AQUATIC INSECTS

Challenges to Populations

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Challenges to Populations

Proceedings of the Royal Entomological Society's 24th Symposium

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Preface

It is customary in the preface or introduction of a book to stress the importance of the subject matter, in order to justify the publication and to encourage readers on to the main text. One of the problems with this is the overuse, and consequent devaluation of 'importance' (Brooker *et al*., 2005). As far as aquatic insects are concerned, we feel that little justification for having an interest in this group is necessary. Their persistent presence in the Earth's fauna (>300 million years since insects invaded aquatic habitats), their numerical dominance in contemporary freshwaters (and some saline waters), and the diversity of roles they perform in aquatic ecosystems speak for the importance of the group. In an academic context, aquatic insects have served as model systems for the development of understanding of many aspects of insect physiology, behaviour, ecology and evolution, so there are many aficionados of this group.

The papers in this book were presented at the 24th International Symposium of the Royal Entomological Society, which was held at the University of Edinburgh, UK, in July 2007. The title of the symposium and this book, *Aquatic Insects: Challenges to Populations*, reflects an unashamed bias of the editors towards processes acting at the population level, but the book's content takes a very broad view of populations. In planning the symposium, our aim was to bring together key workers in diverse fields, to take an integrated view of the challenges facing aquatic insects and to foster a broad appreciation of the links between subject areas that can lead to deeper understanding. It is easy and comforting to stay within the relatively narrow confines of one's own discipline or area of interest, but the greatest prospect for progress and new ideas often comes through discovering connections between apparently unrelated ideas. Thus, this book considers some of the potential influences on individuals and populations (e.g. environmental stresses, parasites, cannibalism, dispersal limitations), the 'cunning tricks' used by aquatic insects to overcome challenges (e.g. polarization vision, life-history strategies, osmoregulation, cold hardiness) and the consequences of those challenges at different levels of organization (e.g. distribution patterns, population structure, population genetics, evolution). Similarly, the set of papers encompass many taxa and all life stages of aquatic insects, not just the ‘aquatic’ stages. It is impossible, in one book, to provide exhaustive cover of all the challenges to populations, and though this set of topics may seem eclectic, we hope it provides a thought-provoking sample. During the symposium, we hoped that the presentations would spark new ideas and synergisms; they certainly sparked conversation! Similarly, we hope that readers will take the opportunity to read multiple chapters and find inspiration for their own work, or simply a wider appreciation for the wonders of aquatic insects.

It is also customary in the preface of a book to acknowledge the people who often work behind the scenes but, without whom, the book never would have existed. We would like to acknowledge our co-convenor of the symposium, Craig Macadam, who was instrumental in getting us involved in the first place, and contributed equally to the success of the meeting. We were also heartened by the eagerness with which the speakers (and subsequent authors) accepted our invitations and by their promptness in producing the required manuscripts. All those who attended the meeting also contributed to its success, and to much lively debate and discussion. Those who agreed to review chapters are also acknowledged for their insightful and constructive comments, which improved the final volume immeasurably.

We would also like to thank the Royal Entomological Society who provided the generous funding, which enabled the meeting of a truly international, and very high quality, set of speakers. Bill Blakemore, Registrar of the Society, and its other staff and officers provided invaluable assistance with the organization of the meeting and the flow of funds. Last, but most certainly not least, we thank Graham Stone (University of Edinburgh) and his team who did so much to ensure that the symposium ran smoothly.

Jill Lancaster
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Aquatic Insect Adaptations to Winter Cold and Ice

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Abstract
Most aquatic habitats in cold regions are frozen or covered by ice during winter. Aquatic insects survive these cold and icy conditions by a variety of adaptations. Different species move seasonally between habitats, choose particular overwintering sites, modify local conditions by constructing shelters, and withstand the effects of ice break-up and flooding during the spring thaw. Limited data indicate that several kinds of aquatic insects withstand subfreezing temperatures while surrounded by ice. Some of these species supercool and others tolerate freezing. A review of the available information in the context of recent discoveries in insect cold hardiness suggests fruitful avenues for research, including the roles of dehydration and of antifreeze proteins. Also required is study of the cold hardiness of individual species in relation to habitat conditions, seasonal movements and mechanical protection by overwintering structures. We need even basic information about the production and interaction of cryoprotectants, which are scarcely known compared with those of terrestrial insects. Therefore, detailed biological information must be collected about individual species of aquatic insects (in contrast to some current preferences for generalized statistics about aquatic systems) and put into a wide life-cycle context.

Introduction

Many aquatic insects live in regions that are cold enough for their habitats to be ice-covered or frozen during winter. Questions to be answered in understanding insect survival in these habitats include: where do aquatic insects go for the winter? What do they do there? And how do they cope with the low temperatures and the ice that it creates in many of the available habitats? I provide ecological context by outlining the patterns of habitat choice and modification, and ways of coping with the fact that ice seals the water surface during winter and greatly disturbs lotic habitats during spring break-up, but focus here on the effects of subfreezing temperatures (Oswood *et al*., 1991; Irons *et al*., 1993; Frisbie and

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Lee, 1997). Surprisingly little detailed biological and physiological knowledge about these effects has been obtained in aquatic systems. Therefore, I emphasize future research directions that are suggested by information on both aquatic insects and insect cold hardiness in general.

Habitat Features

Winter conditions differ widely among different habitats (Table 1.1). Small bodies of water are not well buffered against winter cold, and after formation of surface ice, may steadily freeze to the bottom, especially above arctic permafrost. However, in cool-temperate regions, conditions are ameliorated because overlying snow provides insulation from cold air temperatures and the ice may not get very thick even on small ponds. Provided snowfall is moderate or heavy, large areas of the bottom sediments remain unfrozen even where mid-winter temperatures (December–February) average −8°C for 3 months (Danks, 1971a). In large lentic habitats the sediments also remain unfrozen, typically at 4°C, the temperature at which water is heaviest and stratifies beneath the surface ice.

In lotic waters, flow restricts ice formation, although rivers can freeze into the substrate if flow is low during cold winters (Clifford, 1969; Irons *et al*., 1989). When flow is maintained, river temperatures remain near 0°C and instead of surface ice, frazil ice – suspended crystals that cannot consolidate because of turbulence – is formed (Shen, 2003). The crystals may attach to the bottom and to each other to form anchor ice, but even so the temperature stays close to 0°C. Although winter conditions are not especially harsh in lotic waters of adequate size, the melting of accumulated snow and ice produces major disturbances in the spring, including ice scour, high flows and flooding (Prowse and Culp, 2003).

Winter conditions in aquatic habitats, therefore, depend on how the size, geometry and flow of each habitat, together with the cold, ice and snow in a given region and year, combine to govern winter severity (such as the minimum winter temperature and the duration of ice cover), timing (such as the dates of freeze up and thaw), spring disturbance and other features. Therefore, different species show different habitat choices, habitat modifications, cold hardiness and ways of withstanding other effects of ice.

Choice of Habitat

A major component of insect winter survival is the choice of a place to spend the winter. Aquatic insects can spend the winter in their summer habitats even if these might freeze. Alternatively they can move to different subhabitats within the same water body, to different water bodies and even on to land. The winter habitat dictates requirements for coping with adversity, especially levels of cold hardiness.

Habitats that do not freeze completely, such as deep lakes and groundwater-influenced streams, even allow activity during winter in species adapted for

Table 1.1. Synopsis of conditions created by winter cold and ice in different aquatic habitats in cold regions.

	Lentic habitats			Lotic habitats		
Feature	Small and shallow ponds*	Deep, permanent ponds	Large lakes	Small creeks	Medium rivers	Large rivers
Start of permanent ice cover	Early	Early	Late if at all	Early	Late	Very late
Exposure of organisms to adjacent ice	Common	Varies according to habitat and weather	Infrequent	Common	Occasional; also frazil and anchor ice	Infrequent
Time of thaw	Early	Varies according to size, morphometry, exposure, etc.	Late, especially if ice is thick	Varies according to flow, weather, etc.	Varies	Varies
Bottom condition	Frozen	Unfrozen	Unfrozen	Frozen	Usually unfrozen, depending on flow	Unfrozen
Bottom temperature	0°C to much colder	Below 4°C	4°C	0°C to much colder	Typically close to 0°C	Typically close to 0°C
Winter modifiers	Snow insulation above warmer ground	Winter weather	Winter weather	Snow cover, etc.	Winter weather, water supply	Winter weather
Degree of ice scour in spring	None	None	Some	None	Often moderate to high	High
Other common factors	Anoxia beneath ice					
Peak flow	None	None	Little	Briefly high	Usually high	High
Flooding	Usually yes	Yes	Usually no	Often yes	Yes	Yes

*Including temporary ponds, container habitats, edges of larger water bodies, etc.

growth and reproduction at low temperatures. Indeed, several species complete significant growth in winter, including some black flies, stoneflies, mayflies, caddisflies and chironomids; some emerge in late winter, as in winter stoneflies and some diamesine and orthocladiine chironomids (sample references in Danks, 1991, p. 239).

Relatively few species remain in their summer habitat when it will freeze. Many that do so are chironomid midges from northern ponds, lakes and streams, which survive in habitats experiencing winter temperatures well below freezing (Scholander *et al.*, 1953; Danks, 1971b; Andrews and Rigler, 1985; Irons *et al.*, 1993; Bouchard *et al.*, 2006; Lencioni, 2004). Other species that remain in potentially frozen habitats include some dragonflies from prairie ponds (Daborn, 1971), empidids from Alaskan streams (Irons *et al.*, 1993), caddisflies from tundra pools (Wiggins and Winchester, 1984), midges from pitcher plants (Paterson, 1971) and mosquitoes from tree holes (Copeland and Craig, 1990).

Many insects move within the habitat from summer locations to areas less likely to freeze, for example, from the edge to the centre of streams and ponds (Gibbs, 1979; Olsson, 1982; Irons *et al.*, 1993). Other species move deeper into the substrate for winter, even into the hyporheic zone deep in the bed of streams. However, there are many interspecific differences and it is not possible to conclude that penetration into the substrate is necessarily or commonly associated with protection from cold. The hyporheic zone is preferred for summer growth by some stream species, such as stonefly and mayfly larvae; and some lake and pond species, including chironomid larvae, penetrate the substrate and become dormant in summer when oxygen levels are low. A few species adjust position even during the low temperatures of winter. For example, larvae of *Leptophlebia* mayflies stay close to the ice and move with the ice-front as it changes (Olsson, 1983).

Some species move for the winter to deeper habitats of the same type that are less likely to freeze (Pajunen and Jansson, 1969, for corixids). Several species of beetles and bugs move from the temporary ponds in which they develop to permanent ponds for overwintering, recolonizing temporary ponds in the spring (Williams, 1997), although this strategy is not confined to regions with cold winters. Species of gerrids, mosquitoes, limnephilid caddisflies and other taxa spend the winter as adults in terrestrial habitats, typically sheltered in cavities or litter beneath the snow (e.g. Hudson, 1978; Berté and Pritchard, 1983; Spence and Andersen, 1994).

Species that move to different habitats for the winter return to the original habitats in spring. However, some seasonal movements appear to reflect adaptations against spring disturbance rather than against winter cold (see *Withstanding other seasonal effects of ice*).

Modification of Winter Conditions

Some aquatic insects modify the habitat to improve winter survival, as opposed to simply choosing the most potentially favourable sites. Many species that penetrate the substrate build burrows lined with silk or mucilage. The roles of most such structures in cold hardiness have not been demonstrated, although several unrelated adaptive values have (Danks, 2002), such as the protection against predation afforded by the burrows of chironomids (Van de Bund and Groenenkijk, 1994).

Other species overwinter in cocoons or shelters. Often these structures are more robust or of a different form than the summer equivalents. For example, the distinctive winter cocoons of chironomids enhance survival during experimental freezing (Danks, 1971b). Inside these cocoons the larvae normally fold under at least the posterior segments, presumably to protect the body and especially the anal processes from damage caused by surrounding ice (Danks, 1971b). Cases of some other aquatic insects are attached to the substrate (Hauer and Stanford, 1982) or sealed (Olsson, 1981) for the winter period. Of course, similar adaptations are seen in summer (Hauer and Stanford, 1982) and the shelters protect against predation and other challenges (Dillon, 1985; Danks, 2002).

Finally, females of some species govern the specific winter conditions for their eggs or progeny by selecting and modifying oviposition sites. Eggs of *Lestes* dragonflies that overwinter encased in ice in prairie ponds are inserted into plant stems, which may provide some mechanical protection (Sawchyn and Gillott, 1974). Limnephilid caddisflies deposit their eggs in temporary ponds in a gelatinous matrix that imparts drying and freezing resistance to the eggs (Wiggins, 1973).

Cold Hardiness

Cold hardiness in insects in general has been studied in some detail. For recent reviews and updates see Ramløv (2000), Bale (2002) and Danks (2005).

Low temperatures above freezing are injurious to many insects ('chilling injury'). However, larvae of some stoneflies, mayflies and chironomids from northern regions and from cold habitats such as mountain streams are adapted for activity at temperatures as low as 0.1°C (Brittain and Nagell, 1981). Cold-stream species that are killed by freezing survive winter even when water temperatures are very close to 0°C (e.g. Oswood *et al.*, 1991). Temperatures in most deep lakes are stable at 4°C during winter. Therefore, although there is little information for aquatic species, susceptibility to chilling injury may be less widespread in aquatic than in terrestrial species from cool regions.

Most terrestrial species remain unfrozen in winter, even at temperatures below 0°C, by supercooling. Ice forms in solution by aggregating around a nucleus that encourages crystal formation, so that if nucleators can be masked or eliminated water will supercool to about –40°C, the temperature at which the molecules move so slowly that their aggregation leads to crystallization at the homogeneous or spontaneous freezing point (Vali, 1995).

Nucleators can include internal molecules and surfaces, gut contents and ice crystals that inoculate the body fluids through the cuticle ('inoculative freezing'). Inoculative freezing would be expected in aquatic habitats in which overwintering insects are surrounded by ice (but see below). Of course, the true freezing points of typical insects, depressed by the presence of cell constituents, are up to a few degrees below the 0°C freezing point of pure water. Some aquatic insects freeze in the presence of ice at relatively high subfreezing temperatures (table 3 in Frisbie and Lee, 1997). However, the supercooling points of other aquatic species are still lower even when wet, suggesting that they would tend to remain unfrozen in the aquatic habitat too. For example, supercooling points of empidid larvae overwintering in an arctic stream were between −5 and −10°C (Oswood *et al.*, 1991). Dragonflies from shallow ponds survive only if unfrozen, but have supercooling points of about −4 to −8°C (Moore and Lee, 1991). Larvae of the pitcher plant mosquito *Wyeomyia smithii*, which are killed by freezing, supercool to −5°C (Evans and Brust, 1972). Insulation from still lower air temperatures by ice and snow is important for the winter survival of such species (Danks, 1971a; Farkas and Brust, 1986).

A few species remain unfrozen when surrounded by ice at much lower temperatures. Gehrken and Sømme (1987) showed that eggs of the stonefly *Arcynopteryx compacta* frozen to −29°C in water maintained a supercooled state, apparently through dehydration.

Other aquatic insects tolerate freezing itself. Most of them belong to the Diptera, especially the family Chironomidae. Species living in arctic ponds and lake edges that freeze to −18 or −20°C in winter withstand comparable experimental exposures (Scholander *et al.*, 1953; Danks, 1971b; Andrews and Rigler, 1985), an ability enhanced by the mechanical protection given by cocoons.

Typical terrestrial species that are freezing tolerant manufacture ice-nucleating proteins to initiate freezing at relatively high subfreezing temperatures, preventing the rapid and injurious ice formation in the body that would occur after extensive supercooling (review by Duman, 2001). It is unlikely that such ice-nucleating substances are needed in freezing-tolerant aquatic larvae surrounded by ice. Terrestrial species that are freezing tolerant even though they do not experience very cold temperatures tend to live in very moist places where inoculative freezing is probable (Ramløv, 2000, pp. 32–33), providing a possible parallel with aquatic species.

Supercooling ability and protection against freezing depend partly on cryoprotectants. Very common in terrestrial insects are antifreeze compounds of low molecular weight, chiefly polyhydric alcohols and sugars (Storey and Storey, 1991). These solutes occur mainly in the haemolymph and have several roles, including colligative depression of the supercooling point, binding of water (see below) and control of osmolalities. Some compounds of low molecular weight also stabilize and protect protein molecules or membranes directly (Storey and Storey, 1992). Even in freezing-tolerant species they stabilize molecules (including cell membranes) and control ice formation. Such compounds have not yet been isolated from fully aquatic species, apparently chiefly because no one has looked for them. Adaptive changes in membrane composition also contribute to cold hardiness (e.g. Šlachta *et al.*, 2002; Michaud and Denlinger, 2006): changes in molecular species and increasing levels of unsaturation in fatty acids enhance membrane fluidity at low temperatures by keeping membranes in the liquid crystalline rather than gel state.

A second class of cryoprotective compounds is antifreeze proteins (AFPs), which depress the freezing point especially by inhibiting ice-crystal growth at the ice–water interface (review by Duman, 2001). Various organisms have AFPs of different kinds, but all are characterized by molecular binding to ice (Doxey *et al.*, 2006). AFPs have been reported in aquatic insects only from eggs of a northern stonefly and from a northern adult gerrid (Gehrken and Sømme, 1987; Duman *et al.*, 2004), but undoubtedly are widespread in other species. In terrestrial species, these compounds appear to play multiple roles in controlling or limiting nucleation (including masking nucleation sites) and protecting membranes. They also prevent inoculative freezing through the cuticle by ice on its surface (e.g. Olsen *et al.*, 1998 for beetles; Zettel, 2000 for springtails). Some ice-active proteins inhibit ice recrystallization, a potentially injurious phenomenon whereby large ice crystals grow at the expense of small ones as frozen tissues melt (Knight and Duman, 1986; Knight *et al.*, 1995; Wharton, 2003). Moreover, in some roles AFPs interact with each other in the presence of smaller cryoprotectants such as glycerol (Wang and Duman, 2005).

Involved in all of the biochemical relationships is the status of internal water. Cold hardiness associates some of the internal water with various molecules to make it unavailable for the freezing process (Storey and Storey, 1988; Danks, 2000; see also Block, 2002). Indeed, adaptations for cold hardiness, including an increase of cryoprotectants, habitat selection, and adjustments of water content, parallel those for withstanding dehydration, which share so-called cryoprotectants, notably trehalose (Ring and Danks, 1994, 1998). Also, the need to resist or survive intracellular water loss during dehydration parallels needs when intracellular water is lost to freeze on to extracellular ice. This pathway prevents intracellular freezing, which is almost invariably fatal even in freezing-tolerant species.

Water loss is the key to a different method of cold hardiness, dehydration to ice outside the body that keeps the concentration of body solutes high enough that freezing cannot occur (Holmstrup and Zachariassen, 1996 for earthworm egg cases; Holmstrup *et al.*, 2002). This mechanism relies on the fact that the vapour pressure of ice is less than that of water at the same temperature (cf. Holmstrup and Westh, 1994), favouring dehydration in unfrozen individuals surrounded by ice. Aquatic insects that supercool extensively in the presence of ice might use a version of this strategy (see the section *Key research topics*).

Finally, overwintering terrestrial adults of aquatic species may require resistance to dehydration. For example, diapause females of the mosquito *Culex pipiens* lose water more slowly than non-diapause adults, because of their larger size, metabolic adjustments and greater cuticular waterproofing (Benoit and Denlinger, 2007).

Withstanding Other Seasonal Effects of Ice

A complete layer of surface ice confines the water beneath it and prevents contact with the air, and also freezes out and concentrates solutes particularly in lentic habitats. Therefore, solute concentrations can be high and oxygen levels low in winter especially in small ponds (Daborn and Clifford, 1974). Some insect larvae, including mayflies and chironomids, can withstand anoxia for a long time (Nagell and Brittain, 1977; Redecker and Zebe, 1988). Some species move seasonally in response to anoxia (Brittain and Nagell, 1981). High solute concentrations in water remaining in some ponds as surface ice finally freezes into the substrate appear to favour dehydration and hence cold hardiness (cf. Danks, 2000, pp. 842–843).

A great challenge to lotic insects is the enormous destructive power of ice in high flows during the melt, which adds to the considerable disturbances from meltwater alone. Abrasive broken-up ice is driven by these flows, scouring insect habitats. Moreover, in larger rivers, broken-up ice tends to lock together into dams, resulting in greater flooding than would be caused by the increased flow alone, and typically followed by a final catastrophic flow event. The presence of ice also delays the temperature rise in spring (Prowse and Culp, 2003).

Some species tolerate the high flows (Malmqvist, 1999). Others move away from the main channel to tributaries as break up starts (Clifford *et al*., 1979), avoiding peak flow in the main channel. Stream species in habitats that are not severely frozen may overwinter at the stream edge (Messner *et al*., 1983). Some stream species overwinter in headwater lakes or spring habitats and thus escape disturbances in the outlet channels during spring (Mendl and Müller, 1978). Others oviposit outside the habitat. For example, eggs of the black fly *Simulium pictipes* are deposited on the stream bank (Kurtak, 1974) where they avoid ice formation and spring spates but can drop into accessible habitats upon hatch. The staggered egg hatch of some mayflies and stoneflies, which has often been interpreted as insurance against unpredictable water supply (Danks, 1983), might also insure against loss of the whole population during spates (e.g. Wise, 1980).

Key Research Topics

This brief review shows that winter-related adaptations have been little studied in aquatic insects. Therefore, I recommend research areas (Table 1.2) where more information is necessary to allow the range of adaptations and their interactions to be understood.

Cold hardiness and habitat conditions

A major need for many years has been to associate the winter conditions experienced by insects in nature with mechanisms of cold hardiness (e.g. Danks, 1978, 1991, 1996, 2005), rather than studying the physiological adaptations in isolation. This conclusion applies with particular force to the topic of aquatic habitats, where many questions revolve around habitat temperatures and their variations in relation to the proximity of ice. Compact data loggers that were not available in past years can now record microhabitat temperatures in detail for a whole year (e.g. Bennett *et al*., 2003), but have seldom been deployed in aquatic habitats.

A key element of overwintering habitats is the insulation provided by snow, a result of the air trapped between the snow flakes. Even in cold-temperate regions small container, pond and creek habitats remain partly unfrozen because

Table 1.2. Key research topics about cold hardiness and winter survival in aquatic insects.

Topic	Key themes	Key research needs
Habitat	Actual conditions experienced influence the need for and nature of cold hardiness	Simultaneous measurement of microhabitat conditions and cold hardiness
Mechanical protection	Substrates, burrows and shelters may protect against ice	Assess conditions and the protection afforded inside burrows and cocoons
Dehydration	Water and cold hardiness are closely linked	Measure pre-winter water content, clarify occurrence and influence of water loss to surrounding solute-rich water; clarify water relationships with inoculative freezing; study supercooling through dehydration when surrounded by ice
Time	Characteristically slow temperature changes in aquatic habitats might favour particular cold-hardiness adaptations	Conduct cold-hardiness experiments with suitably slow cooling rates
Cryoprotectants	Cryoprotectants of low molecular weight are very little known	Examine a range of aquatic species for polyhydric alcohols, sugars, etc.
Antifreeze proteins	The occurrence and roles of AFPs are very little known	Examine a range of aquatic species for AFPs. Test potential multiple roles including inhibition of inoculation and recrystallization
Seasonal movements	Habitat choice is a key feature of overwintering	Careful seasonal studies on movement of individual species, and in relation to cold hardiness
Overwintering on land	Many adults of aquatic species overwinter on land	Integrate information about aquatic and terrestrial stages
Winter strategies	Origin of different overwintering strategies	Synthetic analysis of phylogeny, life cycles, elements of cold hardiness, etc.

AFPs, antifreeze proteins.

the warmth of deep substrate layers ameliorates conditions beneath the insulating snow (Danks, 1971a). Precise logging of temperature data would show whether conditions in these places are really as severe as has often been supposed. Indeed, as already noted, it is insulation by snow that permits overwintering survival in plant pitchers of the freezing-susceptible mosquito *Wyeomyia smithii* (Farkas and Brust, 1986).

Conditions in wet habitats are distinctive, because the high specific heat of water and the latent heat of ice slow temperature changes, especially near the freezing point. On one hand, this buffering would ameliorate temperature exposures (as in the wet stumps monitored by Baust, 1976), but on the other it might slow the melting of ice in freezing-tolerant organisms, allowing potentially injurious recrystallizations that appear to be mitigated by certain proteins (see above). Because the temperature of aquatic habitats changes slowly, several features of terrestrial insects that have attracted particular recent attention are less relevant for aquatic stages, including rapid cold hardening (see Danks, 2005) and repair of chilling injury during milder intervals (e.g. Colinet *et al.*, 2006).

In summary, data about winter survival by aquatic species are difficult to interpret because we lack detailed information on habitat temperatures, including patterns of change as well as winter extremes. Furthermore, little actual winter sampling and experiment have been done, as opposed to later recovery of living animals from habitats observed to have been frozen. For example, although some dragonfly larvae survive in frozen prairie ponds (Daborn, 1971), we do not know if they supercool or freeze (compare the discussions of Moore and Lee, 1991; Frisbie and Lee, 1997; Danks, 2007). In addition, responses related to cold-hardiness may differ strikingly within the same terrestrial species according to the conditions experienced (Bennett *et al.*, 2005 for differences in winter diapause and dehydration). By analogy, winter adaptations of chironomid larvae probably differ between arctic and temperate latitudes not only in degree but also in character; however, at present we can only generalize because information is so limited.

Mechanical protection against ice

Adaptations of aquatic insects appear to provide protection against the mechanical effects of external ice. However, both observational and experimental research about the range of possibilities is limited.

Mechanical protection can take several forms. Overwintering in deep layers protects animals beneath a layer of ice above them. Burrowing even to a shallow depth would be expected to mitigate the spread of injurious ice crystals when the substrate freezes (Danks, 2007). This protective effect would be increased in insects that build a substrate burrow. Many aquatic species build cases or shelters in or on the substrate for summer activity, and in winter these would serve as mechanical barriers against ice and against mechanical damage caused by surrounding substrates. Without such protection, most aquatic insects frozen in water are killed by mechanical stresses, as shown by experiments on chironomid larvae and other taxa (Scholander *et al.*, 1953; Danks, 1971b).

