, so we will be watching the fisheries in this area with great interest.

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