It will be difficult to separate any specific functions of these shelters in winter from their general roles in feeding, attachment, and protection against physical factors, natural enemies, toxic substances and so on (Danks, 2002, 2004b), but investigation would be worthwhile especially in the few aquatic species that build special structures for the winter. As noted above, some chironomid larvae make winter cocoons that differ strikingly from the summer feeding cases and are applied tightly to the body. Larvae build and leave the cases as the water cools or rises above temperatures close to freezing (Danks, 1971b; Danks and Jones, 1978). Experiments on case construction in relation to temperature would be instructive. Case building enhances survival during freezing and might also be linked with life-cycle timing such as diapause.

Cold hardiness and dehydration

Water content and water status are closely associated with cold hardiness, so investigations into aquatic insects should test potential similarities with terrestrial species. The internal status of water in relation to inoculative freezing would be of particular interest. Aquatic species that supercool in the presence of ice (Gehrken and Sømme, 1987) might do so either by resisting inoculation, or by losing water to external ice through a mechanism similar to that used by certain soil taxa (see above). That mechanism relies on permeable cuticles that allow the escape of water. It also requires changes slow enough to prevent freezing before vapour–pressure equilibrium is established. Permeable cuticles are normal in the aquatic stages of insects (but not in most terrestrial insects) and relatively slow changes are especially characteristic of freezing aquatic systems, potentially allowing equilibrium to be established between inside and outside. Of course, internal solutes must occur in sufficient concentration that little supercooling is required as dehydration proceeds, so that inoculative freezing does not occur. Assessments of cryoprotectant profiles, as well as experiments on properly conditioned winter aquatic larvae cooled slowly under suitable conditions in the presence of ice, would help to show whether the aquatic insects known to survive in frozen ponds and streams are cold hardy by dehydration, by resisting inoculation, or by freezing tolerance.

Cold hardiness and time

The slow pace of autumn cooling in most aquatic habitats correlates with a number of cold-hardiness traits of aquatic insects. For example, the stonefly eggs just referred to that supercool in the presence of ice can do so only if the cooling is relatively slow, and they die if cooled rapidly (Gehrken, 1989). Chironomid winter cocoons take some time to build, even though this activity does not start until water temperatures fall very close to freezing (Danks, 1971b). Time is required for habitat selection, even when movement takes place just before temperatures become cold (Danks, 1991). Preparations for diapause need time, including the reception of photoperiodic or other inductive signals, changes in developmental pathways and energy storage (Danks, 1987). Many dormant insects cease feeding but then take some time to clear the gut, which is a common source of nucleators.

These findings suggest that ‘conditioning’ plays an important part in seasonal adaptations of aquatic insects, even though temperature changes in aquatic habitats are normally slower than in terrestrial ones. Cold hardiness is not simply a static ‘hardened’ winter state (Danks, 2006), but a component of development, so that ‘acclimation’ is expected. Consequently, detailed studies of habitat conditions and life cycles in the context of the patterns of temperature change will be required to understand the acquisition of cold hardiness. Simple assessments of survival under winter conditions are by no means sufficient.

Occurrence of low molecular weight cryoprotectants

We know very little about the cryoprotectants of aquatic insects. Table 2.1 in Lee (1991) and table 2 in Ramløv (2000) list 28 arthropod species in which cryoprotectants have been characterized, but none of these species is aquatic. Glycerol in particular is known from many other terrestrial insects (Storey and Storey, 1992). Analyses would be especially useful in aquatic species that survive freezing, including some chironomid midges, as well as in species that supercool in the presence of ice. By analogy with terrestrial insects, common compounds that might be expected in addition to glycerol are sorbitol and other polyhydric alcohols, trehalose, glucose and other sugars, and a few other substances, including proline and alanine. Indeed, glycerol was found in the Antarctic (but typically terrestrial) chironomid *Belgica antarctica*, together with sorbitol, trehalose, glucose and fructose (Baust, 1980). The desiccation-resistant African chironomid *Polypedilum vanderplanki* contains high levels of trehalose (Watanabe *et al.*, 2005).

Occurrence of antifreeze proteins

Antifreeze proteins (AFPs) have so far been reported from only two aquatic species (see *Cold hardiness* above), but the known properties and multiple roles of these compounds suggest that they would be especially worthy subjects for investigation in aquatic insects. In addition to depression of the freezing point, AFPs help to prevent inoculative freezing in terrestrial species (see above). Duman (2001) pointed out that AFPs might be able to prevent inoculation through cuticular pores provided the pores are very small, because AFPs are most effective when the potential inoculating ice crystals are very small (Zachariassen and Husby, 1982) – and the way in which AFPs inhibit ice-crystal growth depends on surface geometry. AFPs and cuticular structure might therefore combine to prevent inoculative freezing in aquatic insects surrounded by ice. This potential relationship has not been investigated.

A role for smaller proteins as recrystallization inhibitors (compare Ramløv *et al.*, 1996 and Wharton, 2003 for a nematode) also cannot be ruled out. Such substances might be characteristic of arctic chironomid species frozen into pond or stream substrates that take many days to warm, from a few degrees below freezing to the thaw.

Seasonal movements

Interesting anecdotes, but few specific studies, suggest how seasonal movements help aquatic insects to survive the winter and escape spring flows and ice. Detailed long-term sampling for individual species in carefully chosen multiple locations in one habitat is needed to track seasonal movements. Such studies will be especially complex because although the movements of aquatic larvae as they grow could indeed reflect responses to winter cold or spring disturbances, they might equally be influenced by summer warmth, food availability and predation risk. Tracking the movement of individuals fitted with miniature radio transmitters (cf. Hayashi, 1994 for corydalid larvae) might be a way to gather information efficiently.

Features of aquatic species overwintering on land

The fact that adults of some aquatic species overwinter on land presumably reflects not only ancestral life cycles according to phylogeny, but also the fact that winter conditions in aquatic habitats may be more severe than conditions in sheltered sites beneath the snow in adjacent terrestrial ones. Parallel study of these conditions and the cold hardiness of aquatic species sheltering there would be valuable, but so far we have information only for a few adult mosquitoes and gerrids. Recent molecular studies of the genetic control of cold-hardiness traits in mosquitoes (Kim *et al*., 2006; Rinehart *et al*., 2006) are confined to the terrestrial adult stage.

Cold hardiness and timing in these terrestrial stages resemble those of fully terrestrial species, as might be expected. Because temperature in many terrestrial habitats is less well buffered than in most aquatic ones, such species must manage energy resources well. For example, autumn (after entry into the overwintering site) and spring (before feeding or reproduction is possible) are warm enough to consume substantial energy reserves, even though energy use is reduced during the winter itself (Irwin and Lee, 2003 for a terrestrial species). These requirements are in addition to any metabolic requirements for the manufacture of cryoprotectants. Therefore, studies of the seasonal energetics of aquatic species that consider energy budgets for both larval feeding in water and adult overwintering on land would be particularly helpful.

Evolution of winter strategies

More synthetic questions can be asked once detailed information about cryoprotectants and other aspects of cold hardiness in aquatic insects is known. At the moment, we do not understand how cold hardiness and winter movements correlate with phylogeny, lifestyle, habitat, trophic status, winter temperatures, spring conditions and so on. We do know that the marked cold hardiness of chironomid midges relative to some other taxa stems from their original evolution in cold habitats (Brundin, 1966; Danks, 1971b), for example, but we know relatively little about their diapause (Goddeeris, 2004), winter cocoons (Danks, 1971b), cryoprotectants or other essential components of that cold hardiness.

Climate change

Discussion about the effects of future climate change on insects has focused on terrestrial species (for an introduction to these ideas see Hodkinson *et al*., 1998;

Danks, 2004a, 2006). Most work is concerned with the effect of increased summer temperatures but, as regional climates become less severe, higher winter survival, higher supercooling points, less prevalent freezing tolerance and less complex but potentially more variable cryoprotectant profiles would be expected (Danks, 1992).

Work on aquatic insects has particular value because change alters aquatic habitats in characteristic ways, including the extent and timing of ice cover and spring flow. The relatively limited information on the cold hardiness of individual species hinders biological experiments, but assessing relevant habitat conditions in detail in different climatic regimes, including latitudinal comparisons, would be feasible and instructive.

Conclusions

In habitats likely to freeze, most aquatic insects move to less severe sites for winter (in the same habitat or elsewhere) and only a few, notably chironomid larvae, do not. Other movements in lotic species help to avoid spring disturbances caused by high flows and ice. Most species are dormant for winter, often in burrows or constructed shelters, but a few remain active in cold but unfrozen habitats. How species cope with cold and ice depends on where they spend the winter, but some species can survive body freezing and others can remain unfrozen even when surrounded by ice.

These generalizations are based on surprisingly few data compared with the wealth of detailed evidence about the cold hardiness of terrestrial species. As a result, needed research (summarized in Table 1.2) dwarfs the existing information. Missing in particular is information on the physiological and biochemical basis of cold hardiness, including cryoprotectant production. But concurrent information about ecology and behaviour is also required, because of linkages with habitat conditions, microhabitat choice, seasonal movements, energy use and other requirements to survive the winter.

This conclusion suggests that two particular approaches are most valuable. First, we need detailed biological information about individual species to interpret the linkages between ecology and physiology – despite a tendency in recent studies of aquatic insects to generalize, for example, by inventories made at only a low level of taxonomic resolution – or by analysis only through summary statistics such as biomass and productivity. Second, a wider perspective is needed to provide context for adaptations to cold and ice, giving due weight not only to cold hardiness but also to such features as habitat variability, bet-hedging, food range, dormancy and life-cycle timing (Danks, 2007).

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2 Saline-water Insects: Ecology, Physiology and Evolution

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Abstract
This chapter presents an overview of the numerous genera of insects capable of surviving in saline water, including information on their distribution, ecology and physiology. Detailed description is provided of the two families of insects that have been most intensively studied, namely the mosquitoes (Culicidae) and the brine flies (Ephydridae). The life histories of these groups are well known and the mechanisms of salt and water balance have been examined in considerable detail. Evidence is presented that the primitive condition in mosquitoes is restriction to freshwater. Invasion of saline waters has occurred frequently (at least six times) in the family Culicidae, but the number of species capable of surviving in saline water is small (about 5% of all known mosquito species). The physiological modifications supporting these invasions are discussed.

Introduction

My goal in this chapter is to review interesting aspects of the ecology, physiology and evolution of insects residing in saline waters. Salinity, and more specifically certain ions such as sodium and sulphate, present unusual challenges for insects. Insects are an extremely successful clade; the precise number of species is unknown, but most estimates are for numbers well over 10 million. Insects arose in the terrestrial environment and the current thinking is that ancestral arthropods, similar and related to branchiopods, moved on to land. As such, insects arose in an environment in which plants and detritus were the principal sources of food. Some species eventually evolved forms that could take advantage of freshwater habitats, particularly in the larval stages. The evolutionary advantages of flight for mating and dispersal led most species to retain a terrestrial or aerial adult stage. Whether the food is plant and detrital materials, or the habitat is freshwater, the common feature is a relative paucity of sodium. Most plants do not require sodium and can be grown in environments in which sodium is entirely absent. Animals, however, require sodium for some physiological

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functions, for example, nervous activity. This creates a substantial physiological problem for freshwater and terrestrial animals. The insects got around this problem by reducing the amount of sodium in the body to an essential minimum. Indeed, in some insect species, sodium is restricted to tiny compartments surrounding the nerves. Other osmotically active osmolytes occur in the blood of many insects.

Having evolved as a group supremely adapted to terrestrial and freshwater habitats, the insects have neural and excretory systems geared to obtaining and retaining sodium. As will become clear in text to follow, evolving excretory systems designed not to obtain sodium, but rather to rid the body of sodium, has proven challenging for insects. None the less, some insects have managed to exploit sodium-rich habitats.

Insects in saline waters are subject not only to osmotically stressful conditions, but also to high levels of sodium. Roughly 70% of the Earth's surface is covered by saline water, representing numerous potential habitats for insects. In addition to the oceans, there are saline marshes, large salt lakes, salt ponds and desert pools. Most of these habitats have been invaded and exploited by insects, with the exception of the open oceans. Given the incredible ecological success of insects in most environments on the planet, and indeed their success in places where other groups cannot survive, it is remarkable that the oceans remain largely insect-free.

Marine Insects

Very few insects are found in the open ocean and those few are generally associated with the benthos near the shore. Some insect larvae inhabit coral outcrops, feeding on algae and bacteria on these substrates. The insects with a worldwide oceanic distribution are the marine water striders. These semi-aquatic insects do not live in the water, but walk instead on the ocean surface.

I will describe briefly the most abundant and widely studied groups of saline-tolerant insects. A short review cannot do justice to all of these insect groups and the topic has been reviewed thoroughly by Cheng (1976). Although many papers have been published since that volume appeared, it remains the best source of information on saline-tolerant insects. I will not attempt to provide the level of review contained in a lengthy book but, instead, I will mention the major insect groups that are saline tolerant in order to illustrate that this capacity is not taxonomically limited. I discuss in greater depth two families of insects, the salt-tolerant mosquitoes and the brine flies, that have been the subject of intense study, particularly to determine the physiological mechanisms that permit them to survive and thrive in saline waters.

Collembola

Collembolans are among the most primitive of the insect orders with a fossil record going back 400 million years. The group is thought to be terrestrial in origin, although they are most abundant and diverse in moist habitats. Collembolans tend to accumulate on water surfaces, being largely non-wettable, and they can walk and hop across bodies of water with ease. Collembolans are generally either predacious on other invertebrates and/or feed by scavenging. They are found in all types of substrates, including sea wrack, sandy beaches and rocky shores. Collembolans can survive immersion indefinitely, suggesting that they can obtain adequate oxygen across the integument. They have survived in the laboratory for 14 days with access only to seawater, indicating that they do not require access to freshwater (Joose, 1976).

Thysanura

Marine thysanurans are another abundant and highly successful group of apterygotes able to exploit the ocean shore. These insects are of course ametabolous. All life stages feed on algae on rocky or sandy substrates (Joose, 1976). Weigmann (1973) found that some thysanuran species could tolerate a wide range of salinities – they were osmoregulators in dilute media, but osmoconformers in more concentrated media. The physiological mechanisms associated with this type of osmoregulatory behaviour are described for mosquito larvae below.

Trichoptera

Caddisflies, at least of the species *Philanisus plebeius*, may be among the most fully marine of all insects (Leader, 1972, 1976). The larvae of several species have been investigated with regard to their salinity tolerance and osmoregulatory capacities. *Limnephilus affinis*, which occurs in marine marshes in Europe, can survive in salinities up to 75% seawater. Sutcliffe (1961) found that the larvae osmoregulate in dilute media, but are osmoconformers in more concentrated media. By contrast, *Philanisus plebius*, a species found in New Zealand, was a strict osmoregulator and able to survive indefinitely in full-strength seawater. *Philanisus plebius* spends its entire larval period immersed in seawater, feeds on coralline algae, and the larval silk cases are decorated with sand grains or the coralline algae on which it feeds (Leader, 1976).

Corixidae

Water boatmen can be abundant in coastal marshes, rocky tide pools and coastal marshes. Corixids are often thought to be herbivorous, but the forms in saline waters feed on nematodes, aquatic crustaceans, chironomids and other insects. Several species can osmoregulate in varying osmolarities, including full-strength seawater, and *Trichocorixa* is the only strictly marine genus (Scudder, 1976).

Ephydridae

Shore flies inhabit saline lakes and the ocean shore around the world. In the marine habitat, they tend to be excluded from open oceans, but are abundant in sea wrack, tidepools and marshy sites (Simpson, 1976). In saline lakes, both larvae and adults can be found on sandy and rocky substrates, feeding on algae and bacteria (Bradley and Herbst, 1994). The section below on brine flies describes their ecology and physiology in more detail.

Gerridae

The insects with the widest distribution on the oceans are the water striders in the genus *Halobates*. Of the 1700 species of water striders, 10% are marine. Both the immature and adult stages of marine water striders live atop the ocean waters and, in this sense, their adaptations are similar to those of terrestrial insects. The species that are strictly marine in distribution tend to be wingless, even as adults. Cheng (1976) reviews her many articles examining the ecology and taxonomy of marine water striders.

Ceratopogonidae and Chironomidae

Biting midges (Ceratopogonidae) are a bane to humans and wildlife. Salt marshes and estuaries can be sites of intense production of biting midges and their presence makes many coastal areas distinctly unpleasant for humans. The larvae are fully aquatic and feed on detritus, bacteria and algae. The larvae are fully saline-tolerant, at least up to full strength seawater, and appear to be osmoregulators, but they are never found in the open ocean (Linley, 1976).

Some species of chironomids (non-biting midges) are also fully saline-tolerant. The larvae of many species feed on detritus, algae and bacteria, but some of the saline-water species are carnivorous, a trait attributed to the increased availability of prey in productive saline waters (Hashimoto, 1976). The larvae are osmoregulators and may be the closest thing to a truly marine insect. They have been found on the substrate well below the lowest level of the lowest tide, in some cases in water several metres deep (Hashimoto, 1976).

Other coastal insects

Shore bugs (Saldidae) are abundant on most marine coasts. Although generally less abundant than shore bugs, the beetles (Coleoptera) found in marine coastal habitats are more speciose. Both shore bugs and beetles can withstand prolonged submersion, yet, in terms of morphological and physiological adaptations, they are similar to strictly terrestrial species. Although abundant and ecologically important, they have few adaptations to a saline habitat (Cheng, 1976). Many insect species are found in salt marshes but, as they do not have aquatic life stages, these insects are more accurately considered to be terrestrial than aquatic saline-adapted.

Two Intensely Studied Insects

As the above section suggests, a variety of insects have life stages that are saline-tolerant. Many species are found in coastal marshes and desert pools where the salinity can often exceed that in the open ocean. When insects occur in the ocean, they are generally associated with the intertidal region, with the exception of chironomids that can occur in deep waters, Trichoptera that occur just off-shore in benthic algal mats, and water striders that occur on the ocean surface. Two insects, saline-tolerant mosquitoes and brine flies, have been studied in considerable detail. The former because of their nuisance and medical importance, the latter because of their ecological significance. I will describe what is known about these two insect groups in more detail, thus providing a better understanding of the processes employed by insects to deal with saline waters.

Brine flies

Adult brine flies feed largely on algae, including filamentous algae and diatoms. In many species, the adults are rather long lived and algal feeding is required to support repeated reproductive bouts.

Adult brine flies have a waxy layer on their exterior cuticle and, when they walk along the substrate feeding on algae or ovipositing underwater, they are surrounded by a thin bubble of air. This serves as a source of oxygen and, judging from the length of time they can remain underwater, also serves as a surface for the exchange of respiratory gases. Females lay eggs that are more dense than the surrounding water in rock interstices or in algal mats. The larvae hatch and immediately begin feeding on algae. Bradley and Herbst (1994) demonstrated that several species of algae could support complete larval development. Concretions of calcium carbonate in the Malpighian tubules make the larvae more dense than the medium and allow them to stay on the benthos. The larvae also have hooks on the prolegs, which assist in holding on to the bottom and in locomotion.

Development in ephydrids involves three larval instars. At the end of the last larval instar, the concretions from the lime glands are evacuated through the anus and the larva metamorphoses into a pupa. The pupa, which must remain submerged to survive, is now less dense than the medium and a holdfast near the anus is used for attachment to twigs, rocks or algal mats. The adults emerge directly from the pupal case and, being less dense than water, they float to the surface and emerge from the water.

Physiology

The larvae of ephydrids are astounding for their capacity to survive in highly saline waters. Brine flies from the Great Salt in Utah, thrive by the billions in

NaCl-rich water with a salinity up to 10 times that of the open ocean. At Mono Lake in California, USA, the larvae of *Ephydra hians* also thrive in water three times the concentration of the ocean, but these waters are rich in sulphate and bicarbonate, with a pH of 10!

Given the extraordinary salt concentrations that the larvae experience, the first issue to address is the size of the gradients across the cuticle. All the species of brine fly examined to date are osmoregulators (Simpson, 1976). Table 2.1 shows the concentration of ions measured in the larval haemolymph of *E. hians* reared in water from Mono Lake, as well as the ionic concentrations in the external water (Shimizu and Bradley, 1994). The haemolymph had a total osmotic concentration of about 300 mOsm under these circumstances; the osmotic concentration of the lake was well over 1500 mOsm. It follows that the larvae must lose water across the cuticle due to the large osmotic forces. Studies in our laboratory have shown the cuticle to be permeable, although a quantitative estimate is not available (personal observation).

To replace the water lost through osmosis, the larvae drink the external medium. This replaces the volume they have lost, but poses the additional problem of forcing the larvae to rid themselves of the ingested ions. The very high concentration of sodium, carbonate and sulphate concentrations in Mono Lake water obviously pose serious problems in terms of ionic and pH homeostasis.

Figure 2.1 illustrates the internal organs associated with the gut and with excretion in the larvae of *Ephydra hians*. The fluids and food that are ingested pass into the midgut. In all insects examined to date, the fluid in the midgut rapidly comes into osmotic equilibrium with the haemolymph (Bradley, 2002). In *E. hians*, the ions in the midgut are transported into the haemolymph and water follows osmotically. The Malpighian tubules produce the urine by transporting ions from the haemolymph into the tubule lumen, and water follows this transport osmotically also. The fluid in the Malpighian tubules is, however, isosmotic with haemolymph and therefore does not contribute directly to osmoregulation.

In many insects, crystals precipitate in the lumen of the Malpighian tubules. This is due to shifts in the pH and to the transport of ions, which at low concentrations produce insoluble compounds (e.g. divalent cations and carbonate, or potassium and urate). In *E. hians*, crystals form in the Malpighian tubules and are accumulated in an expanded region of the Malpighian tubules termed the lime

Table 2.1. Ionic concentrations (mm/l) in the larval haemolymph of *Ephydra hians* and in the Mono Lake water in which they were reared.

Ion	Concentration in larval haemolymph	Concentration in Mono Lake water
Sodium	135.7 + 1.0	1224
Potassium	6.9 + 0.4	18
Calcium	5.6 + 0.1	<1
Magnesium	13.2 + 0.5	<1
Chloride	120.0 + 1.4	627
Sulphate	0.6 + 0.1	151

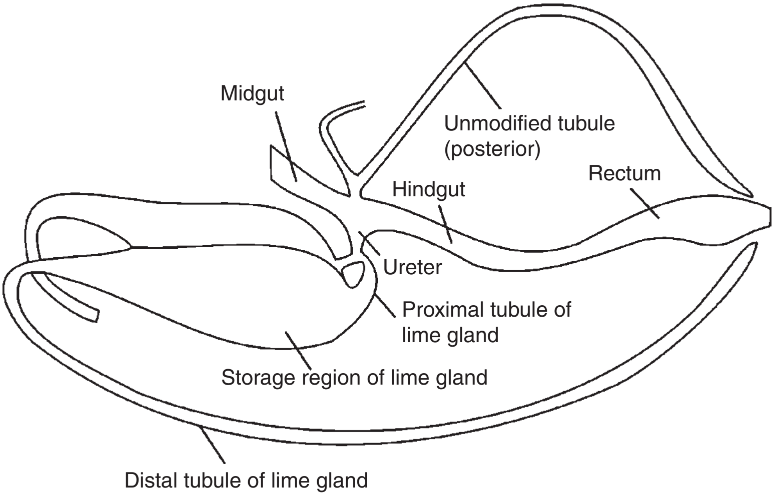

Fig. 2.1. Internal organs of the brine fly *Ephydra hians*. The insect has two pairs of Malpighian tubules, one pair is modified into the lime glands. (Redrawn from Herbst and Bradley, 1989).

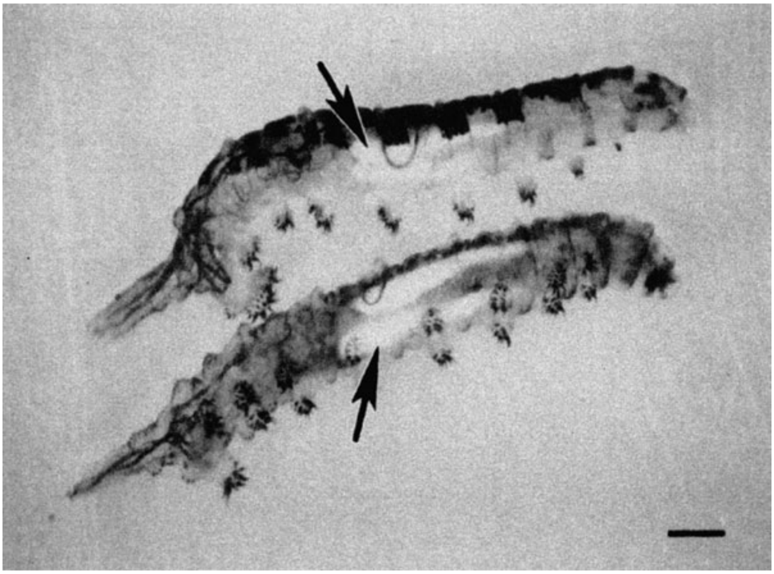

Fig. 2.2. Photograph of two, third-instar larvae of *Ephydra hians*. Note the prominent, white lime glands (arrows) visible through the cuticle of the larvae. – equals 1 mm (from Herbst and Bradley, 1989).

gland. The accumulations of concretions are large enough to form a large white sack in the larva that is visible through the cuticle (Fig. 2.2), and the crystals are composed almost entirely of calcium carbonate (Herbst and Bradley, 1989). The lime crystals serve as ballast, permitting the larva to remain submerged in highly saline water, which is more dense than most biological materials. The precipitation of carbonate and bicarbonate contributes to pH regulation in the larvae.

Sutcliffe (1960) showed that brine flies produce a urine more concentrated than the medium in which they reside. Shimizu and Bradley (1994) demonstrated that the rectum was not the site of hyperosmotic urine formation in *E. hians*. The rectum has a very thin epithelium and the cells do not exhibit the ultrastructural specializations (highly folded membranes and numerous mitochondria) expected in tissues active in ion transport. Instead, the hindgut contains a colon with thick walls and active cells. The authors found that the entire colon was capable of producing a hyperosmotic fluid. The colon was also the site of active transport of sulphate, but this capacity was restricted to the anterior half of the organ.

Survival in highly saline media requires, therefore, transport functions in the Malpighian tubules, particularly for the production of dense concretions. The production of a hyperosmotic and ion-rich urine for osmoregulation is a function of the hindgut and, more specifically, the cells in the colon. In *Ephydra*, hyperosmotic fluid secretion occurs throughout, while sulphate excretion is restricted to the anterior end of the organ (Shimizu and Bradley, 1994).

Saline-tolerant mosquitoes

Saline waters are often extremely biologically productive. Salt marshes along the coast receive nutrients from the sea and also in runoff from the land. In particular, estuaries and coastal swamps are rich in nutrients, benefit from stirring and oxygenation through the shifting tides and exhibit high primary productivity. Although the constantly shifting osmotic concentration can be difficult for animals, these habitats can be extraordinarily productive for mosquitoes. Mosquitoes are unquestionably the most intensively studied of all saline-tolerant insects with regard to their ecology, physiology and evolutionary history. The reasons for this are obvious. Mosquitoes are not only a nuisance to humans, but they also spread a variety of diseases, including the most deadly of all infectious diseases, malaria. Several researchers have examined the ecological distribution of mosquitoes and found that about 5% of all species known have larvae that are capable of surviving in hyperosmotic media, i.e. media more concentrated than about 30% seawater. The degree of salinity that mosquito larvae can withstand varies substantially among species. The reasons for this will be discussed in the section below dealing with physiology. Many species from many genera, however, live in marine waters in rocky tide pools, in salt marshes, which are often much more concentrated than seawater, and in desert pools, which can reach very high salinities and may possess ionic ratios highly different from seawater.

Ecology

Mosquitoes fall broadly into two groups based on their oviposition behaviour. In the first group, which contains the most genera, females lay their eggs directly on the water surface. Species in the genera *Culex* and *Culiseta* form the eggs into an egg raft, whereas species in other genera, such as *Anopheles*, lay the eggs singly. In all cases, the eggs float on the surface until hatching. As the females come into intimate contact with the aquatic medium, it is clear that they test the medium (perhaps by taste) to determine if oviposition should proceed. It has been demonstrated repeatedly, and in many species, that females show marked preferences in oviposition sites with regard to salinity, pH, presence of microorganisms, etc. (O'Meara, 1976). Although the larvae can survive in both fresh and saline waters, salinity preference may be adaptive due to the reduction in competition and predation.

Mosquitoes species in the genera *Aedes* and *Opifex* are referred to as floodwater mosquitoes. These species lay their eggs on the soil adjacent to a body of water, or even at sites that currently contain no water, but will be flooded at some time in the future. The eggs remain in a form of diapause until covered by rising water. This may occur due to rain in inland pools, or due to storm surge or high tide in marine habitats. Oviposition site selection involves selecting a site that will flood during the next rise in water. Both freshwater and saline-water species have an uncanny ability to predict sites that will flood with the next rise in waters, but how the females select these sites is poorly understood. What is clear is that females partial to saline sites often must lay their eggs amidst salt crystals left behind by the receding, drying waters.

The larvae of mosquitoes feed on algae, detritus and microorganisms, either by filter feeding using bristles around the mouth, or by grazing on algae and bacterial mats using the mandibles. Saline-water species benefit from the high productivity of brackish and saline sites. Mosquito larvae are very vulnerable to predation by fish, notonectids, dragonfly larvae, etc. but saline habitats, and particularly those subject to rapid changes in salinity, tend to have few of these predators. As a result, saline-water species of mosquitoes tend to occur in high-nutrient, productive waters with few predators. Saline habitats are famous for their extraordinarily high densities of mosquitoes: in Florida, more than 250,000 mosquitoes were trapped in one location in one night, and egg densities of 10,000/square foot ($>$110,000/m^2) have been recorded (Provost, 1952; Nayar, 1985).

The pupae of mosquitoes are mobile, but lack a mouth and do not feed or drink. The cuticle appears to be quite impermeable as Sheplay and Bradley (1982) showed that pupae could complete their 2-day metamorphosis even in extraordinarily concentrated media. No site of active salt uptake or excretion is known from pupae.

The adults emerge from the water surface and begin a terrestrial and aerial existence. The adults of saline-water forms are indistinguishable from freshwater forms with regard to behaviour. The males feed only on nectar, the females on nectar and blood. Some species are autogenous, meaning that they can produce at least one batch of eggs without feeding, using nutrients carried over from the larval stages. The only behaviour known to vary in the saline-water forms is the preference for oviposition sites.

Physiology of osmoregulators

Biologists have long been fascinated by the capacity of mosquito larvae to survive in saline environments that are much too toxic for any aquatic vertebrate.

Beadle (1939) was one of the first to investigate the physiology of this group and his studies focused on *Aedes detritus*, a species that resides in coastal marshes in northern Europe. He demonstrated that the insects ionoregulate and that organs in the posterior portion of the animal were responsible for that regulation. Ramsay (1950) demonstrated that the rectum was the site of ion concentration and a hyperosmotic urine was excreted via the anus. Similar results were obtained in the species *Opifex fuscus*, a species endemic to New Zealand (Nicolson and Leader, 1974).

On the basis of these studies, it was clear that the species of *Aedes* that had been examined up until that time were osmoregulators, meaning that they regulate the osmotic concentration of their haemolymph at about 300 mOsm, regardless of the concentration of the external medium. As these larvae often are found in saline waters with osmotic concentrations above that of seawater (1000 mOsm), they clearly face large osmotic gradients driving water out of the larva. Bradley and Phillips (1975, 1977b) conducted a series of studies to determine how the larvae were able to maintain osmotic and volume regulation under these circumstances. They found that the saline-water larvae drink the medium at a rapid rate, equal to about their body volume every 10 h. Interestingly, this occurs in freshwater larvae as well, although the rate may be lower. Drinking the external medium therefore occurs in all larvae examined to date, and may be an additional mechanism for obtaining nutrients in the form of dissolved organic material. In the case of saline-water forms, drinking replaces the water lost across the integument by osmosis, as well as any water lost in the urine. This solves the problem of volume regulation, but the high salinity of the water exacerbates the problem of ion regulation. The rectum, therefore, must deal with these ionic and osmotic loads.

An important feature found in the saline-water forms of *Aedes* and *Opifex* is a two-part rectum, in contrast to freshwater forms that have a rectum with only one segment. Bradley and Phillips (1975, 1977a,b,c) conducted several studies examining the process of hyperosmotic urine production in the larvae of *Aedes taeniorhynchus* and *Aedes campestris*. They examined the function of the rectum in detail and found that the anterior rectal segment, that portion resembling the rectum of freshwater forms in its histology, served a similar function in saline-water larvae, i.e. as the site of potassium and chloride uptake from the urine (Fig. 2.3). The posterior segment, namely the portion that is histologically distinct from the freshwater rectum, is unique to saline-water forms and serves as a salt gland. It is the site of active ion transport into the rectal lumen. Ion transport is rapid and, as it is unaccompanied by equivalent amounts of water, the secretion is hyperosmotic. Bradley and Phillips (1975, 1977a,c) found that the concentration of the rectal fluid was always hyperosmotic to the medium in all waters in which the larvae could survive.

The types of ions and rates of ion transport are influenced by the water in which larvae are reared (Bradley and Phillips, 1977a). The larvae can survive in very dilute waters if they hatch in such media. Under these circumstances, the recta presumably function in a manner identical to those of freshwater species. In concentrated media, the recta adjusted the ions transported to match the ions taken in during drinking. In water rich in sodium and bicarbonate, the rectal fluid

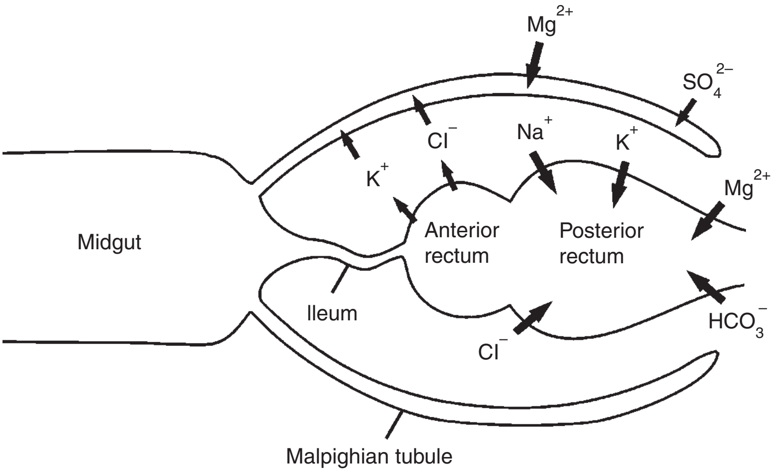

Fig. 2.3. Internal organs of the larvae of the saltwater mosquito *Aedes taeniorhynchus*. The directions of active ion transport are depicted. The rectum is divided into an anterior and a posterior segment, which have highly differentiated roles in ion transport (Redrawn from Bradley, 1985).

was also rich in sodium but low in chloride. When the water was rich in sodium and magnesium sulphate, the rectal fluid was also rich in sodium and magnesium. The only ion which it seems the larval rectum could not transport was sulphate. This large, divalent anion was never transported in substantial amounts by the rectal epithelium. Instead, the Malpighian tubules are the site of excretion of this ion. The Malpighian tubules produce a fluid isosmotic with the haemolymph. As the haemolymph is regulated at a concentration of about 300 mOsm, the amount of sulphate the larvae can eliminate through these organs limits their capacity to survive in sulphate-rich waters.

One remaining question is how larvae obtain physiologically necessary ions from the medium if these are in low supply. For example, in some inland saline waters, the medium can be highly saline, yet be very low in chloride, an ion required for normal physiological function. In dilute media, freshwater species take up sodium and chloride from the external medium using the anal papillae. These are protruberances near the anal opening at which active ion uptake occurs (Patrick *et al.*, 2006, Donini *et al.*, 2006). When saline water species are grown in dilute media, they have enlarged anal papillae that are also likely to be involved in ion uptake. In concentrated media, the anal papillae may be involved in ion uptake if certain ions occur at low concentrations in the media (Phillips and Meredith, 1969).

Physiology of osmoconformers

Not all species of mosquitoes with saline-tolerant larvae engage in osmoregulation; larvae in the genera *Culex* and *Culiseta* osmoconform in all media more concentrated than 30% seawater. This means that, in media ranging from about 300 mOsm to 1000 mOsm (the concentration of seawater), the osmotic concentration of the haemolymph exactly matches that of the external medium (Garrett and Bradley, 1984).

Analyses of the haemolymph of larvae of *Culiseta inornata* and *Culex tarsalis* reared in concentrated media, revealed that the extracellular fluids in these larvae contain high levels of amino acids, particularly proline and serine (Garrett and Bradley, 1984). The haemolymph also contained unusually high levels of trehalose, the common blood sugar of insects. Clearly, these larvae allow high levels of compatible solutes to accumulate in the haemolymph, thereby raising the osmotic concentration of the haemolymph to a level equal to that of the external medium.

Compatible solutes are osmotically active compounds that, although they raise the osmotic concentration of the water in which they are dissolved, do not disrupt proteins and membrane structure in the same manner as salts (Yancey, 2005). Ionized salts such as Na^+, K^+ and Cl^- have high charge densities. These interact with proteins and membranes, often binding to charged sites and disrupting hydrogen bonds that determine the tertiary structure of proteins. Compatible solutes are osmotically active, as they are fully solubilized, but they lack the charge density required to disrupt hydrogen bond and protein structure. As a result, the osmotic concentration of the haemolymph is elevated, but physiological functions in the tissues are not disrupted.

The above studies elucidated the osmolytes that occur in the haemolymph of osmoconforming mosquito larvae. Given that the cells must themselves osmoconform with the haemolymph that bathes them, what are the osmolytes in the intra-cellular compartment? Patrick and Bradley (2000) answered that question by analysing the organic solutes in the extra- and intra-cellular compartments of *Culex tarsalis* larvae acclimatized to 60% seawater. They found that trehalose was restricted to the haemolymph as an osmolyte, but that the intracellular compartment was protected by high levels of proline. This was the first demonstration that the same compatible osmolyte could be used both intra- and extracellularly in any animal.

Garrett and Bradley (1987) speculated on the physiological advantages of the osmoconforming (*Culiseta* and *Culex*) versus the osmoregulating (*Aedes* and *Opifex*) strategy. Osmoconforming larvae do not experience a large osmotic gradient across the body wall and, as a result, do not lose water osmotically to the external medium. This reduces the need for drinking and greatly reduces the need for active ion transport. The strategy of osmoconforming, therefore, should result in a substantial energy savings. Some energy is required to synthesize the organic compounds used as compatible osmolytes, but this does not represent a real energy loss as these compounds are in the body and can be used later, for example, during the pupal or adult stage as sources for metabolic energy. Despite the advantages of this system, Garrett and Bradley (1987) indicate that osmoconforming species have been reported in water only ranging up to about 60% seawater. Since then, we have collected *Culex tarsalis* from the Salton Sea in California, USA, in water that had a concentration of 110% seawater (personal observations). It is unknown, however, if the larvae were always in such waters or could complete development under these conditions.

The osmoregulatory strategy, by contrast, rests on the notion that the internal fluid compartment will be strictly and rigorously regulated with regard to ionic and osmotic strength. Substantial energy output will be devoted to that purpose and specialized organs (the posterior rectal segment) must evolve to meet these demands. The advantage of this mechanism is that the mosquitoes can survive in any medium. Ion pumps exist for most of the major ions found in the environment and the larvae can use the rectum and Malpighian tubules to remove these from the haemolymph, should they enter through ingestion. The disadvantage, that energy is expended in active ion transport, may be overcome by the rich nutrient levels in the water and the abundance of food in the form of algae and bacteria. The support for these notions resides in the fact that the osmoregulating larvae of *Aedes taeniorhynchus*, *A. sollicitans* and *A. campestris* are routinely found in salt marshes and saline ponds ranging in salinity up to 200% seawater. Bradley and Phillips (1977b) examined larvae that could complete their development in NaCl-rich water with a concentration equivalent to 300% seawater. On the basis of these observations, it would seem that osmoregulation is a viable strategy for invading highly saline media. The energy cost this strategy engenders can seemingly be overcome if the environment is sufficiently rich in food for the larvae.

Evolution

In recent years, my collaborators and I have been investigating the evolutionary pathways by which saline tolerance arose in mosquitoes (Grueber and Bradley, 1994; Albers and Bradley, 2005). The first step was to establish the primitive condition in the family Culicidae. The first clue is that 95% of all mosquito species are restricted to freshwater, i.e. they possess a one-part rectum, can only produce urine that is iso-osmotic or hypo-osmotic to the haemolymph, and cannot survive in media more concentrated than about 30% seawater. The rectum of these species can only transport ions into the haemolymph, not out. In addition, the two families of insect most closely related to the Culicidae are both strictly freshwater. Taken together, these observations argue that the freshwater condition is primitive in the Culicidae. This conclusion is further supported by the observation that salt tolerance occurs in many genera (nine genera are listed by O'Meara, 1976) yet, in most genera, saline tolerance is a rare and derived trait. The most likely scenario, therefore, is that mosquitoes were initially restricted to freshwater and that saline tolerance arose repeatedly and fairly recently in several lineages in the family.

To examine the process in more detail, we chose a group of mosquitoes formerly in the genus *Aedes*, but now considered to be in the genus *Ochlerotatus*. Many of the species discussed above (*Aedes taeniorhynchus, A. campestris, A. sollicitans, A. detritus*) have now been placed in the genus *Ochlerotatus*. We mapped the ecology and physiology of the species in this group on to a phylogeny provided by Schultz *et al.* (1986); the results are shown in Fig. 2.4. Note

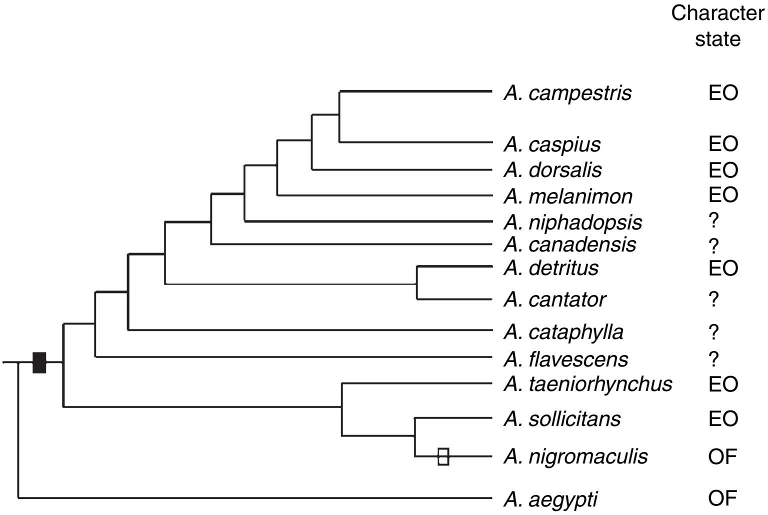

Fig. 2.4. The phylogeny of species of *Aedes* (now *Ochlerotatus*). Salt-tolerant species are indicated by a character state of EO (euryhaline osmoregulators). Freshwater species are designated by OF (obligate freshwater) (Redrawn from Grueber and Bradley, 1994). The filled box indicates a change of character state to salt tolerant; the open box indicates reversion to the obligate freshwater condition.

that the saline-tolerant species are scattered throughout the phylogeny. Assuming that the freshwater condition was ancestral, saline tolerance apparently arose repeatedly in the group. Alternatively, the entire clade may have been saline-tolerant with several cases of reversion to the freshwater condition.

The species *Aedes melanimon* provides an interesting situation. The larvae of this species have a two-part rectum and can survive in full-strength seawater. In nature, however, the larvae are found in freshwater habitats in flooded pastures in Southern California. It seems, therefore, that the physiology and ecology of the species do not always map precisely on each other.

The species *Aedes nigromaculis* is also an interesting case. *Aedes nigromaculis* (a freshwater species with a one-part rectum) is a sister species to *A. sollicitans* (a saline-water species), and their closest relative is *A. taeniorhynchus*, another saline-water species. This species cluster provides the strongest evidence that reversion to the freshwater condition has occurred in this clade, with reversion involving behavioural, physiological and morphological traits.

We are left, therefore with the surprising result of multiple evolutionary steps, forward and back, as species move in and out of a variety of ecological niches. The changes involve complex genetic influences on behaviour and physiological capabilities.

Our understanding of the evolution of enhanced saline tolerance in this clade will improve as we gain further molecular information regarding the phylogenetic relationships. Even now, however, it is evident that the evolutionary process by which saline tolerance arises in mosquitoes is complex and governed by stochastic events as much as by environmental pressures.

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3

Larval Cannibalism and Population Dynamics of Dragonflies

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Abstract

Cannibalism, the process of killing and eating conspecifics, is common among odonate larvae and is believed to influence odonate population dynamics. Here we attempt to summarize and consider interactions among key factors linked to cannibalism at both the individual and population levels. Through cannibalism, odonate larvae receive energy directly from the consumption of the conspecific, and indirectly from reduced exploitation competition because the per capita food supply may increase. Cannibalism might, however, also incur costs such as risk of death and pathogen infections. Alternative food availability, population density and size structure of the cannibalistic population, and habitat structure are environmental factors that affect cannibalism rate in odonate larvae on a short-term basis. Theoretical models predict that cannibalism reduces size variation under most cannibalism intensities and life histories. The models also show that cannibalism can – but will not always – stabilize population dynamics. Unfortunately few long-term studies examining the population dynamics on dragonfly larvae have been performed, and we urge more such studies.

Introduction

Cannibalism is the process of killing and eating a conspecific individual. It was not until the influential reviews by Fox (1975) and Polis (1981) that ecologists started to recognize cannibalism as a ubiquitous phenomenon in natural systems. The two reviews also sparked a lot of interest in the relationship between cannibalism and such phenomena as behaviour, sexual selection, life history, competition, and population dynamics and structure. In this chapter we show that studies of dragonflies have widely contributed to the increased understanding of these relationships. In cases where no evidence of cannibalism has been found in dragonflies, we will turn to examples from other organisms.

Aquatic Insects: Challenges to Populations (eds J. Lancaster and R.A. Briers)

Our focus is on the ecologically important larval stage of dragonflies, but we would like to encourage the study of cannibalism in adult dragonflies as well. Such studies are to our knowledge non-existent, though we both have personal observations of this phenomenon. A well studied aspect of cannibalism that we will not address here is sexual cannibalism (Elgar, 1992), as we are aware of no examples in dragonflies. We start our chapter by evaluating the costs and benefits of cannibalism. After that, we look at mechanisms that affect cannibalism rate, and then we focus on implications of cannibalism for population dynamics and structure, and, finally, we provide some suggestions for future research on the topic.

Cannibalism Evidence from Diet Data

Diet data show that predation by odonate larvae on other odonate larvae is frequent in nature, suggesting a potential for cannibalism to affect population dynamics. A literature survey covering six studies showed that the highest percentage occurrence of any odonate species in the diet was 18, 5, 8, 10, 38 and 0% in studies by Pritchard (1965), Thompson (1978), Folsom and Collins (1984), Merrill and Johnson (1984), Blois (1985), Dudgeon and Wat (1986), respectively. Cannibalism intensity also varies within species. Van Buskirk (1992) found that the frequency of cannibalism changed during development in natural environments. His study found that cannibalism ranged from 0 to 14.7%, being low in small larvae and higher in large larvae (Van Buskirk, 1992). Laboratory studies and short-term semi-field experiments that have explored the various aspects of cannibalism are common, but more studies that estimate cannibalism of odonate larvae across species in the wild are clearly needed to identify factors influencing the frequency and impact of cannibalism.

Benefits and Costs of Cannibalism

By cannibalizing other individuals, odonate larvae could accelerate development and increase growth rate. Accelerated development leads to earlier emergence, which has important fitness implications (Anholt, 1991; De Block and Stoks, 2005). A higher growth rate (all else equal) would result in a larger size at emergence, another important fitness factor in odonates (Banks and Thompson, 1987; Anholt, 1991; De Block and Stoks, 2005). By shortening the dangerous aquatic larval stage, early emergence also reduces risk of larvae being cannibalized themselves.

Energy gain

The most obvious benefit of cannibalism is the extra energy and nutrients gained from consuming a conspecific, yet few experimental studies have actually shown an increase in growth as a result of the extra energy gain from the consumption of conspecifics. Cannibalism may also result in increased feeding rate with the removal of a competitor – either because of reduced distraction or risk from neighbours (Crowley *et al.,* 1988), or because of increased per-capita food availability (De Block and Stoks, 2004). De Block and Stoks (2004) managed to separate these two effects in a manipulative laboratory study (Fig. 3.1). They did this by manipulating the food availability of the cannibals. In Fig. 3.1, per capita food availability was corrected after cannibalism occurred, so that cannibals and non cannibals received the same per capita food level after cannibalism. In the case of no food correction, the cannibal received double the amount of food, since the food of the victim was available to the cannibal. They found that cannibalism increased growth rate, increased mass at emergence and decreased time to emergence. Figure 3.1 shows that mass at emergence increases in the case of food correction (so that cannibals and non-cannibals received the same amount of food after cannibalism to permit estimation of the direct gain from cannibalism). Interestingly, De Block and Stoks (2004) also found that cannibalism early during ontogeny had a large impact on size at emergence (Fig. 3.1). The increased per capita food availability is an indirect benefit of cannibalism because it may reduce competition by removal of a potential competitor, potentially increasing feeding rate. This indirect benefit is a special case of the indirect food web phenomenon ‘thinning’ (Abrams *et al.*, 1996; Van Buskirk and Yurewicz, 1998). De Block and Stoks (2004) explicitly examined the effect on growth and development when a competitor was eliminated by cannibalism. Their study found that cannibalism increased growth rate and mass at emergence and decreased time to emergence. Figure 3.1 shows that cannibals grew to a larger size at emergence by eating the food that would have gone to the cannibalized competitor. This result shows that thinning benefits are possible, but tells us little about their potential importance in nature.

Other studies on odonate larvae have also shown that growth and development increase via cannibalism. These include laboratory experiments (Hopper *et al.*, 1996; Johansson, 1996) and semi-field experiments (Anholt, 1994). In the tree-hole-living damselfly *Megaloprepus coerulatus*, Fincke (1994) found no difference in growth between individuals that cannibalized one smaller individual compared with a control, indicating no advantage gained from the cannibalism. None of these studies separated the direct effect of eating the victim from the indirect effect of reduced exploitation competition, but both factors may have contributed to the life-history responses observed.

Injury or death

One potential cost of cannibalism is that engaging in a cannibalistic interaction might result in an injury and, in the extreme case, the potential cannibal might end up being the prey. There exists no direct evidence of this cost in the odonate literature. However, indirect evidence comes from the fact that similar sized individuals often engage in staring contests against each other, resulting in an apparent war of attrition (Crowley *et al.,* 1988). These contests usually end with one of the contestants withdrawing. One interpretation of the withdrawal could be that it is too costly and risky to attack. In contrast, cannibalism between individuals

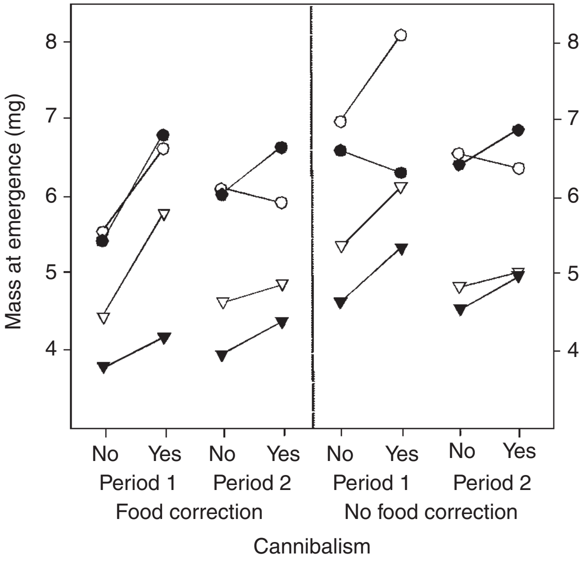

Fig. 3.1. The effect of cannibalism on mass at emergence of female larval *Lestes viridis*. Circles denote high food level and triangles low food level. White symbols indicate early photoperiod (low time stress) and dark symbols late photoperiod (time stress). Period 1 denotes if cannibalism occurred during the first half of the developmental period (before 50 days), and Period 2 if cannibalism occurred during the second half of the developmental period (day 51–104). See text for explanation of food correction. Modified from De Block and Stoks (2004).

differing in size is common even in the case where staring contests are going on initially (Baker and Dixon, 1986), suggesting that risk for the large individual is less in interactions. It could be argued that individuals do not have the physical capacity to prey on similar-sized individuals, but one of us (F. Johansson) has observed final instar larvae of *Aeschna juncea* cannibalizing each other under starvation. This observation suggests that there exists a negative relationship between aggressiveness and condition, and theory predicts that animals should be more risk prone when in poor condition (Houston *et al.*, 1988).

Pathogens and parasites

As individuals might be more likely to acquire pathogens from conspecifics than from heterospecifics (Freeland, 1983), we can assume that cannibals incur a higher risk of pathogen infection. Though no studies of cannibalistic transmission are available, there are examples from other organisms showing transmission of pathogens via cannibalism (references in Pfennig *et al.*, 1998). Such transmission might cause death or reduced fitness. For example, Pfennig (2000) elegantly demonstrated a reduced growth rate by tadpoles fed infected conspecifics in an experiment. However, recent theoretical modelling suggests that pathogens transmitted by cannibalism might be rare except under certain circumstances (Rudolf and Antonovics, 2007).

Loss of fitness

Another potential cost of cannibalism is that it might reduce inclusive fitness because of the risk of eating close relatives. As eggs of odonates are often attached together or deposited close together, there is a high risk of siblicide. On the other hand, cannibalizing a sibling reduces future resource competition, and hence sibling cannibalism might be beneficial in certain circumstances (Mock and Parker, 1997). From a theoretical point of view, we should thus expect cannibalism on relatives to be dependent on resources (Mock and Parker, 1998). No studies have been undertaken with odonates to determine whether they can discriminate among relatives with respect to cannibalism. From other invertebrates we know that such discrimination is possible (Michaud, 2003), but in many cases kin may tend to be similar in size and therefore cannibalism is less probable, even in the absence of sib discrimination (Wise, 2006).

In summary, we have good evidence that cannibalism provides benefits in dragonflies. Besides the costs of injury and death, we have little or no evidence of potential costs of cannibalism in dragonflies, though such costs occur in many other organisms. Certainly, more research is needed concerning these other costs.

Factors Affecting Cannibalism

Intraspecific density

If intraspecific density is high then we should expect frequent encounters between individuals, which could increase cannibalism. Such encounters are determined by the movement activity of the larvae. Support for higher rates of cannibalism at higher densities in odonate larvae has been found in simple laboratory studies (Fischer, 1961; Van Buskirk, 1989; Hopper *et al.*, 1996; Claus-Walker *et al.*, 1997; De Block and Stoks, 2004). In Fig. 3.2a, for example, it can be seen that cannibalism is more frequent at high densities of *Epitheca cynosura* under laboratory conditions. Field experiments, field enclosure experiments and mesocosm experiments suggest that the pattern observed at the laboratory level is found at larger-scale experiments as well (Johnson *et al.*, 1985; Van Buskirk, 1989, 1993; Anholt, 1994; Fincke, 1994). For example, survival rate of *Epitheca cynosura* was dependent on intraspecific density, and this effect was not attributed to prey density as food was not limited (Johnson *et al.*, 1985). A laboratory study by Crowley and Martin (1989) showed that per capita cannibalism rate went down with increasing density of potential cannibals. This suggests that similar sized and large cannibals engage in interactions that reduce cannibalism, though not enough to eliminate or reverse the density-dependent effect at the population level. But, a study by Van Buskirk (1992) did not find any density-dependent effects of cannibalism in field experiments run for 10–15 days.

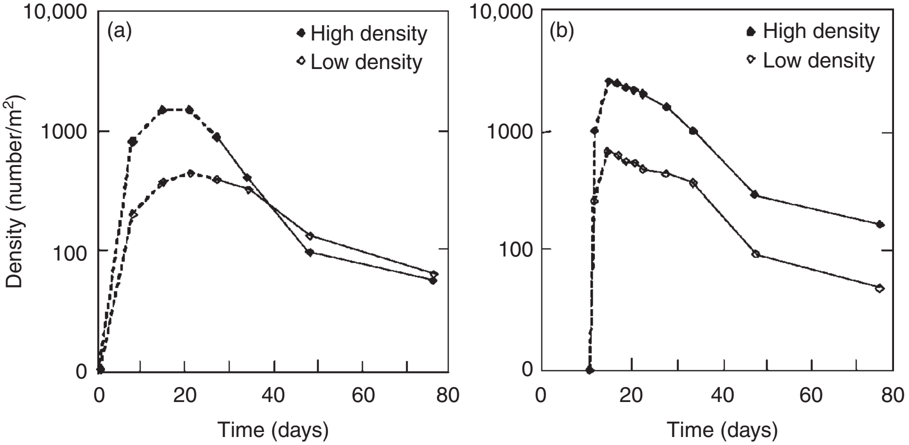

Fig. 3.2. Survival of high and low density cohorts of larval *Epitheca cynosura*. In (a), larvae were hatched asynchronous, and in (b) larvae were hatched synchronous. Dashed lines denote the span of the hatching period. Modified from Hopper *et al.* (1996).

In summary, density-dependent cannibalism is common in odonate larvae, but exceptions can occur. We suggest that the exceptions may arise from factors such as size distribution of larvae, habitat structure and behaviours, which will be discussed below.

Alternative prey

We define alternative prey as other species available for consumption. Alternative prey are likely to affect cannibalism through hunger level. If we assume that cannibalism is risky, then cannibalism should increase with decreasing alternative prey densities. The reason is that as density of alternative prey goes down, consumption of those prey goes down as well, increasing hunger. An increase in hunger usually triggers active and riskier foraging (Johansson, 1991, 1993; Werner and Anholt, 1993), which results in more encounters among conspecifics and more cannibalism. Support for this scenario has been found in odonates (Johansson, 1992; Hopper *et al.*, 1996). Though hunger increases cannibalism, starvation seems unlikely in the field, as odonates can withstand long periods of starvation (Lawton *et al.*, 1980; Wissinger, 1988). The incidence of cannibalism suggests that the benefits of a fast development and growth rate can outweigh the associated risk. Even if the risk of cannibalism is low, hunger level should increase cannibalism as encounters with conspecifics will be more common than encounters with alternative prey.

Habitat structure

Prey capture success declines with increasing habitat complexity, primarily because predator mobility and detection of prey are hindered by structure (Diehl, 1988).

Similarly, cannibalism rate in odonate larvae may go down as complexity increases. We have no direct evidence of this, but we provide examples from odonate systems where predation on alternative prey is reduced by habitat structure. First, Folsom and Collins (1984) found that predation by *Anax junius* on amphipods decreased with increasing habitat complexity. Second, predation rate on the damselfly *Coenagrion puella* by the backswimmer *Notonecta glauca* was lower at high habitat complexity compared with low complexity (Thompson, 1987). Thus, if predation success by odonate larvae goes down and their susceptibility as prey goes down as complexity increases, this suggests less cannibalism in complex habitats. Anholt (1994) found support for this prediction: survival of small larvae of the damselfly *Enallagma boreale* in the presence of large larvae was 10 times higher in a high complexity habitat compared with a low complexity habitat. But greater habitat structural complexity can sometimes reduce prey numbers (Warfe and Barmuta, 2006). Similarly, we suggest that cannibalism could increase with greater habitat complexity under certain circumstances. For example, for sit-and-wait cannibals, a higher habitat complexity might allow for a higher access to prey swimming in the water column.

Size structure

Cannibalism generally increases with relative size difference between the cannibal and the victim. Predators prefer to prey on prey smaller than themselves, presumably because smaller prey are less dangerous and easier to subdue. This preference is supported in studies on odonate larval cannibalism (Crowley *et al.*, 1987a; Wissinger, 1988; Fincke, 1994). Hopper *et al.* (1996) showed that cannibalism was low if larvae did not differ in instar, intermediate if larvae differed by one instar and high if the difference was two instars. A similar increase in cannibalism as an effect of instar difference between larvae was found by Wissinger (1988). His study showed a positive relationship between number of small larvae cannibalized and the size of cannibal in two species of dragonflies (Fig. 3.3). This pattern suggests that asynchronous hatching of eggs should increase the rate of cannibalism. In a laboratory experiment, Hopper *et al.* (1996) showed that asynchronous hatching (resulting in a broad size distribution) of larvae resulted in higher cannibalism compared with synchronous hatching. The results of their study can be seen in Fig. 3.2 where per capita death rate (the slope of the curve) is higher at high densities and asynchronous hatching. A high cannibalism intensity on small instar larvae can alter the size structure and developmental synchrony of the population (Crowley and Hopper, 1994).

Time constraints

Most odonates live in seasonal environments that impose time constraints, as larval development must cease with the onset of sufficiently severe conditions. Species that must emerge before winter should speed up their development and growth rates to keep size at emergence as large as possible (Rowe and Ludwig, 1991). One way of speeding up growth rate under time constraint is to increase

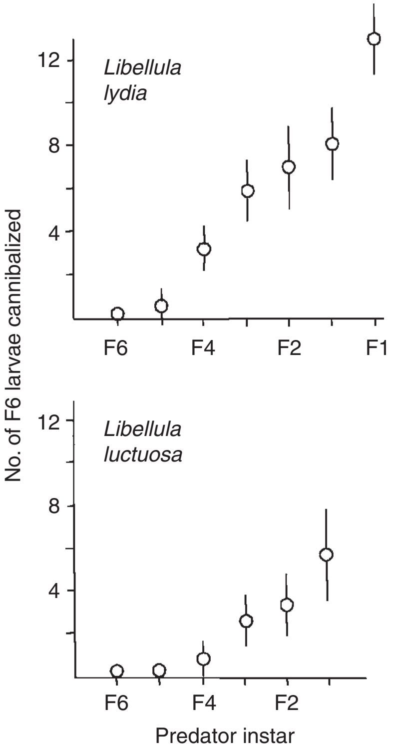

Fig. 3.3. Number of F-6 instar larvae cannibalized by *Libellula lydia* and *L. luctuosa* larvae in different instars. F denotes final instar larvae, F1 first instar from the last, F2 second from the last and so on. Vertical bars represent 1 SD. Modified from Wissinger (1988).

foraging activity. However, an increase in foraging activity usually results in a higher encounter rate with predators and conspecifics (Brodin and Johansson, 2004). We should therefore expect cannibalism rate to increase under time stress. For example, larvae that are late in their development with regard to the onset of the winter, should forage more actively and hence experience higher cannibalism.

Time constraints can be imposed by rearing larvae under a photoperiod simulating late season light conditions to which damselflies react by speeding up development. Johansson and Rowe (1999) found that cannibalism was higher among time-constrained than non-time-constrained larvae of *Lestes congener*. The larvae under time constraint in that study had a higher foraging activity, suggesting that a high encounter rate between individuals was the cause of the increased cannibalism. Moreover, time-constrained larvae may have been more willing to accept the risk of attacking a conspecific, possibly subjecting the attacker to counter attacks. Cannibalism was also more frequent under time constraint in larvae of *Lestes viridis*; in individuals with a high rate of cannibalism, development and growth rates both increased (De Block and Stoks, 2004).

Other factors

There are many other factors that can also affect cannibalism intensity. We will mention two additional ones. First, dragonflies are not always the top predators, and it is well known that top predators reduce activity of other predators that are potential prey via intraguild predation (e.g. Schmitz *et al.*, 1997). Such reduction in activity should result in less cannibalism in the presence of fish. Claus-Walker *et al.* (1997) found a trend indicating reduced cannibalism in *Epitheca cynosura* in the presence of fish scent in a semi-field experiment. Behavioural observation in the laboratory supported the observed trend, as larvae of *E. cynosura* reduced activity in the presence of fish.

Second, odonate larvae do differ in their 'lifestyle', *sensu* Sih (1987). A slow lifestyle is characterized by low activity, restricted microhabitat use, low feeding rate and low growth rate, whereas a fast lifestyle implies the opposite. In a suite of six species of odonate larvae, Johansson (2000) showed a strong difference in activity and microhabitat use. The study found a continuum from relatively inactive species exploiting the bottom as a microhabitat to relatively active species using the water surface as their microhabitat. The fast lifestyle odonate species were associated with fishless lakes while the slow lifestyle species were associated with lakes containing fish (Johansson, 2000). We should expect cannibalism to be reduced in the slow lifestyle species with reduced activity living on the bottom. No empirical studies have examined how such lifestyle differences among species relate to cannibalism rates. However, a study on the effect of intraguild predation among species found differences between odonate species in intraguild predation rate (Johansson, 1993). The difference in intraguild vulnerability in that study yielded equivocal results on the relationship between lifestyle characteristics and intraguild predation.

The primary challenge for ecologists is to determine which of the above factors and others are the most important and how they affect population structure, population dynamics and distribution of species (Crowley *et al.*, 1987b). Figure 3.4 provides an overview on how cannibalism might influence these population effects. The basic life cycle moves early instar (small) larvae by growth and development into the later instars (large larvae), contingent on survival, and the surviving late-instar individuals mature and reproduce, yielding the next generation after a time-lag of days to months. Prey availability (an alternative to eating conspecifics) generally speeds these vital rates with little effect on survival; but under food scarcity, survival can be reduced by risky foraging (shown as positive effects of growth and development or maturation and reproduction on survival). In general, however, survival and developmental processes trade off, depending especially on seasonal constraints and the influence of top predators. To the extent that larvae of different sizes maintain similar diets (perhaps more typical of slow than fast lifestyles), there may be competition for food, though evidence for exploitation competition in odonate larvae is limited. Cannibalism influences these processes in important ways, strongly increasing in intensity with density of potential cannibals (larger larvae) and victims (smaller larvae), producing density dependence that can help stabilize odonate population dynamics. Because cannibalism is often risky, exposing the potential cannibal to counter-attack or to other predators or parasites, the frequency of cannibalism is generally expected to be inversely related to the abundance of alternative prey. By evaluating the relative importance of these processes and effects on different species, especially with respect to slow and fast lifestyles, seasonal constraints,

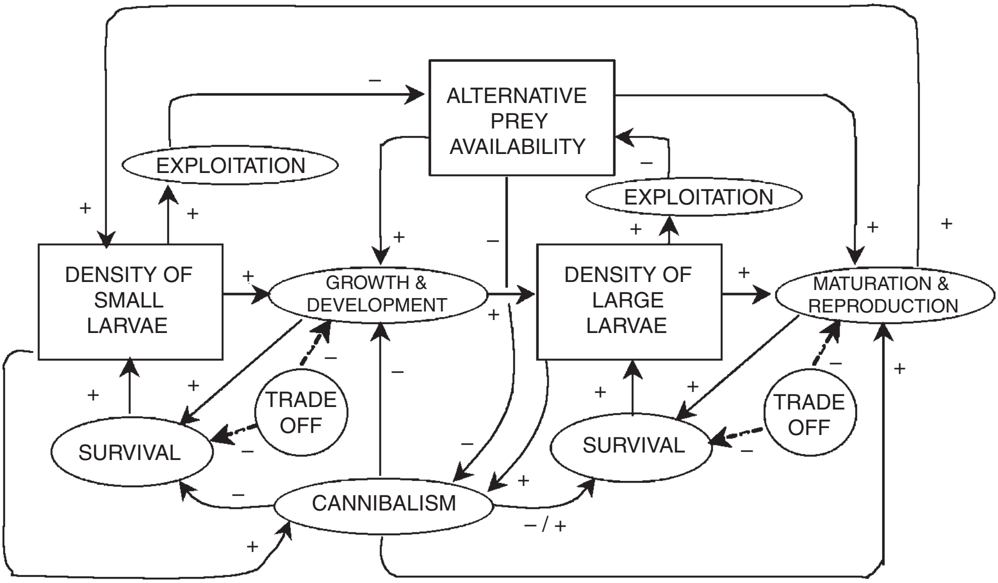

Fig. 3.4. An overview of how cannibalism influences densities and individual-level processes in larval odonates, based on literature reviewed in this chapter. The primary patterns and processes are indicated within elipses; environmental factors and state variables are shown in rectangles.

and predation regime, different dynamic patterns produced by different species can be better understood.

Population Size Structure and Dynamics

Models

Cannibalism can affect the size structure and dynamics of a population. A comprehensive review of general theoretical models on cannibalism and the population dynamics associated with different models is given in Claessen *et al.* (2004). Many of the studies they address indicate that cannibalism has a strong regulatory effect by strengthening density dependence. However, regulation of population density depends on the number and size of victims a cannibal can eat and, if saturation of the functional response is too abrupt, then cannibalism fails to control and can even destabilize population dynamics (Claessen *et al.*, 2004). Claessen *et al.* (2004) conclude that when population cycles are induced by density-dependent effects other than cannibalism (e.g. size-dependent competition for a common resource) cannibalism is more likely to act as a stabilizing mechanism. In contrast, age-dependent cannibalism with a time delay may cause population cycles.

Cannibalism could also serve as a ‘lifeboat mechanism’ (van den Bosch *et al.*, 1988). Under this scenario a cannibalistic population is able to persist under severely reduced food availability, whereas it would have gone extinct if the population was non-cannibalistic. In this case there are two stable states: extinct and persistent. The lifeboat mechanism allows the population to survive at low resource densities through a positive feedback in which the cost of cannibalism (mortality of victims) is smaller than the benefits gained from consuming victims (cannibalism). Hence the population survives a bottleneck situation of low food availability and thereafter recovers again as resource density goes back up. Claessen *et al.* (2004) end their review by concluding that: (i) cannibalism tends to be destabilizing with little or no competition for resources between cannibals and victims, and (ii) if competition is present, cannibalism is stabilizing when the juvenile victims are the stronger competitors for resources.

We are aware of only one model that considers the size structure and dynamics of dragonfly populations. Crowley and Hopper (1994) developed a density-dependent dynamic game model to explore the population consequences of cannibalism using parameter values from the cannibalistic dragonfly *Epitheca cynosura*. Their model showed that cannibalism decreased size variation within the population at low to moderate cannibalism intensities if cannibalism increased with *relative* size of the cannibal. Cannibalism increased the size variation when cannibalism was very intense and intensity depended on the *absolute* size of the cannibal. The model also showed that, at high alternative prey availability and low to intermediate fecundity, stable population dynamics were generated. But at low alternative prey availability and high fecundity, the population dynamics were more prone to be irregular.

As odonate systems can be viewed as metapopulations, cannibalism seems likely to dominate population dynamics only in rare circumstances, such as when the focal species is an abundant top predator with limited alternative prey available (see Van Buskirk, 1992 and below). Yet cannibalism (and the threat of cannibalism) may often influence phenological patterns, especially for species with plastic life histories and high population densities (Fig. 3.5). This influence hinges to a considerable extent on the feedback loop from cannibalism, to intra-cohort developmental synchrony, to instantaneous size variation and back to cannibalism – potentially facilitated by the effect of synchrony on cohort splitting (Fig. 3.5). When cannibalism desynchronizes the cohort by speeding the growth of the large cannibals relative to smaller at-risk individuals, this becomes a positive feedback loop that could help generate between-year variation. The typically strong damping effects of dispersal influx, other sources of density dependence (e.g. predators), and physiologically mediated seasonal forcing (Gurney *et al.*, 1992, 1994), however, should generally prevent major year-to-year fluctuations.

Nevertheless, odonates with circum annual life cycles capable of surviving the high stress season (winter or dry season) as larvae may cycle through complex seasonal patterns across generations under seasonal forcing (Gurney *et al.*, 1992, 1994). The result will be multimodal size distributions within years that will repeat each year, but with individual lineages reaching different modes in different years. These life histories usually result in overlapping stable limit cycles, though not of the period-doubling type. Multimodality is especially susceptible to shaping by cannibalism resulting from size asymmetries.

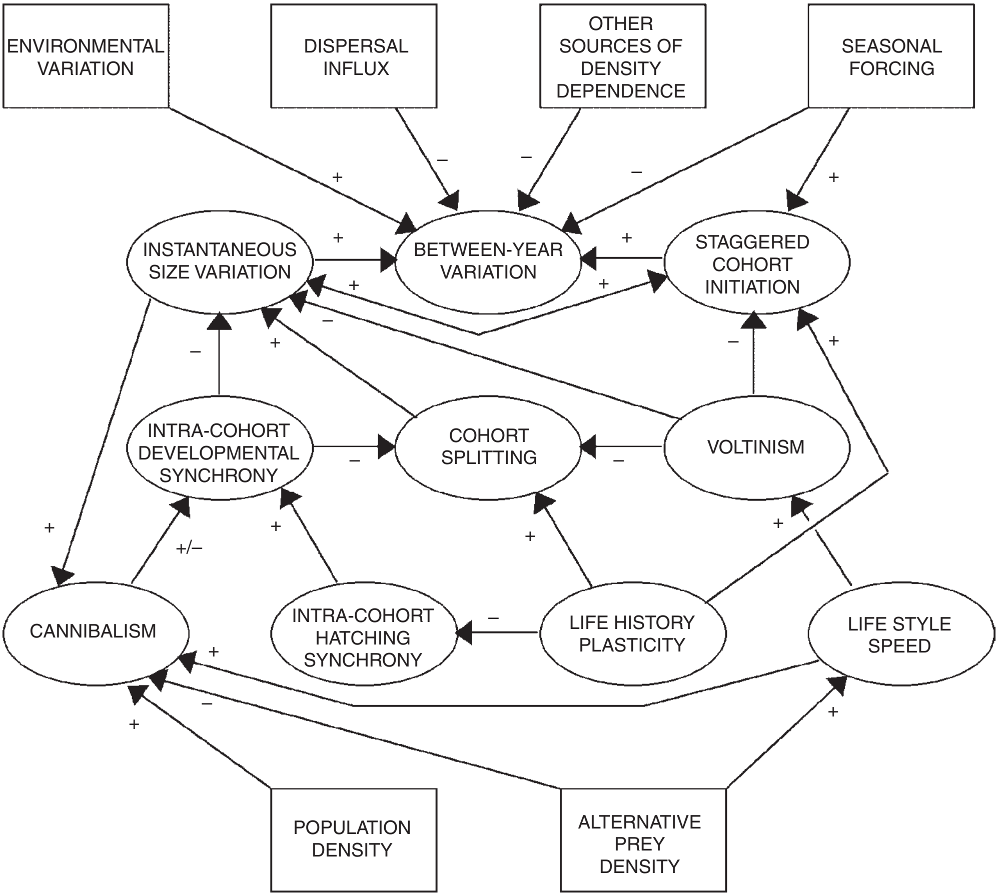

Fig. 3.5. Cannibalism and its implications at the population level. The primary patterns and processes are indicated within elipses; environmental factors and state variables are shown in rectangles. All influences are primarily unidirectional except for the bi-directional link between instantaneous size variation and staggered cohort initiation. Voltinism is the number of generations per year, which may be fractional.

Empirical evidence for models

Few studies have focused on the population dynamics of cannibalism in dragonflies, but see Van Buskirk (1992, 1993) for an exception. Most studies have addressed one generation or less, and those studies have focused on size structure and density dependence of cannibalism.

Support for the model prediction that cannibalistic species should feature low size variation within a cohort has been found in several studies on dragonfly larvae (Wissinger, 1988; Van Buskirk, 1989; Fincke, 1994; Hopper *et al.*, 1996). However, this pattern might simply reflect hatching synchronization and initial size distribution of larvae. If hatching is asynchronous, cannibalism might spread the size distribution out, probably as a result of a combined effect of competition and cannibalism (Hopper *et al.,* 1996).

Support for the model prediction that density-dependent survival might synchronize population dynamics has also been found in dragonfly larvae. Larvae of *Epitheca cynosura* showed stabilizing density dependence when hatching of larvae was asynchronous (Hopper *et al.*, 1996). Seventy-eight days after the first larvae had hatched, the initial high and low densities of larvae had converged to similar densities (Fig. 3.2). Interestingly, mortality from cannibalism was present in larvae when hatching was synchronous, but cannibalism did not result in convergence of densities (Fig. 3.2), suggesting that relative size distribution between larvae is an important factor that affects dynamics (Crowley and Hopper, 1994). Density convergence of larvae has also been found in field experiments (Johnson *et al.*, 1985).

Cohort splitting, where for example one part of a cohort may be on a 1-year life cycle track and another part on a 2-year life cycle track, is a common phenomenon in dragonflies (Norling, 1984; see also the models of Gurney *et al.,* 1992, 1994). Cohort splitting could result from competition among larvae or hatching asynchrony (references in Claus-Walker *et al.*, 1997). As cannibalism is common in odonate larvae and has the potential to act in a density-dependent fashion, we suggest that without cannibalism odonate larval density in natural habitats could show much larger variation among years than generally observed (Crowley and Johnson, 1992), but effects of cannibalism on within-year and within-cohort synchrony are more ambiguous. Cohort splitting may result in part from a behavioural response of the smaller larvae. In the presence of large larvae, small larvae reduce their activity and increase their hiding behaviour as an antipredator response (Van Buskirk, 1992; Johansson, 1993; Crowley and Hopper, 1994). With enough shelter and habitat complexity, this behaviour would slow down growth and development, resulting in a longer development time compared with the cannibals. A semi-field experiment by Claus-Walker *et al.* (1997) found that larvae from initially high densities with a high degree of cannibalism varied more in head width compared with larvae at initially low densities where cannibalism was less. An additional behavioural experiment in their study showed that the small larvae reduce their activity in the presence of large larvae. This finding supports the possibility that an antipredator response could increase size variation.

An intriguing population dynamical pattern in odonate larvae that might be driven by cannibalism comes from a field study by Van Buskirk (1992). The study showed a striking 2-year cycle in the age structure of *Aeschna juncea* populations (Fig. 3.6). Van Buskirk suggested that a large final (third-year) cohort suppresses the second-year cohort, thus releasing the first-year cohort. Once a large third-year cohort emerges, the eggs that are laid by them will comprise a subordinate cohort suppressed by the immediately preceding cohort. This 2-year cycle in age structure appears to be a period-doubling instability attributable to intense cannibalistic interactions between annually successive cohorts. The synchrony of the 2-year cycle may be maintained, in part, because the population studied is on an isolated island with presumably little impact from migrants. This can be visualized in Fig. 3.5 as a case with

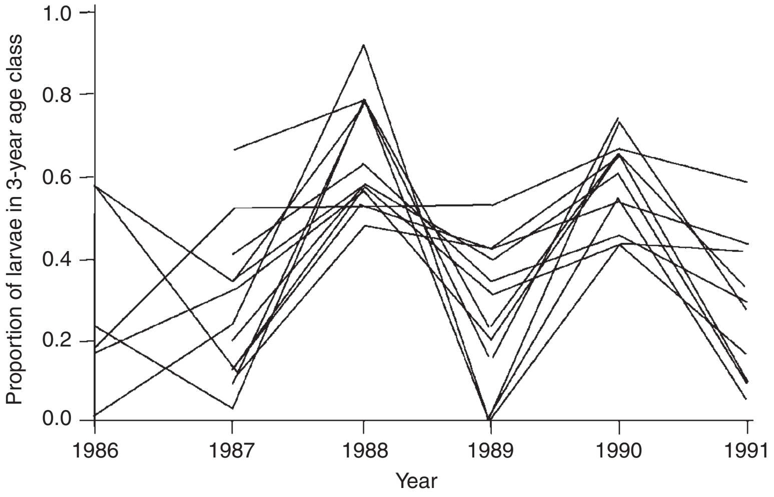

Fig. 3.6. Two-year cycle in the age structure of *Aeschna juncea* at Isle Royal. Each line represents a single pool. Modified from Van Buskirk (1992).

negligible dispersal influx or other sources of density dependence, but low voltinism and thus high size variation. The size variation results here in between-year variation but within-cohort synchrony maintained by intense relative, size-dependent cannibalism.

In summary, empirical results over a short timespan suggest that cannibalism reduces size variation within a cohort. However, the long-term dynamics of size distribution are less known. There are also important consequences for community structure resulting from cannibalism, and some of these are reviewed in Claessen *et al.* (2004) and Crumrine *et al.* (2008).

Future Directions

In this chapter we have shown that cannibalism is common in dragonfly larvae, and that cannibalism has several advantages for successful cannibals, such as faster growth and development. One of the potential costs of cannibalism is that it can reduce inclusive fitness. Many species of dragonflies deposit their eggs in clumps or other aggregates, and hence there is a high probability that cannibalism occurs among siblings upon hatching of eggs. We should therefore expect selection to act on traits to reduce kinship cannibalism. Many studies have shown that potential cannibals can recognize kin and therefore minimize kinship cannibalism (Pfennig, 1997); however, no such studies have been performed in dragonfly larvae. Two basic types of kin recognition have been identified (Pfennig, 1997). In the first type, 'phenotypic recognition', the cues are produced by the organism itself. Such cues may often be chemical. In the second type, 'non-phenotypic recognition', the cues are based on time and place, which influence cannibalism rate. For example, eggs within an egg clutch might hatch synchronously and this timing might decrease cannibalism, as cannibalism is reduced for synchronously hatching larvae compared with when hatching is asynchronous (Hopper *et al.*, 1996). Laboratory experiments with manipulation of egg clutches and their hatching synchrony should be able to explore this issue in dragonfly larvae.

Some organisms feature polyphenism, such that one morph is cannibalistic while another is non-cannibalistic (e.g. Pfennig, 1992). Such differences are usually induced by the environment and thus express phenotypic plasticity. Genetic differences with regard to cannibalism do also occur in some organisms (Baur, 1994; Stevens, 1994; Wagner *et al.*, 1999). Some of the genetic differences in cannibalism have been attributed to environments. For example, heritable differences in cannibalism intensity were expressed at low food levels but not at high food levels in the ladybird beetle *Harmonia axyridis* (Wagner *et al.*, 1999).We are not aware of any studies on genetic difference in cannibalism rate within or between populations in dragonfly larvae. As dragonflies disperse between habitats, such genetic patterns could be evident in dragonflies as well. For example, in years of harsh conditions with few resources and rapid pool drying, cannibalistic genetic lines would be at a selective advantage. But, in years with abundant resources and little risk of pool drying, cannibalistic genetic lines would be less favoured. However, genotypes could also respond to resource and pool drying among years by adjustments in phenotypic plasticity. Whether a fixed or a flexible genotype is favoured depends on several factors, such as predictability of the habitat quality and cost of plasticity (e.g. Sultan and Spencer, 2002). Two interesting questions would be: (i) is there genetic variation in the intensity of cannibalism? (ii) Is there an interaction with environment? These questions could be studied at the level of differences between populations as well as between species.

Using a combination of modelling and empirical studies, more work needs to address the way that cannibalism shapes size distributions and the timing of life cycles in natural populations. From field patterns and laboratory analyses of size-related intensities of cannibalism and magnitudes of behavioural shifts, models can begin to reveal the precise contributions of cannibalism to the dynamics of odonate populations.

Life-history dynamics also need to be addressed from a game-theoretic perspective: What is the role of cannibalism in making one life cycle pattern invasible by another within populations? And, how are these patterns influenced by the metapopulation structure and seasonal forcing typical of most odonate populations?

Finally, we emphasize the need to study cannibalism in the adult stage. For example, cannibalism on egg-depositing females should have a major impact on the dynamics, as the death of a female eradicates the whole clutch of offspring that potentially could be deposited into the system.

Acknowledgements

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4 The Ecology of Host–Parasite Interactions in Aquatic Insects

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Abstract

The importance of parasites in affecting characteristics at the individual, population, community and ecosystem levels in natural systems has been increasingly recognized and documented. A literature survey of the interactions between parasites and aquatic insects revealed strong taxonomic biases with respect to both hosts and parasites studied. Some relatively speciose and ecologically important groups (e.g. aquatic Coleoptera, Ephemeroptera, Plecoptera, Trichoptera) were poorly represented while others (e.g. Odonata, Culicidae) dominated the literature. Similarly, some groups of aquatic insects appear to be parasitized by relatively few parasite groups, and some parasites were studied from a narrow range of hosts. Studies on the ecological effects of parasites were dominated by those addressing effects on host fitness, but utilized a narrow range of hosts (largely odonates and mosquitoes) and parasites (largely gregarines, microsporidia, nematodes and water mites). Less than 5% of the 551 papers surveyed addressed population- or community-level effects of parasites. Because all host–parasite interactions take place within the framework of a larger set of species interactions occurring in a community, I discuss examples that address the context-dependent effects of parasites, and their effects at the population and community levels.

Introduction

It is an exciting time to be interested in the ecology of host–parasite interactions. Since the early 1990s, there has been a tremendous increase in interest in the effects of parasites on hosts, effects of hosts on parasites and interactions between parasites. Following the appearance of several highly influential models of host–parasite population dynamics that showed that, under realistic conditions, parasites should commonly have strong effects on host populations (Anderson and May, 1978, 1981), there has been a growing body of theory and empirical examples demonstrating the importance of parasites at the individual and population levels (Hudson, 2005; Hudson *et al.*, 2006).

Aquatic Insects: Challenges to Populations
(eds J. Lancaster and R.A. Briers)

Recent reviews (Thomas *et al.*, 2005b; Collinge and Ray, 2006) suggest that the study of parasites is even becoming part of mainstream community and ecosystem ecology.

By contrast, general reviews of aquatic insect ecology (Resh and Rosenberg, 1984; Ward, 1992; Williams and Feltmate, 1992; Allan, 1995; Hershey and Lamberti, 2001) either largely ignore host–parasite interactions or discuss parasitism in the context of aquatic insects that are themselves parasites or parasitoids (e.g. the aquatic Hymenoptera). Thus, although several reviews focused on particular parasite groups or host–parasite systems are available (e.g. Hominick and Welch, 1980; Molloy, 1981, 1988; Beier and Craig, 1985; Smith, 1988; Rolff, 2001; Smith *et al.*, 2001), it seemed appropriate to take a broader view of the literature here. In this chapter, I first survey the literature to identify general patterns in the nature of research conducted on host–parasite interactions in aquatic insects. I then highlight examples of research focusing on effects of parasites at the individual and, especially, population and community levels. I conclude with some recommendations for future studies.

Literature Survey

The Web of Science was used to survey the literature on host–parasite interactions in aquatic insects. Initially, I used a search strategy such as: (ephemeroptera OR mayfl*) AND (parasit* OR diseas* OR infect*). This was followed by a more focused search on each of the major parasite groups encountered. These searches were supplemented by examining references cited in many papers, and papers that cited those works. These searches were performed for each of the wholly aquatic orders (Ephemeroptera, Plecoptera, Odonata, Trichoptera and Megaloptera), and for the largely aquatic families in the partially aquatic orders (Hemiptera, Coleoptera, Diptera, Lepidoptera and Neuroptera). I excluded papers from the voluminous literature dealing with aquatic insect vectors of human or wildlife diseases, or that dealt with the use of pathogens, such as *Bacillus thuringiensis* in biocontrol programmes. I categorized the resulting papers by host group (order or family), parasite group (e.g. microsporidia) and by the nature of the study. Study type categories included: description, prevalence, several categories dealing with effects of the parasite(s) on host fitness (growth, condition, survivorship, fecundity, morphology, physiology, behaviour, mating), host range, host immune response, context-dependent effects, population-level effects, community-level effects, parasite behaviour, parasite fitness and coevolution. Most papers were classified as representing two or more of these categories. Studies classified as 'descriptive' often described one or more new parasite species and presented information on the parasite's life cycle or nature of the host–parasite relationship. Studies classified as 'prevalence' presented information on the proportion of the host population infected by a parasite. To be classified as presenting 'population-level effects' the paper needed to present information, often time-series data, on both parasite prevalence and host population size.

A total of 551 papers was considered to satisfy the search criteria and was included in the survey. However, this list of papers is far from exhaustive. In particular, a number of papers cited in World Health Organization summaries of pathogens of biting flies (e.g. Clark, 1977; Federici, 1977; Hazard and Chapman, 1977; Strand *et al.*, 1977) did not appear in my searches. None the less, most of those papers present descriptive information and little, if any, information on ecological effects on host individuals or populations.

There was appreciable variation among aquatic insect orders/families in the number of papers reporting information on host–parasite interactions (Table 4.1). For example, only 9.4% of the papers reported on interactions in Ephemeroptera, Plecoptera and Trichoptera, three orders that are especially important in the structure and function of running water ecosystems (Allan, 1995), figure prominently in measures of stream ecosystem health (Wallace *et al.*, 1996) and represent about 25% of aquatic insect species considered in this survey. The three stonefly studies reported on somewhat atypical parasites: chironomid (Diptera) larvae (Giberson *et al.*, 1996; Doucett *et al.*, 1999) and gordian worms (Nematomorpha) (Winterbourn, 2005). Even more striking is the dearth of studies on a very speciose group, the Coleoptera. Sprague (1977) reported microsporidia from only one stonefly and none from aquatic Coleoptera, but over 100 mosquito (Diptera: Culicidae) hosts, which suggests that my survey results for these group may not be strongly biased. It is unclear whether the relative paucity of reports on these groups indicates they are seldom parasitized, or that they have been poorly studied with respect to host–parasite interactions. Given that most workers expect that every species is host to at least one parasite (Dobson *et al.*, 2006), lack of study seems the most likely explanation. None of the papers encountered in this survey reported the results of surveys to determine the incidence of parasites in a broad range of potential hosts.

Similarly, some groups of aquatic insects appear to be parasitized by relatively few parasite groups (Table 4.1). For example, 85% of the papers on odonates reported on interactions with gregarines (phylum Apicomplexa) or water mites (Arachnida), and in nearly all of those papers the host was a damselfly. In another well-studied group, the black flies (Diptera: Simuliidae), a high proportion of studies involved either nematodes, especially the family Mermithidae or microsporidia. Finally, some parasites were studied from a narrow range of hosts. Most studies on gregarines come from odonates or mosquitoes, and most studies on viruses are from Diptera. By contrast, studies of microsporidia, nematodes and water mites are reasonably well represented in most aquatic insect groups.

There was considerable variation among parasites in the nature of studies that were reported. Overall, 59% of the studies presented only descriptive information or information on disease prevalence, but that varied substantially among parasites (Table 4.2). A high proportion of studies on microsporidia fell into this category, and that held true for nearly all host groups except the Culicidae. It would be a mistake to dismiss such studies as not reporting information of ecological interest, as several report substantial information on disease prevalence (e.g. Andreadis, 1999, 2002) that can be useful in determining when and under what conditions epizootics occur.

One hundred and sixty studies (27.5%) presented information on parasite effects on host fitness (Table 4.3). 70% of these studies came from just four

Table 4.1. The number of studies satisfying the literature search criteria by host and parasite taxonomic groups.

			Parasite											
Taxon	World species	Total papers	Virus	Bacteria	Gregarine	Ciliate	Trypanosomatid	Fungus	Microsporidia	Nematode	Helminth	Water mite	Chironomidae	Other
Ephemeroptera	3,100	28	1		1	2			1	15	6		2	
Plecoptera	2,000	3	1										2	1
Odonata	5,500	89	1		41				5	1	4	35		5
Hemiptera	2,600	27	1		1		4		1		2	18		1
Trichoptera	11,000	21						1	13	2	1	3		
Megaloptera	300	5				1				1	2			1
Coleoptera	9,500	4								2		2		
Diptera														
Ceratopogonidae	5,300	13	3				3	2	2	6				
Chironomidae	5,000	68	7	3				7	15	22		15		
Culicidae	3,500	216	16	9	30	13		17	78	33	11	13		
Simuliidae	1,800	62	12			2		9	17	33	1	1		
Other Diptera	>15,000	20	1	4	1		2	2	4	3		4		

Table 4.2. The per cent of studies reporting only descriptive information or information on disease prevalence. The number of studies in each category is in parentheses. The total number of studies (582) is greater than the total number of papers in Table 4.1 because some papers reported on >1 parasite group.

	Parasite											
Taxon	Virus	Bacteria	Gregarine	Ciliate	Trypanos-omatid	Fungus	Micro-sporidia	Nematode	Helminth	Water mite	Chirono-midae	Other
Ephemeroptera	100 (1)		100 (1)	0 (2)			100 (1)	40 (15)	83 (6)		100 (2)	
Plecoptera											100 (2)	100 (1)
Odonata	100 (1)		63 (41)				100 (5)	100 (1)	75 (4)	14 (35)		0 (5)
Hemiptera	100 (1)		0 (1)		25 (4)		100 (1)		100 (2)	44 (18)		100 (1)
Trichoptera	100 (1)					100 (1)	77 (13)	100 (2)	100 (1)	100 (3)		
Megaloptera				0 (1)				100 (1)	50 (2)			100 (1)
Coleoptera								50 (2)		100 (2)		
Diptera												
Ceratopogonidae	67 (3)				100 (3)	0 (2)	100 (2)	67 (6)				
Chironomidae	86 (7)	33 (3)				86 (7)	73 (15)	77 (22)		47 (15)		
Culicidae	44 (16)	56 (9)	43 (30)	23 (13)		71 (17)	65 (78)	32 (33)	18 (11)	15 (13)		
Simuliidae	83 (12)			100 (2)		56 (9)	88 (17)	79 (33)	0 (1)	100 (1)		
Other Diptera	100 (1)	100 (4)	100 (1)		50 (2)	100 (2)	100 (4)	100 (3)		100 (4)		

parasite groups: water mites, nematodes, microsporidia and gregarines. Furthermore, nearly all (96%) of the studies addressing gregarine effects on host fitness came from two host groups, odonates and mosquitoes, and 78% of the studies on microsporidia are from mosquitoes. Mosquitoes account for 52% of the studies addressing affects of parasites on host fitness and odonates account for an additional 19%. Twenty-six studies (4.5%) addressed the context dependence of host–parasite interactions (see below), and nearly 60% of those studies were conducted using mosquito hosts. Finally, <4% of studies addressed population- or community-level effects of parasites.

This survey indicates that considerable effort in the study of host–parasite interactions in aquatic insects has been directed at the effects of parasites on host fitness and, to a substantially lesser degree, effects of the host on parasite fitness. However, all host–parasite interactions take place within the framework of a larger set of species interactions occurring in a community. Because it is clear that both the strength and outcome of interactions can change as a function of their biotic and abiotic context (Agrawal *et al.*, 2007), it is important to address host–parasite interactions in a broader context to better understand their importance for populations and communities. I next consider studies that have begun to do this in aquatic insect–parasite systems.

Context-dependent Effects of Parasites

Most models of host–parasite population dynamics assume that parasite virulence (the rate of parasite-induced mortality, often represented as α) is a constant that does not vary with prevailing environmental conditions (Anderson and May, 1981, but see their model E where this assumption is relaxed). Currently there is considerable interest in whether the response of hosts to parasite infections varies with environmental conditions, such as host food availability, conditions in the habitat, such as temperature, and host sex (Sheridan *et al.*, 2000), and this interest is reflected in several recent studies involving aquatic insects. Most of these studies have examined whether food availability for hosts influences effects of a parasite on one or more fitness-related attributes of hosts, such as survivorship and adult size. The studies manipulate host food availability (or host density, which should affect per capita food availability) and parasite infection level in factorial designs, and test for a significant interaction between food and infection. These studies, most of which have been conducted in the laboratory, can be placed in three groups: those that find condition-dependent effects for all response variables, those that find condition-dependent effects for some but not all host attributes, and those that did not detect any condition-dependent effects. Agnew and Koella (1999a,b) provide good examples of the first group. Both studies examined effects of the microsporidian *Edhazardia aedis* on the mosquito *Aedes aegypti* in laboratory experiments. In both cases they found that the magnitude of parasite effects increased as food availability decreased. Several other studies have found consistent condition-dependent effects of food availability (Arnqvist and Maki, 1990; Braune and Rolff, 2001; Nguyen *et al.*, 2002). More commonly, studies find condition-dependent effects for some response variables,

Table 4.3. The number of studies reporting results in one or more study categories (see text for a description of the categories). The total number of studies (582) is greater than the total number of papers in Table 4.1 because some papers reported on >1 parasite group.

Parasite	Host fitness	Host range	Immune response	Context dependence	Population	Community	Parasite behaviour	Parasite fitness
Virus	8			1	3			
Bacteria	5				1			
Gregarine	24	3	5	7		1		
Ciliate	12		1	1				1
Trypanosomatid	2			2				
Fungus	8	1			3			
Microsporidia	23	4	1	6	7	1		4
Nematode	26	5	4	3	3			3
Helminth	10		2	2	1		1	
Water mite	39	1	8	3	2		4	6
Other	3		4	1				

but not all. For example, Comiskey *et al.* (1999) found that a gregarine parasite significantly reduced survivorship of the mosquito *Aedes albopictus* only when mosquitoes experienced low food availability. All other host attributes (emergence time, adult size, female fecundity) were significantly affected by food availability and infection status, but there were no interactive effects. Studies reporting similar results include: Lanciani (1975), Walker *et al.* (1987), Bedhomme *et al.* (2004) and Tseng (2004). Finally, only three studies reported condition-independent effects of food availability on host responses to parasites: Nasci *et al.* (1992), Klingenberg *et al.* (1997) and Agnew *et al.* (1999). Klingenberg *et al.* (1997) found no effects of gregarine load on body size or developmental time in a water strider, even when reared with low food availability. The other studies in this latter group found significant effects of both food level and parasite infection, but no interactive effects. Studies addressing the effects of abiotic conditions on host–parasite interactions are less common (Petersen and Willis, 1970; Mercer and Anderson, 1994; Taylor and Merriam, 1996; Van Rhein *et al.*, 2000; Gurski and Ebbert, 2003). Only Mercer and Anderson (1994) employed an experimental design allowing condition-dependent effects to be detected but, unfortunately, only two individuals became infected in their field experiment, which prevented meaningful tests of condition-dependent effects. Collectively, these studies suggest that much greater attention should be paid to the ecological context of host–parasite interactions involving aquatic insects.

Population-level Effects

Strong effects of a parasite on the dynamics of its host population imply, by definition, that the parasite exerts strong effects on the fitness of individuals in the population. However, even if strong effects of a parasite on the fitness of host individuals can be demonstrated, it does not necessarily follow that the parasite will have demonstrable effects on host population dynamics. The reason, of course, is that the host will nearly always be embedded in a food web and, as a consequence, direct and indirect interactions with other community members may play a more important part in shaping the dynamics of the host than interactions with the parasite (Washburn *et al.*, 1991; Washburn, 1995).

The processes influencing host population dynamics can be complex, even in seemingly simple communities that support few species. For example, the population dynamics of mosquitoes whose larvae develop in containers (e.g. treeholes and other phytotelmata, tyres) are influenced by several processes affecting larvae directly and indirectly, such as intra- and interspecific competition (which is influenced by larval density and food availability) and the presence of natural enemies (predators, parasites). Long-term dynamics are also influenced by periodic recruitment of new individuals into the population, which depends on female oviposition into the habitat. This process is also complex, as it is influenced by larval density, e.g. females oviposit preferentially in habitats containing an intermediate density of conspecific larvae (Zahiri and Rau, 1998), and by whether an oviposition repellent is being produced in the habitat, either as a result of larvae being stressed (by competition) or infected by parasites

(Lowenberger and Rau, 1994; Zahiri *et al.*, 1997; Zahiri and Rau, 1998; but see Reeves, 2004).

Schwab *et al.* (2003) performed a large-scale laboratory experiment in which several of these factors were manipulated simultaneously. They followed populations of *Aedes aegypti* for 14 days where adult females had the choice of ovipositing in containers that either contained larvae or did not. Containers with larvae were exposed to no, low or high levels of cercariae from a digenean trematode parasite, and all such containers received high levels of food to minimize intraspecific competition. They found strong effects of the parasite on *Aedes* population dynamics, largely achieved through much higher pupal mortality in the parasite treatments relative to the control, which resulted in substantially lower production of adults in the parasite treatments. Interestingly, females oviposited preferentially in habitats containing larvae in the final days of the experiment but, in contrast to other studies, did not discriminate among the parasite treatments.

Observations on the population dynamics of hosts in natural settings are made under much less controlled conditions than can be achieved in the laboratory, which affects what inferences can be drawn regarding the role of parasites in host population dynamics. Observations of host population collapses in the absence of accompanying data on parasite prevalence in the population (e.g. Hunter, 1968) or of disease epizootics without accompanying data on changes in host population density (e.g. Glenn and Chapman, 1978), while suggestive, do not demonstrate causation. Patterns in changes in host population density over time along with changes in parasite prevalence in the population has been used repeatedly to argue that parasites regulate host population dynamics (e.g. Molloy, 1981; Majori *et al.*, 1986) but, as discussed below, such data must also be interpreted with caution. Because the majority of population-level data on host–parasite interactions in aquatic insects are of this form, I will briefly consider patterns that have been observed, and then explore more generally the problem of inferring the role of parasites in the dynamics of host populations.

Micieli *et al.* (2001) reported on dynamics in an interesting system in which the parasite (the microsporidian *Amblyorspora albifasciati*) has a complex life cycle with two hosts, requiring that both host populations and disease prevalence in both hosts be monitored. *Amblyospora* is transmitted vertically from infected adult females to their progeny. These larvae develop lethal infections, releasing thousands of meiospores into the water. The meiospores are infective to the copepod *Mesocyclops annulatus* and produce lethal infections in adult females, which also release spores into the environment upon their death. These spores are infective to mosquito larvae, producing benign infections targeting female gonadal tissue. Micieli *et al.* monitored the dynamics of this system in an ephemeral floodwater habitat for one year, during which eight mosquito broods were produced as a result of periodic drying and filling of the habitat. They observed disease epizootics in the copepod, but not in the mosquito. Transovarial transmission was detected in five of eight broods, but disease prevalence in vertically infected larvae never exceeded 7%. Despite the occurrence of disease epizootics in the copepods, horizontal transmission from copepods to mosquitoes was detected only twice and appears to be the main factor limiting the impact of the disease on the mosquito population (see also Larkin *et al.*, 1995). The authors concluded that the disease may significantly affect the copepod population, but not the mosquito. Copepods were largely absent from the system from September through May, following a period (May–September) where several major epizootics occurred. Circumstantial evidence supporting this conclusion was that, in 50 other pools in the area and that were monitored over the same time period, no infections in *Mesocyclops* were observed and copepods were abundant throughout the year.

Especially striking dynamics were observed in a somewhat atypical system: the cholera bacterium (*Vibrio cholerae*) associated with egg masses of *Chironomus* sp. (Diptera: Chironomidae) (Halpern *et al.*, 2006). *Vibrio cholerae* occurs naturally as a free-living organism in aquatic habitats and has been found associated with zooplankton, especially copepods. An additional natural reservoir for *V. cholerae* is chironomid egg masses (Halpern *et al.*, 2004) and a haemagglutinin/protease enzyme secreted by the bacteria can degrade the egg masses, preventing the eggs from hatching (Halpern *et al.*, 2003). Halpern *et al.* (2006) monitored chironomid egg mass density and *V. cholerae* in the egg masses at two sites, a river and a waste stabilization pond. A striking pattern was observed at both sites: increases in chironomid egg mass density were followed by increases in *V. cholerae* density in the egg masses and a subsequent reduction in egg mass density (Fig. 4.1), suggesting that *V. cholerae* was driving the dynamics of midge egg masses and, hence, the dynamics of the midge populations.

Similar dynamics, although not always quite so striking, have been observed in a wide variety of systems and a diverse array of hosts and parasites: an entomopoxivirus in chironomid larvae in flood-control channels (Harkrider and Hall, 1978); nematodes in black fly larvae in streams (Phelps and DeFoliart, 1964; Takaoka, 1981); a fungus in ceratopogonid larvae (Diptera: Ceratopogonidae) in canal beaches (Wright and Easton, 1996); a microsporidian in mosquito and copepod hosts in bromeliad leaf axils (Micieli *et al.*, 2007); an iridescent virus in black fly larvae in streams (Hernandez *et al.*, 2000); and a baculovirus in mosquitoes in ponds (Becnel *et al.*, 2001). All of these cases are similar to the examples described above in greater detail in that they are, at best, suggestive that the parasite plays a major role in the dynamics of its host population(s). I will now consider approaches that can provide stronger evidence that a parasite is responsible for driving the dynamics of its host.

If a parasite plays a major role in regulating the population dynamics of its host, we should observe: (i) strong density dependence in the dynamics of the host, and (ii) strong evidence of density-dependent parasitism (Murdoch, 1994). Kohler and Hoiland (2001) monitored the population dynamics of the univoltine caddisfly *Brachycentrus americanus* (Trichoptera: Brachycentridae) and the prevalence of a microsporidian disease in the population for 15 years. The microsporidian is an undescribed species, tentatively placed in *Microsporidium*, which, based on its SSU rDNA gene sequence, appears to be more closely related to *Cougourdella* (Microsporidia: Cougourdellidae) than any other microsporidia. The disease attacks the fat body and eventually spreads to other tissues, resulting in host death, generally before pupation. The *Brachycentrus* population was

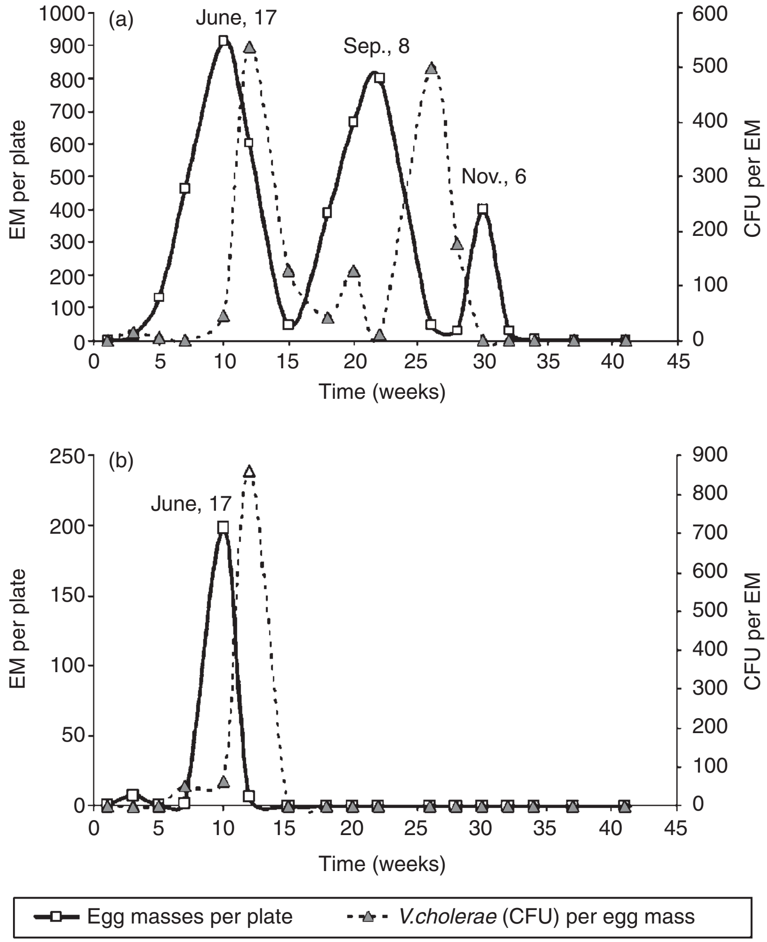

Fig. 4.1. *Chironomus* sp. population dynamics, as the number of egg masses (EM) per Styrofoam plate, and *Vibrio cholerae* population dynamic, expressed as colony forming units (CFU) per *Chironomus* sp. egg mass, in (a) a waste stabilization pond, and (b) the Kishon River, Israel between April 2003 and January 2004 (week 41). From Halpern *et al.* (2006).

censused annually near the time of peak pupation (pupation and adult emergence are both fairly synchronous), while disease prevalence and *Brachycentrus* density were also measured frequently in each generation to determine when epizootics occurred and to obtain weighted-average estimates of prevalence in each generation. Both the host and its pathogen appeared to exhibit cyclical dynamics over the 15-year period (Fig. 4.2), and statistical analyses of both time series supported this conclusion. For example, the autocorrelation function for the detrended time series of (ln-transformed) *Brachycentrus* population density exhibited a significant negative spike at a lag of two generations and a positive spike at a four-generation lag, suggesting that the population exhibited cyclic

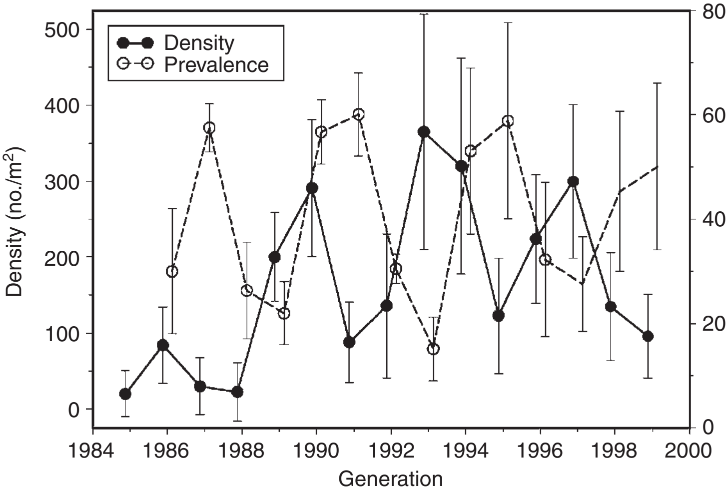

Fig. 4.2. *Brachycentrus americanus* population density (mean ± 95% confidence interval) in 15 consecutive generations (years) and the mean prevalence of *Microsporidium* in *Brachycentrus* larvae and pupae within each generation. Prevalence is the mean over all sampling dates in a generation, weighted by *Brachycentrus* population density on each date. Error bars are 95% confidence limits. Figure redrawn from Kohler and Hoiland (2001).

oscillations in density with a period of about four generations. The autocorrelation function for *Microsporidium* disease prevalence behaved similarly. A set of well-accepted statistical procedures provided strong evidence for density dependence in *Brachycentrus* population growth from the annual census data. While all tests provided evidence for significant direct density dependence, even stronger support was provided for the hypothesis of delayed density dependence with a lag of one generation (i.e. density in the previous generation significantly affected per capita population growth rate in the next generation). Finally, Kohler and Hoiland (2001) found no relationship between disease prevalence in a generation and *Brachycentrus* population density at the start of the generation, but disease prevalence in a generation increased markedly with increasing population size at the start of the previous generation (Fig. 4.3). Thus they observed strong evidence of delayed density-dependent parasitism with a lag of one generation, which is consistent with the pattern of density dependence in the host. Overall, their observations provided strong support for the hypothesis that the microsporidian disease is largely responsible for driving observed *Brachycentrus* population dynamics in this system.

Ultimately, the strongest tests of the role of parasites in affecting the dynamics of host populations will come through controlled manipulations of parasites (Hudson *et al.*, 1998; Tompkins and Begon, 1999; Redpath *et al.*, 2006) but, in many host–parasite systems, such experiments will be difficult if not impossible to perform, except in the laboratory. In lieu of controlled experimental manipulations in field settings, natural experiments, in which dynamics in systems with

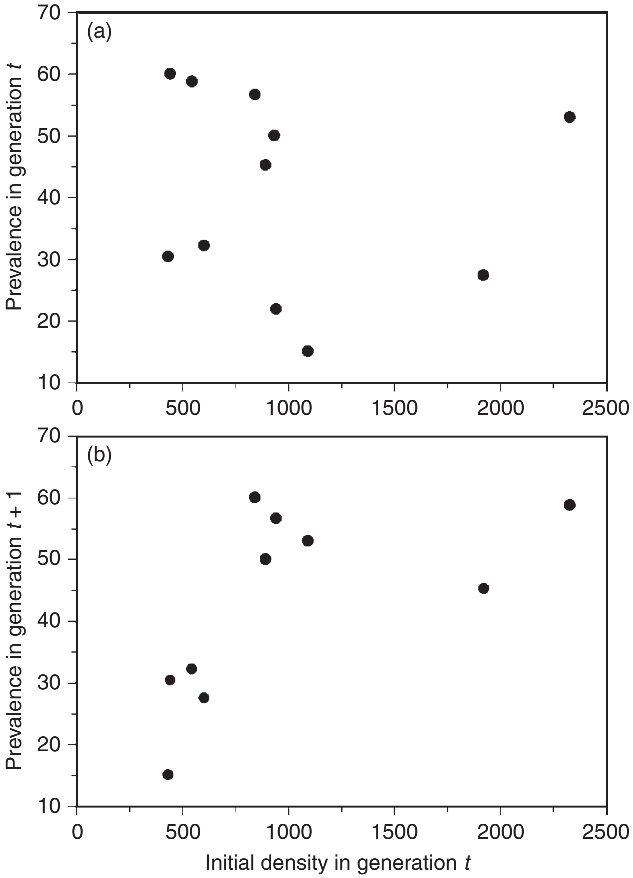

Fig. 4.3. The relationship between disease prevalence in a generation and *Brachycentrus* population density (a) at the start of the generation, or (b) at the start of the previous generation. Figure redrawn from Kohler and Hoiland (2001).

and without the parasite are compared, could be used much more frequently to gain insight regarding the importance of parasites in host population dynamics. Although the limitations of natural experiments are well known, their use in combination with other approaches to causal analysis, such as structural equation modelling, could provide a powerful alternative to controlled experiments when manipulations cannot be performed.

An example of the use of natural experiments is provided by the studies of the caddisfly *Glossosoma nigrior* (Trichoptera: Glossosomatidae) infected by the microsporidian *Cougourdella* sp. in coldwater streams (Kohler and Wiley, 1992). *Glossosoma* dynamics in ecosystems where *Cougourdella* is present are strikingly different from those in systems where *Cougourdella* infections have not been detected (Fig. 4.4). In systems where *Cougourdella* appears to be absent (or *Glossosoma* is highly resistant to infection), *Glossosoma* populations are relatively stable and do not exhibit marked fluctuations in size. In systems where

Cougourdella infections have been detected, *Glossosoma* populations appear to occur in either of two conditions or states: (i) a high density state where *Cougourdella* prevalence is consistently low, and (ii) a low density state where the population is maintained at low density by recurrent *Cougourdella* epizootics (Fig. 4.4a). These striking differences in patterns of dynamics between systems with and without the pathogen strongly suggest that the pathogen can play a major role in driving *Glossosoma* population dynamics.

The time-series data in Fig. 4.4a are not long enough to address the interesting question of whether, in the long term, *Glossosoma* populations in systems supporting the pathogen will continue to oscillate between high and low density states. To begin addressing this question, Kohler and Wiley (unpublished results)

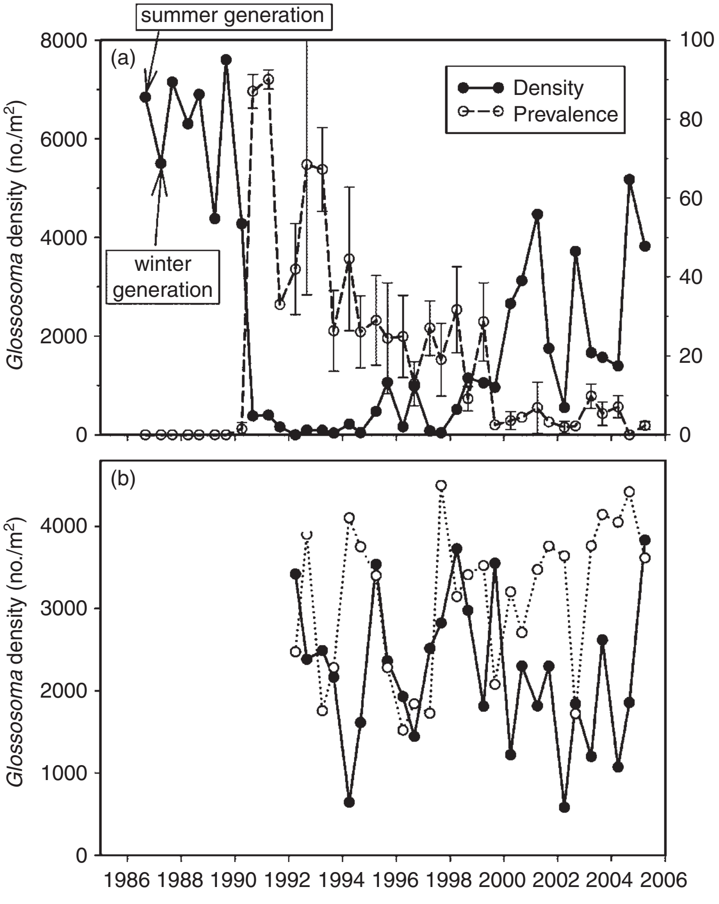

Fig. 4.4. (a) *Glossoma nigrior* population density at the end of overwintering and summer generations, and the prevalence of *Cougourdella* sp. in *Glossosoma* larvae and pupae in Seven Mile Creek, Michigan. Error bars are 95% confidence limits. (b) *Glossosoma nigrior* population density at the end of overwintering and summer generations in two nearby streams where *Cougourdella* infections have not been detected. Data are unavailable for these streams prior to 1992.

have applied a replicated, space-for-time substitution approach. They selected 62 streams at random from the >200 streams supporting *Glossosoma* in the lower peninsula of Michigan and, beginning in 1991, sampled the streams at generally 3-year intervals in the spring (at the end of *Glossosoma*'s overwintering generation), measuring *Glossosoma* population density and disease prevalence. In agreement with Fig. 4.4a, they found that none of the streams maintained *Glossosoma* at high density (>1000/m^2) between 1991 and 2004, and that <5% of the populations remained at low density throughout the period. In all 3-year periods, a high proportion of the populations either collapsed (declined in size by at least an order of magnitude) or recovered (increased by at least an order of magnitude). However, on average, in any given 3-year period, the proportion of populations that collapsed was nearly balanced by the proportion recovering. These patterns suggest that: (i) at the regional scale *Glossosoma* populations are relatively stable (although they clearly fluctuate markedly at the scale of individual streams), and (ii) the long-term trajectory in any given stream may be one of regular oscillations in state (i.e. from high density, low disease prevalence to maintenance at low density by recurring pathogen epizootics). Because *Cougourdella*'s complete life cycle is unknown (Heilveil *et al.*, 2001), it is not possible to test hypotheses regarding mechanisms responsible for state transitions (i.e. are state transitions driven by coevolutionary dynamics?).

Community-level Effects

While a rich literature addresses effects of parasites at the individual and, to a lesser extent, population levels, our understanding of how parasites affect community structure and ecosystem function is in its infancy (Marcogliese and Cone, 1997; Hudson, 2005). Dobson *et al.* (2006) suggest that 'developing a deeper understanding of the role that parasites and pathogens play in food webs is perhaps the greatest empirical challenge in food web biology.' Examples have appeared only recently demonstrating the important roles of parasites in natural communities, both in terms of food web topology (Thompson *et al.*, 2005; Lafferty *et al.*, 2006a,b) and community structure (Kohler and Wiley, 1997; de Castro and Bolker, 2005; Mouritsen and Poulin, 2005b; Mouritsen and Polml, 2006; Wood *et al.*, 2007). In this section, I consider examples of both of these approaches (i.e. food web topology, direct and indirect interactions between species) of addressing the roles of parasites at the community level.

Food web topology

Topological food webs depict the trophic relationships (who eats whom) among consumers, producers and non-living material in ecosystems, while bioenergetic webs focus on the flow of energy among species, and interaction webs identify species and trophic links that most strongly influence community structure (Winemiller and Polis, 1996). Several statistics are used to describe topological webs (e.g. link density, connectance, chain length, predator to prey ratio) and considerable effort has been directed to determine if general patterns in these metrics occur among food webs. Parasites have only recently been incorporated into topological webs (Huxham *et al.*, 1995; Thompson *et al.*, 2005; Lafferty *et al.*, 2006a) and no published examples include systems with parasite–aquatic insect links. Recent work suggests that food webs are more sensitive, in terms of secondary extinctions, to the loss of highly connected species, and that increased connectance (the number of observed links relative to the number of possible links) helps buffer systems against secondary loss of species from either random or selective removal of species (Dunne *et al.*, 2002). Lafferty *et al.* (2006a) found that inclusion of parasites increased connectance, but the parasites in the largely marine systems they analysed were dominated by helminths, which commonly have complex life cycles involving several hosts (Lafferty *et al.*, 2006b). It will be interesting to see if this pattern holds in systems having greater insect representation (e.g. rivers, wetlands), as the life cycle characteristics of parasites in such systems may be markedly different (Thompson *et al.*, 2005).

Species interactions and community structure

In the topology approach to food webs, parasites are, like other species, nodes in a food web. In the interaction web approach for addressing the effects of parasites at the community level, a stronger emphasis is placed on the nature of the interactions between parasites and their hosts and how those interactions can affect other members of the community. The effects of a parasite on other community members will probably be least important when the dynamics of the parasite are driven by its host (i.e. there are strong bottom-up effects of the host on the parasite population, but not strong top-down effects of the parasite on the host population; see Briggs *et al.* (1995) for several examples from terrestrial insects where the host appears to drive dynamics of its pathogen, but not vice versa). Effects of parasites on other community members should be strongest in either of two situations. First, if the parasite has strong top-down effects on the abundance of their hosts, even regulating host population dynamics (Anderson, 1979; Anderson and May, 1981; Hudson *et al.*, 1998; Kohler and Hoiland, 2001), effects of parasites on their host can extend indirectly to other community members. In such situations, parasites can assume roles in communities similar to those of predators in density-mediated interactions, such as trophic cascades, apparent competition and keystone parasitism (Thomas *et al.*, 2005a; Holt and Dobson, 2006). Second, by influencing traits of their hosts such as behaviour (Mouritsen and Poulin, 2005a; Wood *et al.*, 2007) and morphology (Mouritsen and Poulin, 2005b), parasites may have significant trait-mediated indirect interactions with other community members (Werner and Peacor, 2003).

Trait-mediated indirect interactions

One common form of trait-mediated indirect interaction occurs when two natural enemies share a resource (Werner and Peacor, 2003). By affecting traits (e.g. behaviour) of the resource, one natural enemy can affect the other, even without changing the abundance of the resource. Of course, this sort of interaction is common with parasites, as parasites often influence the behaviour of their hosts to facilitate their transmission to predators that serve as subsequent hosts (Dobson, 1988). Two interesting cases involving aquatic insects that do not fit the typical parasite transmission model bear mentioning.

Vance and Peckarsky (1997) studied the impact of a mermithid nematode on the vulnerability of its host, the mayfly *Baetis bicaudatus* (Ephemeroptera: Baetidae), to two invertebrate predators, a stonefly (*Kogotus modestus*) and a caddisfly (*Rhyacophila hyalinata*). In streamside artificial streams, the stonefly fed preferentially on parasitized *Baetis* larvae, while the caddisfly did not discriminate between parasitized and uninfected prey. Parasitized *Baetis* were less likely to evade an approaching stonefly by entering the water column and drifting downstream, and thus were captured more frequently by the stonefly than unparasitized larvae. Thus, the mermithid should have a positive indirect effect on stoneflies in this system by increasing *Baetis* vulnerability through its effects on *Baetis* behaviour. By contrast, the prevalence of nematode infections in the mayfly *Deleatidium* was much greater in drifting individuals than in animals on the stream bottom in a New Zealand stream, suggesting that nematode infection increased the tendency of *Deleatidium* to drift (Williams *et al.*, 2001). Because drifting individuals are more vulnerable to drift-feeding predators such as trout (Allan, 1978), the mermithid should facilitate trout by increasing the vulnerability of its prey. However, in both systems, because the predator facilitated by the nematode is not used by the nematode as a host, the changes in prey behaviour induced by the nematode appear to have negative fitness consequences for the nematode (because the nematode is killed along with the mayfly when consumed by a stonefly or trout). While drifting, parasitized larvae are more vulnerable than uninfected larvae to trout (Vance, 1996) and, in general, trout account for much greater mayfly mortality than do stoneflies (Kerans *et al.*, 1995). Therefore, from the parasite's perspective, parasite-induced changes in prey behaviour may reflect a trade-off between the risks of being eaten by stoneflies or trout (Vance and Peckarsky, 1997).

Apparent competition

Apparent competition is frequently described as an indirect interaction between prey species that share a predator, in which increased abundance of one prey species enhances predation on the second species, and vice versa. Thus the prey species appear to be competitors, even though they do not interact, either directly or through shared resources (Holt, 1977). Of course, such indirect interactions can also occur between hosts that share a generalist parasite (Holt and Pickering, 1985) and the potential importance of such interactions in shaping host community structure has received increasing interest (Hudson and Greenman, 1998; Poulin, 1999; Hudson *et al.*, 2006). None the less, to date only two experimental studies of apparent competition in animal host–pathogen (excluding parasitoids) systems have been reported (Chaneton and Bonsall, 2000) and one of these involves aquatic insects (Copeland and Craig, 1992; see also Grosholz, 1992).

Copeland and Craig (1992) studied two closely related treehole mosquitoes, *Aedes triseriatus* and *A. hendersoni*, that exhibit relatively strong niche segregation: *A. hendersoni* avoids ovipositing in sites near the ground and each species specializes in the types of treeholes occupied. Each species is infected by a different gregarine species, but cross-infections are known to occur with both parasites. Copeland and Craig conducted laboratory experiments to determine if ongoing interspecific competition between the mosquitoes accounted for the distribution patterns and whether the outcome of competition was influenced by a shared parasite. The competition part of the experiment followed a replacement series design in which the total density of larvae in experimental chambers was held constant. Food availability per larva was also held constant in their experiments at a relatively high level. All of the *Aedes* species combinations were observed in both the presence and absence of parasitism. The parasite used was *Ascogregarina barretti*, which occurs naturally in *A. triseriatus*. In the experiment, both mosquito species were infected by the gregarine, but infection intensity (number of trophozoites per larva) was much higher in *A. triseriatus*. However, gregarine infection had no effect on *A. triseriatus* survivorship, the size of emerging adults or female developmental rate, but there were highly significant effects on *A. hendersoni*. Moreover, the competitive effects of *A. triseriatus* on *A. hendersoni* were greater with the parasite present than in its absence. In other words, there were significant interactive effects between competition and infection, especially for female developmental rate and female size. By contrast, the presence of the parasite did not alter the competitive effects of *A. hendersoni* on *A. triseriatus*. These results illustrate complex indirect interactions between the mosquitoes. When food availability was relatively high, *A. triseriatus* had strong competitive effects on *A. hendersoni*, but only when the shared gregarine parasite was present. Thus the species exhibit apparent competition but the interaction is highly asymmetrical: only *A. hendersoni* was affected by the presence of the alternate host species. Asymmetrical apparent competition has been observed more frequently than symmetrical indirect interactions, in which each 'prey' species is affected by the other species (Chaneton and Bonsall, 2000). The mechanisms producing these effects in Copeland and Craig's (1992) study are unclear. In Grosholz (1992), apparent competition appeared to result from greater disease prevalence in the presence of an alternate host (and potential competitor), but such data were not reported by Copeland and Craig (1992).

Trophic cascades and keystone parasitism

Parasites may have keystone effects in a community if they strongly affect the dynamics of other, strongly interacting species in the food web. Such effects have been observed at large temporal and spatial scales in Michigan (USA) trout streams. In these systems, the herbivorous caddisfly *Glossosoma nigrior* is a particularly strong interactor, because foraging activity of its larvae maintains the biomass (and productivity) of attached algae at very low levels throughout the year, which results in *Glossosoma* having strong competitive effects on most other primary consumers (Kohler, 1992). As described above, *Glossosoma* is also host to a host-specific microsporidian microparasite, *Cougourdella*. Recurrent outbreaks of *Cougourdella* have resulted in whole-stream reductions in *Glossosoma* population size by one to two orders of magnitude and maintained *Glossosoma* density at low levels for years (Fig. 4a). Fortuitously, such outbreaks have been observed in many streams that were already the subject of long-term monitoring, allowing community-level effects of the pathogen to be assessed at large scales. Pathogen-induced reductions in *Glossosoma* abundance resulted in increased abundance of *Glossosoma*'s food resource (attached algae), and increased population sizes of most other algal consumers, including grazers and filter-feeders (Kohler and Wiley, 1997). Whole-stream reduction of *Glossosoma* by the pathogen revealed competitive effects of *Glossosoma* that could not have been anticipated from the results of more typical smaller-scale experiments (e.g. Kohler, 1992). For example, several algal grazers (primarily other caddisfly species) that had been extremely rare or absent, increased markedly following *Glossosoma*'s decline, indicating that they had been competitively excluded from these systems. *Cougourdella*'s effects in the community extend beyond the primary producer and primary consumer trophic levels. Because pathogen-induced reduction in *Glossosoma* results in increased algal productivity and increased abundances of relatively vulnerable prey (*Glossosoma* itself is relatively invulnerable to invertebrate and vertebrate predators), presence of the pathogen should facilitate top-level carnivores and perhaps intermediate-level carnivores as well. Population dynamics of predacious invertebrates (intermediate-level carnivores) suggests that their populations are often strongly resource-limited. Populations of predacious caddisflies (*Rhyacophila*) and stoneflies (*Paragnetina*, *Isoperla*) have increased over twofold following the collapse of *Glossosoma* populations in several streams. Thus *Cougourdella* plays a keystone role in this system because it strongly affects the abundance of a dominant competitor, *Glossosoma*. As a consequence, the long-term dynamics of the community should be strongly tied to the long-term dynamics of the host–parasite interaction, and will ultimately depend on the, as yet, poorly understood mechanisms driving long-term patterns in the interaction.

Conclusions

Hudson (2005) asks a series of insightful questions that should help frame future research in parasite ecology in a broad range of systems: how might removal of parasites affect community structure and the flow of energy and materials in an ecosystem? How do parasites influence biodiversity in a system? How do parasites interact with other natural enemies and what are the consequences of these interactions? How do reductions in biodiversity influence host–parasite interactions? Addressing these questions in systems where aquatic insects play important structural and functional roles (e.g. streams, wetlands, lake benthos and littoral communities) will require attention to a few key areas. First, studies to date have been highly skewed in terms of the taxonomic distribution of hosts and parasites studied. Greater attention to species that are suspected of interacting strongly with other community members, or who have a relatively large number of links with other species, would be beneficial. Second, more studies are needed that go beyond asking whether a parasite affects host fitness and explore more broadly the context dependence of host–parasite interactions, especially in field settings. Third, our understanding of the population-level effects of parasites on aquatic insects is in its infancy and remains a major challenge. Because controlled manipulations are difficult to perform, progress in this area will often require a well-designed combination of field observations and mathematical or statistical modelling (e.g. structural equations). Finally, questions regarding the roles of parasites in structuring communities and affecting the function of ecosystems dominated by aquatic insects and other invertebrates are largely unexplored, but observations in other systems (Mouritsen and Poulin, 2002, 2005a) suggest it will be well worth the effort.

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5

Effects of Drought on Stream Insects and its Ecological Consequences

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Abstract

Global climate change scenarios predict more frequent and extended droughts, especially in the mid-latitudes. For many stream insects, these increasing periods of drought are likely to cause local if not regional extinctions, with potentially severe consequences for stream ecosystem function. Drought is a steadily-intensifying 'ramp' disturbance that disrupts lateral, longitudinal and even vertical hydrological connectivity, depending on the spatial patterns of drying and drought severity. These hydrological changes affect many stream insects via impacts on refuges and water quality interacting with changes wrought by human activities. Selective extirpation of specific groups of insects during drought may alter benthic food web linkages or fundamental ecosystem processes such as organic matter breakdown. Management of flowing waters must consider these impacts, seeking to protect natural resilience (e.g. refuges) and explicitly acknowledging how drought affects aquatic insect community composition and function. However, there is much still to learn about drought and its impacts on stream insects. For example, we lack data from long-term studies that illustrate lag effects or other repercussions of droughts. Factors affecting rates and trajectories of post-drought recovery by stream insect communities are also poorly understood, hampering assessments of resistance and resilience to this increasingly common disturbance.

Introduction

Stream insects play central ecological roles in virtually all running waters. They underpin in-stream, riparian and flood plain food webs, processing organic matter and transporting energy along stream channels, laterally to the flood plain and even vertically into the stream bed (Hynes, 1970; Malmqvist, 2002). For example, in many forested streams, aquatic insects mediate leaf litter breakdown, supplying nutrients, carbon and energy to the stream and adjacent ecosystems

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(Cummins and Klug, 1979; Williams and Feltmate, 1992). Their activities can alter water quality, patch dynamics and flow patterns across multiple scales (O'Connor and Lake, 1994; Wiens, 2002) while their biological interactions often have significant repercussions on community structure (Williams and Feltmate, 1992; Williams, 2006). So ubiquitous and fundamental to riverine processes are aquatic insects that their assemblage composition is routinely assessed as an indicator of the 'health' of running waters (reviews in Wright *et al.*, 2000; Bonada *et al.*, 2006a).

Natural disturbances such as flooding and drought also affect virtually all running waters, impacting on aquatic biota and altering water quality (Resh *et al.*, 1988; Lake, 2000). Although the effects of floods on riverine fauna are relatively well-documented (Lytle, 2000; Lake *et al.*, 2006), far less is known about the impacts of drought, despite the fact that prolonged declines in flow or loss of water have severe consequences for freshwater ecosystems and aquatic insects. Part of this ignorance stems from the practical difficulties of studying ecological responses to drought; most studies to date have been serendipitous, phenomenological assessments hampered by limited replication and inappropriate design (Lake, 2003, 2006). It is difficult to predict when a drought will commence, and the realization that it is occurring usually only emerges some time after the disturbance has started. Droughts are also complex 'ramp' disturbances (defined below) whose intensity, history, variability and extent across multiple catchments confound attempts to generalize about their impacts or to dissociate these from concomitant changes in catchment condition and anthropogenic activities during the drought (Boulton, 2003; Lake, 2003).

Forms of Drought and their Perturbation Dynamics

Given the plethora of definitions of drought (review in Wilhite, 2000), we define it here as 'an extended period (seasons to years) of deficit precipitation compared to the statistical long-term average in a region' (cf. Druyan, 1996). This precipitation deficit is termed a *meteorological* drought when rainfall in a region declines below some threshold determined from long-term records. Inevitably, meteorological drought leads to *hydrological* drought, where the reduced precipitation fails to sustain normal volumes in standing waters or flows in rivers and streams, typically defined at the basin or regional scale (Svoboda *et al.*, 2002). Hydrological drought can also arise from water deficits due to land use, and water abstraction and storage. *Groundwater* drought occurs when groundwater storages or hydraulic heads decline relative to those normally expected (van Lanen and Peters, 2000) and reflects reduced groundwater recharge, also frequently impacted by human activities.

Droughts start with meteorological drought followed by hydrological and then groundwater droughts. This sequence depends on the duration of below-average precipitation and losses through evapotranspiration, human extraction, and other causes of water deficits. When a meteorological drought breaks, it invariably takes longer before the hydrological drought breaks and much longer before the groundwater drought breaks, as there is a lag time required for recharge of groundwater aquifers and recovery of flows (Lake, 2006).

A disturbance (cause) and the subsequent ecological response (effect) together constitute a perturbation. In aquatic ecosystems, spates are seen as pulse disturbances where the strength of the disturbing force (in this case, flow) increases and declines as a pulse. In contrast, press disturbances arise sharply and then plateau at a constant level, whereas ramp disturbances (Lake, 2000) occur when the strength of disturbance increases steadily over time and space. Droughts are a prime example of a ramp disturbance, intensifying over an increasing area until broken by adequate precipitation. As droughts progress, variations in rainfall and water use cause irregularities in the trajectory of the ramp disturbance, some of which may coincide with the onset of hydrological and groundwater drought. Ramp responses may also be irregular or even 'stepped' when certain critical thresholds (e.g. flow cessation, pools drying) are crossed (Boulton, 2003), resulting in sharp changes in variables such as species richness or the abundance of certain taxa. For example, mean numbers of taxa of aquatic invertebrates from sites along two intermittent streams in Victoria, Australia, declined abruptly when flow ceased and again when pools dried during a severe drought (Boulton and Lake, 1992b). A similar stepped response in invertebrate taxon richness was observed between the same phases during a drought in a Spanish stream (Acuña *et al.*, 2005).

Droughts can be classified as 'seasonal' or 'supra-seasonal' depending on whether the drying is a reasonably predictable, periodic event versus longer, less predictable and more destructive disturbances (Lake, 2003). Seasonal droughts typify streams in regions such as the wet–dry tropics (e.g. Rincon and Cressa, 2000; Douglas *et al.*, 2003) and Mediterranean climes (e.g. Gasith and Resh, 1999; Bonada *et al.*, 2006b). In these areas, many streams are intermittent and cease flow predictably (Gasith and Resh, 1999), selecting for adaptations by the stream biota to survive the predictable waterless period. In contrast, supra-seasonal droughts occur virtually anywhere, may persist over multiple seasons, and their unpredictability militates against evolution of adaptive life-history responses to drying; impacts on stream biota tend to be more severe during supra-seasonal than seasonal drought (Boulton, 2003; Lake, 2003; but see Lind *et al.*, 2006).

Impacts of Drought on Stream Insects

Sequential losses of hydrological connectivity

The ramp disturbance of drought causes a sequence of changes in hydrological connectivity and wetted habitat in streams that affects the aquatic (and potentially terrestrial) stages of many stream insects. Depending on the severity and intensity of the drought as well as the river's size and shape, there will be a progressive decline in flow and volume that first severs lateral and then longitudinal hydrological connectivity, ultimately resulting in complete drying of the streambed (Fig. 5.1). During drying, water quality typically deteriorates, especially in

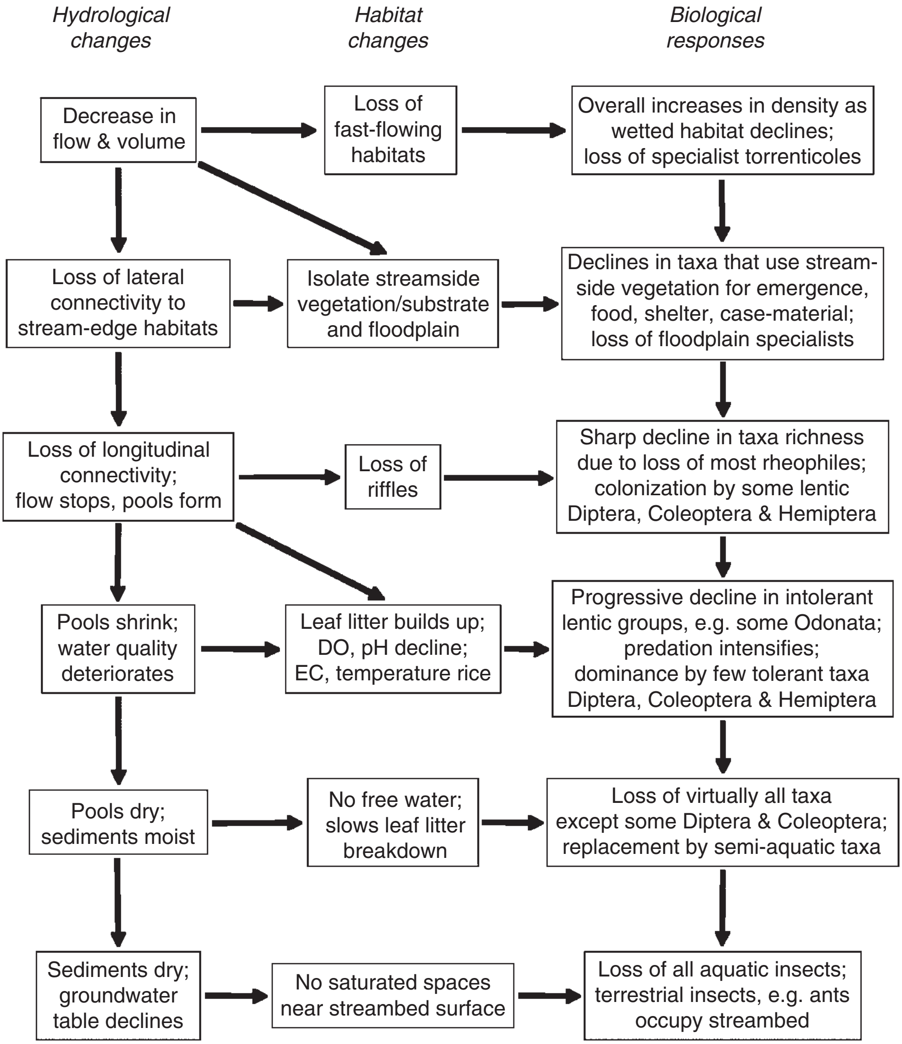

Fig. 5.1. Changes in stream habitat and biological responses during the progressive hydrological stages of drought. DO = dissolved oxygen; EC = electrical conductivity. Table 5.1 lists representative Australian aquatic insect families impacted by these stages of drought.

remnant pools along the streambed. Leaf litter accumulating in these depositional habitats accelerates declines in pH and dissolved oxygen (Towns, 1985; Caruso, 2002), rendering the pools uninhabitable except by stream insects capable of respiring air directly (e.g. dytiscid beetles and corixid bugs; Gooderham and Tsyrlin, 2002) or with physiological adaptations for enhanced uptake of oxygen (e.g. haemoglobin used by some chironomid 'bloodworms'; Hynes, 1970) (Table 5.1). When surface water completely disappears, a few stream insects can refuge in moist sediments (see below) but, during especially severe

Table 5.1. Occurrence of common families of Australian aquatic insects, listed by sequential stages of habitat change as drought progresses (Fig. 5.1). The pool stage is divided into early and final stages to reflect differing tolerances by insect families to the deteriorating water quality; families present in the final stages are usually present in early stages of drying too.

Habitat or habitat change: ecological group	Family or subfamily
Decrease in flow/volume: specialist torrenticoles or need fast-flowing, oxygenated water	Blephariceridae D Ameletopsidae E Coloburiscidae E Siphlonuridae E Eustheniidae P Notonemouridae P Hydrobiosidae T Philorheithridae T
Loss of lateral connectivity: uses stream-edge habitats or vegetation	Hydraenidae C Thaumaleidae D Pyralidae L Lestidae O Synlestidae O Hydroptilidae T
Loss of longitudinal connectivity (flow ceases): Rheophiles	Psephenidae C Ptilodactylidae C Empididae D Simuliidae D Baetidae E Leptophlebiidae E Corydalidae M Neurorthidae N Austroperlidae P Gripopterygidae P Notonemouridae P Calocidae T Conoesucidae T Glossosomatidae T Helicopsychidae T Hydrobiosidae T Hydropsychidae T Leptoceridae T Philopotamidae T Philorheithridae T Polycentropodidae T Tasimiidae T
Early stages of pools shrinking: moderately tolerant leutic taxa (or extremely versatile lentic taxa)	Elmidae C Hydraenidae C Hydrochidae C Athericidae D Tanypodinae D

(*Continued*)

Table 5.1. *continued*

Habitat or habitat change: ecological group	Family or subfamily
Early stages of pools shrinking: moderately tolerant lentic taxa (or extremely versatile lotic taxa)	Orthocladiinae D
	Tipulidae D
	Tabanidae D
	Dolichopodidae D
	Psychodidae D
	Baetidae E
	Caenidae E
	Leptophlebiidae E
	Naucoridae H
	Sialidae M
	Sisyridae N
	Coenagrionidae O
	Isostictidae O
	Lestidae O
	Protoneuridae O
	Synlestidae O
	Hemicorduliidae O
	Libellulidae O
	Gomphidae O
	Gripopterygidae P
	Atriplectididae T
	Calocidae T
	Conoesucidae T
	Ecnomidae T
	Hydroptilidae T
	Leptoceridae T
	Odontoceridae T
Final stages of pools drying: highly tolerant lentic taxa	Dytiscidae C
	Gyrinidae C
	Hydrophilidae C
	Scirtidae C
	Ceratopogonidae D
	Chironominae D
	Culicidae D
	Ephydridae D
	Muscidae D
	Stratiomyidae D
	Leptophlebiidae E
	Belostomatidae H
	Corixidae H
	Gerridae H
	Hydrometridae H
	Nepidae H
	Notonectidae H
	Veliidae H

(*Continued*)

Table 5.1. *continued*

Habitat or habitat change: ecological group	Family or subfamily
Final stages of pools drying: highly tolerant lentic taxa	Mesoveliidae H Calamoceratidae T Leptoceridae T
Pools dry: taxa with desiccation-resistant stages or able to survive in moist stream bed	Dytiscidae C Ceratopogonidae D Tabanidae D Simuliidae D Gelastocoridae H Gripopterygidae P

Order abbreviations are as follows: C, Coleoptera; D, Diptera; E, Ephemeroptera; H, Hemiptera; L, Lepidoptera; M, Megaloptera; N, Neuroptera; O, Odonata; P, Plecoptera; T, Trichoptera; and groups are arranged alphabetically.

drought, even this habitat desiccates as groundwater tables fall below the reach of burrowing taxa.

The sequential local extinction of stream insects during drought is largely a function of their resistance to changing abiotic and biotic conditions, although other factors such as the initial species pool, whether the stream typically dries and the extent of human disturbance are also important. The first aquatic insects to be impacted are those requiring either very fast-flowing water, or at least cool, well-oxygenated flowing water, as these conditions disappear when volume and flow declines during the early stages of drought. The combination of reduced current velocity and decreased oxygenation through loss of physical turbulence soon eliminates torrenticoles such as blephariceriid dipteran larvae and several families of mayflies, stoneflies and caddisflies (Table 5.1).

These groups usually inhabit spring-fed streams in montane areas that are seldom subject to drought (Hynes, 1970) and take a long time to recolonize when supra-seasonal drought causes local extinction (Williams, 2006). This long recovery time is presumably because the spring heads are geographically isolated and there has been little evolutionary selection for effective dispersal of species restricted to this usually reliable water source. In especially severe drought, there may be widespread drying across many springs (Erman and Erman, 1995), reducing the pool of potential colonists and increasing the recolonization distances of springs that had dried.

Aquatic insects of spring-fed systems appear especially vulnerable to groundwater drought and discharge fluctuations. Erman and Erman (1995) sampled 21 cold springs in Sierra Nevada, California, for several years prior to an extended drought and then re-sampled the springs after 4 and 6 years of drought. They found two to 18 species of caddisflies per spring with nine species restricted to constant-temperature spring sources (36 caddisfly species were collected overall). Before the drought, caddisfly species richness was positively correlated with spring discharge. However, after 6 years of drought, there was a stronger negative relationship between species richness and long-term fluctuations in discharge. In particular, springs that had few caddisfly species dried completely during the drought, whereas water in the species-rich springs persisted (Erman and Erman, 1995).

Loss of lateral connectivity

Stream margins become exposed as flow and stream volume decline to critical levels (Stanley *et al.*, 1997), affecting insects that rely heavily on hydrological linkages to lateral habitats, ranging from flood plain wetlands connected to the river through to emergent streamside vegetation (Table 5.1). Stream insects that use macrophytes along the edge of the channel to pupate and emerge, feed or for shelter (Harrison, 2000) are the species most impacted when water recedes from these habitats. Even mobile lentic taxa that scurry and hunt on the water's surface (e.g. veliid and gerrid water bugs) may be disadvantaged as they potentially become more prone to predation from birds and fish when lateral fringing vegetation is isolated from the water's edge during the early stages of drying and lateral contraction.

Loss of lateral connectivity in larger rivers and contraction of aquatic habitat away from the stream margins also reduce prey subsidies and arthropod densities in the riparian zone (Ballinger and Lake, 2006), constraining this important pathway for energy and nutrients. Conversely, the exposure of streambed sediments and lateral gravel bars may provide access for terrestrial insects. The ecology of semi-aquatic insects of this lateral transition zone is poorly understood and this would be a useful avenue for further research during seasonal and supraseasonal drought. Streams that dry regularly have a 'clean-up' crew of semi-aquatic insects (e.g. ants, staphylinid and carabid beetles) that inhabit the dry stream bed (Williams and Hynes, 1977), but it is unclear whether the composition of this community overlaps substantially with that of the insect assemblages along the margins of permanent streams. If so, their populations may be favoured by drought where increased habitat is available when water shrinks from stream margins.

Loss of longitudinal connectivity

The most dramatic change occurs when flow ceases and pools form, a process that may occur over several weeks across different river sections. Many stream insects have aquatic stages that rely on flow to provide feeding currents, enhance respiration, enable passive movement, import detritus, deliver prey, aerate water through turbulence, and sustain biofilms for herbivores (Hynes, 1970). These rheophilous ('flow-loving') groups (Table 5.1) soon disappear, unlikely to find suitable refuges except in nearby flowing habitats within dispersal reach. Most studies of drought on aquatic insects in streams have reported marked changes in community composition when flow ceases (Williams and Hynes, 1977; Miller and Golladay, 1996; Filho and Maltchik, 2000; Acuña *et al.*, 2005), primarily due to the disappearance of nearly all the rheophiles and declines in many other species.

Boulton and Lake (1992a,b) tracked changes in taxon richness and composition of stream insect assemblages at four sites on two streams in Victoria, Australia, during seasonal drought. Although the sites varied markedly in flow duration, there was a consistent sharp decline in taxon richness when flow ceased. This was due to the loss of species of filter-feeding midge larvae (Chironomidae) and net-spinning caddisflies, as well as many free-living caddisflies (e.g. hydrobiosids). There were also sharp declines in abundance of other groups of midge and other dipteran larvae, mayfly and stonefly nymphs, and some odonates (Boulton and Lake, 1992b). Similar marked declines in stream insect density and taxon richness in response to seasonal flow cessation were described in a Spanish stream (Acuña *et al.*, 2005) for many of the same broad taxa.

The break in longitudinal connectivity also severs an important dispersal pathway in most streams – invertebrate drift (Williams and Hynes, 1976) – preventing recolonization of even remnant flowing sections. In many gravel-bed streams, flow will cease in only a few reaches first yet continue elsewhere along the stream, sustained by hyporheic discharge. None the less, stream-scale movement of aquatic stages is inhibited, with major effects on predators that rely on a supply of food imported from upstream (McIntosh *et al.*, 2002). Furthermore, the cessation of flow often promotes the settlement of fine sediment (Wright, 1992; Wright and Symes, 1999). Siltation stresses many aquatic insects by coating their respiratory surfaces and smothering their food sources, such as diatoms or benthic organic matter (Angradi 1999; Wood and Armitage, 1999), slowing post-drought recovery in some streams (Wood and Armitage, 2004).

Shrinking pools and ‘predator soup’

As the pools along the stream bed shrink, their worsening water quality imposes a ramp disturbance on the remaining resistant denizens. Soon, the only taxa that persist are those capable of tolerating extremely poor water quality. This highly-tolerant group of stream insects that persists in the dwindling pools primarily comprises beetles, true bugs and dipterans (Table 5.1), although some mayflies, e.g. *Atalophlebia* (Leptophlebiidae), and case-building caddisflies, e.g. *Lectrides varians*, some *Triplectides* (Leptoceridae), also have a surprising capacity to persist in such stagnant warm water (Towns, 1983, 1985). Many of these tolerant taxa are also highly mobile, able to escape from shrinking pools to seek larger ones for refuge (Williams and Hynes, 1977; Boulton, 1989; Velasco and Millan, 1998).

The remnant pools also become a ‘predator soup’ where the biological interactions of predation and competition intensify (Stehr and Branson, 1938; Hynes, 1975; Stanley *et al.*, 1994), fuelled by diminishing wetted habitat and increasing densities of stream insects. For example, Extence (1981) reported that contraction of wetted benthic habitat in a lowland English stream during drought concentrated prey densities and led to increases in numbers of predators. In drying Australian streams, many of these predators apparently invade stream pools from nearby lentic sources such as farm dams and ponds (P.S. Lake, unpublished data). When flow resumes, they are able to fly back to the original water bodies.

Refuge use in the dry stream bed

In the final stages of drying, an array of refuges may be used by stream insects (Table 5.2). Remaining pools typically harbour the most taxa (Boulton, 1989), but some stream insects such as midge larvae and small mayflies persist within the burrow water of crayfish (as 'pholeteros' *sensu* Lake, 1977) or in moist microhabitats under bark, in leaf litter, or under rocks. Although many stream insects survive dry periods as terrestrial adults during prolonged supra-seasonal droughts, even these individuals are likely to die as food resources decline, habitat

Table 5.2. Refuges (from Fig. 9.5 in Boulton and Brock, 1999) and examples of their use by stream insects during seasonal and supra-seasonal drought. Taxa using remnant pools are listed in Table 5.1.

Refuge	Stream insect taxa	Example references
Under bark and in rotting wood	Mining insects such as some Elmidae and Chironomidae (e.g. *Stenochironomus*), Tipulidae	Boulton, 1989
Moist microhabitats in leaf litter	Adult Dytiscidae; larval Psephenidae, Tipulidae, Chironomidae, Leptoceridae	Larimore *et al.*, 1959; Boumezzough, 1983; Boulton, 1989
Burrow water of crayfish ('pholeteros')	Collembola, Chironomidae, Ceratopogonidae	Lake, 1977; Boulton, 1989; Williams, 2006
Hyporhoeic zone and buried in moist sediments	Plecoptera, Chironomidae, Tipulidae, Tabanidae, Ceratopogonidae, Psychodidae	Harper and Hynes, 1970; Gray and Fisher, 1981; Boulton *et al.*, 1992; Tronstad *et al.*, 2005
Resting stages in dry sediments	Eggs: Ephemeroptera, Chironomidae, Simuliidae, Leptoceridae; Plecoptera Larvae/nymphs: Chironomidae, Plecoptera, Leptoceridae	Towns, 1983; Miller and Golladay, 1996; Fritz and Dodds, 2004; Tronstad *et al.*, 2005
Aerial adults	Trichoptera, Ephemeroptera, Hemiptera (e.g. Corixidae, Notonectidae), Coleoptera (e.g. Dytiscidae, Hydrophilidae), Odonata, Plecoptera, Diptera (e.g. Chironomidae, Simuliidae Ceratopogonidae)	Harrison, 1966; Williams and Hynes, 1977; Delucchi, 1989; Paltridge *et al.*, 1997; Velasco and Millan, 1998; Shivoga, 2001

is lost, and the waterless period starts to exceed the lifespan of aerial recolonizers and egg-laying females.

Even after all surface water has disappeared, some aquatic insects can persist in either moist sediments (e.g. dytiscid beetles, tabanid fly larvae; Gray and Fisher, 1981; Boulton, 1989) or within the fully saturated alluvial aquifer just below the streambed (Boulton *et al.*, 1992; Clinton *et al.*, 1996; Table 5.2). In a Sonoran Desert stream, soon after surface water had dried but hyporheic sediments remained saturated, numerous ceratopogonid midge larvae (*Bezzia* and *Probezzia* spp.) persisted in the interstitial water (Boulton and Stanley, 1995). However, in a later study by Clinton *et al.* (1996) in the same stream, ceratopogonid and chironomid larvae did not move deeper into the sediments during later stages of drying, implying a limit to the use of even this refuge.

Ecological Consequences of Progressive Loss of Stream Insects During Drought

Organic matter processing and carbon transfer

As stream insects are the most common and species-rich macroinvertebrate component in nearly all headwater streams (Hynes, 1970; Williams and Feltmate, 1992), including those that dry regularly (Boulton and Lake, 1992a,b; Acuña *et al.*, 2005), they play a number of key ecological roles in stream ecosystems. They are pivotal in the food web as prey for many vertebrates as well as feeding on micro- and meso-benthos, microbes, algae and diverse biofilms. They also process detritus and organic matter entering from forested catchments. In many streams, functional feeding groups of detritivores termed ‘shredders’ comminute leaf and other coarse particulate organic matter into smaller particles that sustain ‘collectors’ and ‘filterers’.

In forested streams, shredding insects are represented primarily by caddisflies, mayflies and stoneflies, most families of which are vulnerable to drought. However, a few genera, e.g. *Triplectides* and *Lectrides* (Leptoceridae), have representatives able to survive deteriorating water quality in pools in drying streams in Australia where they shred accumulated leaves and wood. None the less, loss of flow or water in most streams can substantially slow the breakdown of coarse particulate organic matter, partly due to the local extinction of drought-intolerant insect shredders (e.g. Kirby *et al.*, 1983; Maamri *et al.*, 2005), with major repercussions for higher trophic levels and the conversion of detritus to energy to fuel in-stream ecosystems (Acuña *et al.*, 2005).

Many filterers rely on currents to feed passively (e.g. hydropsychid caddisflies) and are eliminated when stream flow ceases during drought, removing this pathway of processing and uptake of fine particulate organic matter. However, some actively filter-feeding stream insects, e.g. mosquito larvae (Culicidae), proliferate in standing waters (Boulton, 1989) and tolerate poor water quality to take advantage of the food resource provided by fine suspended organic matter and bacteria in remnant pools. Similarly, some benthic insects that feed by ‘collecting’ fine organic matter from the sediments (e.g. midge larvae in the genus

Chironomus) thrive in stagnant waters, relatively free of competitors, and can reach high abundances in drying pools (Boulton and Lake, 1992a; Acuña *et al.*, 2005). Despite this ability by some stream insects to persist, cessation of flow and eventual drying markedly reduce the overall diversity of detritivorous insects in streams during drought (Bogan and Lytle, 2007), restricting this heterotrophic pathway that is so important in providing energy to the denizens of most forested running water ecosystems.

Food web dynamics, aquatic–terrestrial linkages and succession

In-stream and riparian food web dynamics also change dramatically during the sequence of hydrological changes that occur during drought. As streams dry and pools become isolated, predation pressure intensifies (Stehr and Branson, 1938; Hynes, 1975; Stanley *et al.*, 1994). The decline in water quality soon eliminates all but the hardiest fish, while voracious insect predators such as dytiscid and hydrophilid beetles, dragonflies, and corixid, notonectid, nepid and veliid bugs proliferate (Boulton and Lake, 1992a; Stanley *et al.*, 1994; Acuña *et al.*, 2005). Predation by terrestrial and semi-aquatic insects also increases as they feast on prey stranded by declining water levels; ants and some beetle families (e.g. Carabidae, Staphylinidae) are especially common in many drying stream beds (Stanley *et al.*, 1994; Williams, 2006).

The variable tolerance by aquatic insects to drying alters the succession process when flow resumes and is likely to vary from year to year, even when drying is a predictable, regular event (Gasith and Resh, 1999). Post-drought community composition reflects the type of drought (seasonal versus supra-seasonal), its intensity and duration, the availability of refuges (Table 5.2) and the condition of the catchment and stream channel. In a small Spanish stream, the Fuirosos, subject to seasonal drought, severe flow reduction and drying led to an increase in worms, ostracods and *Chironomus* sp. midges, whereas during a less harsh dry period when more refuges persisted, baetid mayflies, black flies and several different chironomid genera dominated invertebrate biomass and density (Acuña *et al.*, 2005).

Similarly, Boulton and Lake (1992a,b) working in two seasonally-drying Australian streams during a drought and the following wetter year found that some genera of stoneflies, dragonflies and free-living caddisflies were either absent or much less common a year after the drought. This was interpreted as the result of failed recruitment, producing a 'lagged' response that affected the post-drought recovery phase. However, in a study of invertebrate recovery after a 4-year drought in six headwater streams in Georgia, Churchel and Batzer (2006) did not find significant differences between streams where residual water persisted and those that dried completely, indicating that the presence of refugial pools is not always a strong determinant of post-drought community composition. These variable findings across different streams indicate the need for caution when attempting to draw generalizations regarding the responses of stream insects to drought.

Recovery after seasonal drought in most intermittent streams follows a rather predictable sequence where early colonists with short life cycles (e.g. chironomids, simuliids) are joined by longer-lived collectors and grazers (mayflies and caddisflies) and taxon richness rises steadily as flows establish (Harrison, 1966; Boulton and Lake, 1992a,b; Fritz and Dodds, 2004). Conversely, recovery after supra-seasonal drought is less predictable because previously common drought-intolerant taxa may be extinguished (Wood and Armitage, 2004), whereas new habitat may be created for taxa that were rare before the drought. In a small acid stream in England, post-drought recovery was dominated by the tanypod chironomid *Zavrelimyia* sp. that was previously uncommon, although it became rare again when the macroinvertebrate community returned to its pre-drought composition after high flows in winter (Ledger and Hildrew, 2001). Loss or change in composition of aquatic macrophyte beds in perennial streams during supra-seasonal drought can also contribute to unpredictable responses (Wood and Armitage, 2004).

Indirect effects of drought

Drought can affect stream insects and ecosystem processes indirectly. From 2001 to 2004, severe drought in western USA coincided with earlier emergence of adult *Baetis bicaudatus*, a montane mayfly (Harper and Peckarsky, 2006). Increasing water temperatures rather than stream drying were the cue for this accelerated emergence. Large-scale climate changes with an increasing frequency of supra-seasonal drought were predicted to shift the timing of mayfly metamorphosis, with negative impacts on populations that play a key role in stream ecosystems (Harper and Peckarsky, 2006). Mayflies emerging in dry years also tend to be smaller than in wetter years when emergence is delayed and nymphs can feed for longer (Peckarsky *et al.*, 2001).

Drought does not have a negative impact on all aquatic insects. A normally perennial stretch of Waterston Stream, southern England, ceased flowing from August 1973 to January 1974, virtually eliminating very common taxa such as the amphipod *Gammarus pulex*, whereas other taxa such as the mayfly *Ephemerella ignita* increased in abundance (Ladle and Bass, 1981). This pattern was interpreted as a response to the timing of the drought and the availability of recolonizers. In a Welsh mountain stream, two stonefly and a mayfly species steadily increased in density after drought reduced the numbers of several other common stream insects (Hynes, 1958). Depending on the ecological roles of those aquatic insects favoured by drought, some stream ecosystem processes may be altered, especially if previously dominant taxa are eliminated or if different feeding groups are favoured by high or low flows (Bogan and Lytle, 2007).

Human Activities and the Effects of Drought

Humans compete with the other biota of aquatic ecosystems for water, especially during drought and especially in arid areas. As conditions become drier, human demands intensify. Aided by ever-increasing technological efficiency, extraction of surface and groundwater accelerates the onset of, and slows recovery from, hydrological and groundwater droughts. For example, in English chalk streams, maximum groundwater abstraction coincides with natural periods of low flow (Agnew *et al.*, 2000), prolonging the waterless periods in the channel. These 'artificial droughts' (droughts created by human activity, Boulton, 2003) exacerbate the stress of natural drought on aquatic insects (Wright and Berrie, 1987) and may cause permanent extinction of some groups in rivers subjected to heavy extraction of water. Where serious groundwater droughts occur, recovery of the stream community may take several years because of the need for recovery of flow associated with recharge of the aquifer (Wood and Armitage, 2004).

Economic hardship due to drought prompts social pressure to 'drought-proof' landscapes, usually by engineering schemes to redirect water or dam rivers, and seldom through more appropriate land use or planning for future droughts. These inter-basin transfers and dams have numerous deleterious effects on stream insects (reviews in Boulton and Brock, 1999; Allan, 2004) and are the inevitable by-product of seasonal and supra-seasonal droughts when humans seek a more reliable surface water supply. Multiple small storages on feeder streams further disrupt longitudinal connectivity and reduce total runoff, rendering rivers downstream more drought-prone than normal and leading to longer periods when flood plains remain dry, with negative impacts on the aquatic biota (review in Jenkins and Boulton, 2007).

During severe drought, although humans are generally aware of dwindling surface water supplies, there is seldom the same appreciation of the concurrent groundwater drought. Excessive groundwater extraction from alluvial aquifers during drought reduces river baseflows with reach and catchment-scale impacts on the biota of these groundwater-dependent ecosystems (Wood and Armitage, 2004; Boulton and Hancock, 2006). The stream insects of perennial springs and groundwater-fed rivers are particularly vulnerable to drought and often lack mechanisms to recover after loss of surface water (Williams, 2006). In two German karstic streams, their perennial springbrook sources supported different taxa from those in the seasonally-dry reaches downstream and contributed substantially to overall species richness (Meyer *et al.*, 2003).

In streams under human pressure, the condition and availability of refuges are impaired by direct water extraction during the drought, pollution by anthropogenic toxicants, or excessive sedimentation that fills deeper pools and clogs bed sediments. In-stream wood removal and bank slumps, coupled with excessive grazing and loss of surface vegetation exacerbated during drought, hasten sedimentation and create 'sand-slugs' that smother the stream bed and fill crucial refugial pools (Downes *et al.*, 2006). Remnant pools are one of the most important refuges during drying, and their loss through sedimentation severely impacts on post-drought recovery in sand-slugged streams. Excessive siltation in the perennial section of an English chalk stream sampled during the 1976 drought constrained macroinvertebrate habitat quality and availability, reducing the abundance of benthic insects such as black flies and baetid mayflies (Wright and Berrie, 1987). Ecological effects were considered most severe where the impacts of siltation on aquatic invertebrates persisted into the autumn of 1977, but recovery was complete by 1978 (Wright and Symes, 1999). Similarly, Lind *et al.* (2006)

suggested that salinization due to human activity pushed the disturbance posed by drought beyond the tolerance of many invertebrates in the Wimmera River, Australia.

Drought may favour the spread of some diseases for which aquatic insects are the vector. During severe drought, streams and wetlands shrink to isolated pools where mosquito populations proliferate. Such areas also attract unusually high aggregations of birds. Drought and this population concentration effect greatly heightens the likelihood of contact between the mosquitoes and birds, allowing arboviruses (arthropod-borne viruses), such as St Louis encephalitis (Shaman *et al.*, 2002) and West Nile virus (Shaman *et al.,* 2005), to be amplified in the bird hosts. When the drought breaks, the mosquitoes and birds disperse, promoting virus transmission and often triggering an epidemic of the viruses in humans (Epstein and DeFilippo, 2001; Shaman *et al.*, 2002). Global warming and the resultant cycles of more extreme floods and droughts may thus serve to increase the distribution and severity of these mosquito-borne diseases (Epstein, 2001).

Avenues for Further Research on Drought and Stream Insects

While preparing this chapter, we were struck by the scattered nature and lack of synthesis of research on the effects of drought on stream insects and their ecology. Most of the work we found was phenomenological, opportunistic, restricted in time and space, and seldom extended beyond a description of some aspect of response to drought (either the effects of progressive drying or the response after the drought had broken and flow resumed). This limited data set poorly equips us for preparing for the likely effects of climate change scenarios that predict increasing aridity and drought across much of the globe (Dai *et al.*, 2004). Along with accelerated ‘artificial drought’ as humans extract or pollute surface and groundwater reserves, droughts will become more frequent disturbances and deserve more attention and research than they currently receive.

One of the best sources of information about the effects of drought on stream insects is well-planned, long-term monitoring studies that reveal changes in stream communities across a multiple spatial scales, have sufficient pre-drought information to identify trends in different streams, and continue long enough to detect ‘lagged’ responses and even localized extinctions from especially severe droughts (Boulton, 2003; Wood and Armitage, 2004). If such studies are combined with monitoring of anthropogenic effects on streams during drought, it may be possible to tease out the main synergistic processes and manage streams to reduce environmental impacts at times of severe water deficit. We predict that the most severe impacts will be on refuges such as remnant pools or groundwaters that become heavily extracted or polluted as reserves dwindle and are not protected during the ‘panic’ of water shortages. Research is needed on refuge use by stream insects and ways to sustain these refuges during drought when human pressures on them intensify.

Part of effective protection of refuges will hinge on some understanding of the ecological strategies used by stream insects, and it is striking how few autecological data exist for most aquatic invertebrate species. Perhaps some form of 'ecological trait' analysis (e.g. Bonada *et al*., 2007) will be a fruitful approach. By assessing the ecological traits of a suite of stream insects at a catchment or regional scale and comparing those with the suite exhibited by survivors after a drought, we may identify some characteristic features that promote survival in various refuges. From these sorts of studies may emerge generalizations that can be used worldwide to enhance management and protection of stream insect populations from increasing frequency of natural and artificial droughts.

More work is needed to understand the full impacts of drought on ecosystem processes, such as organic matter breakdown and transport, which are severely impaired when streams dry, removing a crucial pathway of energy in these systems. Longitudinal and lateral hydrological fragmentation also sever pathways of stream insect colonization and redistribution among habitats. Fish and terrestrial predators, reliant on these pathways for prey, suffer during drought, with repercussions for riparian and flood plain ecosystems. Drought may also weaken, if not eliminate, prey subsidies consisting of aquatic insects eaten by terrestrial predators and terrestrial insects being prey for stream predators, such as gerrid and veliid hemipterans and gyrinid beetles (Ballinger and Lake, 2006).

Recent studies (Chadwick and Huryn, 2007) have demonstrated that drying severely constrains insect production in some streams, interpreted as selection against ecological traits such as large body size and longevity (Huryn and Wallace, 2000). In streams in Maine, large-bodied taxa such as the dragonflies Aeshnidae and Gomphidae and the stoneflies Perlidae and Pteronarcyidae are eliminated by drying, resulting in extremely low secondary production (Chadwick and Huryn, 2005). We need more research that integrates ecological traits, refuge use, and the effects on stream-scale secondary production to predict how the trophic transfer of energy will be affected by drought in streams.

Predicting the full suite of ecological effects of drought is hampered by our limited understanding of stream insect responses to this complex ramp disturbance, the effects of which are mediated by site-specific features (e.g. location, size and shape, nature of bed sediments, groundwater reliance). For example, while drought may dry upland streams completely, lowland rivers may continue to flow slowly, but lose all lateral connectivity with flood plain and riparian zones. Pools in rivers with porous beds may be maintained by hyporheic flow (Stanley *et al.*, 1997) or springs (Dahm *et al.*, 2003), sustaining a refuge that would be absent in rivers with less pervious sediments. It is critical that future research into refuge use and the effects of drought on stream insects and their production acknowledges the importance of patterns of hydrological drying. Our 'model' of sequential changes in insect community composition in response to drying (Fig. 5.1) is a starting point for refinements, and it would be useful to characterize how stream types and drying patterns influence the severity of impacts of loss of lateral, longitudinal and vertical hydrological connectivity. For example, in upland streams the loss of longitudinal connectivity via flow may be more severe than lateral disconnections with inundated stream-side vegetation, whereas in lowland rivers, lateral connections may be more important.

Conclusions

Our review has illustrated that while there may be relatively predictable changes in aquatic insect assemblages as drying progresses, the ecological consequences of these changes are less predictable because of the complex interactions with human impacts and the modifying effects of stream location, morphology and groundwater linkage. As drought is a natural part of all stream ecosystems, we must tailor our management strategies accordingly. 'Hard' and reactive engineering approaches to resist the effects of drought are less likely to be successful than proactive strategies that seek to improve our resilience to this ramp disturbance. As droughts are always large-scale disturbances and as global climate change is a very large-scale phenomenon, the synergism between these two ramp disturbances brings the grim prospect of severe and prolonged 'mega-droughts' with potentially devastating impacts on aquatic insects and associated ecosystem processes.

We lack autecological data on the responses of most stream insects to drying and resumption of flow. This makes it difficult to predict changes in organic matter transfer, secondary production and food web dynamics in response to increasing frequency and severity of drought. As most stream insects are resilient (rather than resistant) to drought, refuge use is especially important to their survival. Effective management and protection of stream ecosystems and their aquatic insects therefore relies on preserving functional refuges and making difficult decisions about allocations of water for environmental purposes during times of severe water scarcity.

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6 The Effect of Floods on Aquatic Invertebrate Communities

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Abstract

Almost all rivers experience increases in discharge, although whether this results in a flood depends on the size of the increase, channel morphology and hydrology. High flows have many effects on aquatic invertebrates both directly and indirectly through changes to habitat. Shear stress on the stream bed increases, removing organisms or forcing them to seek refuge among substrates or in the drift. Substrates can be moved, scouring invertebrates and their periphyton food source. Numerous studies have shown that floods reduce invertebrate abundances and diversity, although the threshold flows at which this occurs still remain contentious. However, recovery from most floods is relatively rapid and invertebrates persist even in very flood-prone streams. This is a result of many taxa having morphological, behavioural and life-history strategies to cope with the effects of floods. Although we have been aware of the community-level effects of floods on aquatic invertebrates for decades, it still remains unclear how many individual taxa respond, what motivates that response and what drives the recovery process. Understanding these patterns is key to our ability to manage flow variability to maintain ecosystem integrity in the face of increasing pressure to remove floods from a river's hydrology regime.

What is a Flood and Does it Represent a Disturbance to Stream Invertebrates?

Floods are a unique characteristic of almost all natural rivers and streams (Lake, 2000; Robinson *et al.*, 2002) although the predictability, frequency, magnitude and duration can differ markedly between rivers, regions and continents (Robinson and Uehlinger, 2003; Poff *et al.*, 2006). Many stream ecologists see floods as one of the principal structuring forces on stream invertebrate populations and communities (Resh *et al.*, 1988; Reice *et al.*, 1990; Lake, 2000). This has led a number of ecologists to advocate the return of natural flood regimes (the natural flow paradigm) to regulated rivers as one mechanism for maintaining the ecological integrity of downstream reaches (Poff *et al.*, 1997). Hydrologists define a flood as a flow

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that overtops stream banks, with the term 'spate' associated with high flows that do not overtop the banks (Gordon *et al.*, 2004). However, whether or not an increased discharge overtops the banks is unlikely to alter the effects of the increased flows on invertebrates; therefore, the word flood is used in an ecological sense to mean any increase in discharge, not just increases that overtop the stream bank.

To what extent these increased discharges represent a disturbance to stream invertebrate communities has been an area of debate (Resh *et al.*, 1988; Poff, 1992; Death and Winterbourn, 1994). Some people reason that the relative predictability and lack of lasting effects of many high-discharge events (see below) indicate that stream invertebrates are 'adapted' to these events, which therefore are not disturbances (Resh *et al.*, 1988). However, the focus now is on quantifying the degree of habitat alteration and concomitant changes in invertebrate communities, even if short lived, rather than the predictability of the discharge event (Poff, 1992; Death and Winterbourn, 1994; Angradi, 1997). Nevertheless, not all increased discharges disturb stream invertebrates; identifying what physical changes in the environment caused by floods represent disturbances to stream invertebrates and how to quantify these changes remains a challenge. Most researchers acknowledge that increases in flow that move substrates comprise disturbances for stream invertebrates, but identifying such flows for particular rivers is much more difficult (Clausen and Plew, 2004; Matthaei *et al.*, 2004).

What do Floods do?

Floods result from high rainfall events, snowmelt, dam release, removal or breakage (Minshall *et al.*, 1983) and lead to large volumes of water moving rapidly downstream. The volume and speed of the water creates high shear stress on the stream bed and surrounding channel that scours, abrades or moves substrates, suspends sediment in the water column, deposits logs and detritus, can alter channel shape and results in a patchwork of both scoured and infilled stream bed (Carling, 1987; Lake, 2000; Matthaei and Townsend, 2000b).

These changes in habitat structure have corresponding effects on the biotic component of rivers and streams. Periphyton, macrophytes and bryophytes are washed away, scoured or buried (Fisher *et al.*, 1982; Biggs *et al.*, 1999; Suren and Duncan, 1999; Downes and Street, 2005). Even thin epilithic biofilms can be scoured by flood-induced substrate movement (Scrimgeour *et al.*, 1988). Surprisingly, the quantity of benthic organic matter seems to be largely unaffected by floods, possibly because similar volumes of material are deposited as are washed away (Death and Winterbourn, 1995; Lytle, 2000; Robinson *et al.*, 2003). However, leaf accumulations in forest streams can be reduced by floods (Angradi, 1997).

Benthic invertebrate density, biomass and diversity are usually reduced by flood events (e.g. Jones, 1951; Maitland, 1963; Scrimgeour *et al.*, 1988; Robinson *et al.*, 2003) as individuals shift out of the rising channel, are washed away, or are crushed by moving substrate and debris. Abundance of animals can be reduced by 70–95% (Siegfried and Knight, 1977; Brooks and Boulton, 1991; Giller *et al.*, 1991; Matthaei *et al.*, 1997a). However, floods do not always have deleterious effects. Invertebrates in the Fraser River, Canada are unaffected by flooding because they simply move up the shoreline to more stable substrates as the water level rises (Rempel *et al.,* 1999). Similarly, invertebrates in streams of the Indian subcontinent are not affected by monsoonal floods because of synchronized seasonal changes in abundance (Arunachalam *et al.,* 1991; Brewin *et al.,* 2000).

Increases in invertebrate drift as a result of increased flows, often termed 'catastrophic' drift, have been recorded in several studies (e.g. Irvine, 1985; Brittain and Eikeland, 1988; Poff and Ward, 1991). Entrainment of substrates at flows above critical is one of the main reasons for this increased drift as the surface to which an animal clings is removed into the water column (Giberson and Caissie, 1998; Bond and Downes, 2003; Gibbins *et al.*, 2005). However, increased shear stress from high flows can also remove animals into the water column (Lancaster and Hildrew, 1993; Bond and Downes, 2000, 2003), as can physical abrasion from entrained fine sediment particles (Downes *et al.*, 1998; Bond and Downes, 2003). Multifactorial experiments by Bond and Downes (2003) on Australian invertebrate communities indicated that flood-induced drift was predominantly a result of shear stress from increased flows rather than fine-sediment abrasion. Gibbins *et al.* (2005) studied induced drift of baetid mayflies and concluded that, while increased shear stress does increase drift at higher flows, the entrainment of animals along with mobile substrates is much greater. Bed movement is the principal instigator of catastrophic drift from floods but, in streams that experience smaller increases in discharge or where substrates are tightly embedded, shear stress alone can lead to changes in the benthic invertebrate communities (Boulton *et al.*, 1992; Rempel *et al.*, 1999). Disturbance may also potentially alter the fitness of invertebrate populations, without any mortality or displacement, by increasing the metabolic costs associated with activities such as reconstructing food-catching nets (Beveridge and Lancaster, 2007).

There are fewer studies of flood effects on invertebrates in tropical streams (Turcotte and Harper, 1982; Flecker and Feifarek, 1994; Rosser and Pearson, 1995), although the responses and outcomes seem broadly similar to those in temperate streams. One exception is subtropical Nepalese streams where invertebrates are relatively unaffected by monsoon floods, possibly because of the seasonal predictability of the floods (Arunachalam *et al.*, 1991; Brewin *et al.*, 2000).

How do Invertebrates Respond During Floods?

Despite the morphological and behavioural characteristics of many stream invertebrates to maintain themselves in high flows, invertebrate communities exhibit low resistance to floods (Grimm and Fisher, 1989; Lake, 1990; Lancaster and Belyea, 1997). Many invertebrates drift or are washed away by floods. It has long been hypothesized that invertebrates actively or passively seek refuge before or during high flow events (Sedell *et al.*, 1990; Townsend and Hildrew, 1994), but there has been relatively little observational or experimental research to evaluate whether or how this occurs. Such research is fraught with difficulties: predicting when floods will occur, being able to work during high flows and observing what invertebrates do in swollen turbid rivers (Winterbottom *et al.*, 1997). Furthermore, invertebrates may accumulate in refugia or simply maintain densities relative to less stable surrounding substrates.

Some species of coleopterans and hemipterans leave desert streams in response to rain storms to avoid floods (Gray, 1981; Lytle, 2000; Lytle and Poff, 2004). Many invertebrates are washed into or actively move into the flood plain or river margins during floods (e.g. Bishop, 1973; Scrimgeour *et al.*, 1988; Rempel *et al.*, 1999). Although Matthaei and Townsend (2000a) concluded, from work in a New Zealand river, that flood plains only provide temporary refuge for stream invertebrates and many are stranded as the flood plain dries. Whether flood plains act as refugia depends on surface or hyporheic connectivity being maintained with the main channel. Refugia in river margins, in contrast, can prevent or ameliorate the effects of increased shear stress from flooding (Rempel *et al.*, 1999).

It has been widely held that animals seek refuge in the hyporheic zone during high flow events (Resh *et al.*, 1988; Poff and Ward, 1990; Sedell *et al.*, 1990). Few studies have tested whether this occurs. Studies in North America and New Zealand concluded the hyporheic zone did not act as a refuge during floods (Giberson and Hall, 1988; Palmer *et al.,* 1992; Olsen and Townsend, 2005). In contrast, work in the Rhône River found that refuge-seeking in the hyporheic zone during floods does occur, but is not universal and depended on the geomorphic complexity of a stream, substrate size and thickness of the sediments (Marmonier and Chatelliers, 1991; Dole-Olivier and Marmonier, 1992; Dole-Olivier *et al.*, 1997).

Invertebrates are also known to accumulate in areas of the stream channel where hydraulic forces are reduced, ‘dead zones’, although whether they do so actively or passively is still unclear (Lancaster and Hildrew, 1993; Winterbottom *et al.*, 1997; Lancaster, 2000). Stable substrates, such as debris dams and embedded stones, also provide refugia during high flows (Robertson *et al.,* 1995; Palmer *et al.,* 1996; Matthaei *et al.,* 2000). Matthaei *et al.* (2000) postulated that invertebrates may be able to sense a stone vibrating just before it becomes entrained and use this cue to move to more stable areas of the stream bed. Brooks (1998, cited in Lake, 2000) found a glossosomatid caddisfly *Agapetus kimminsi* moved from the tops of stones to the sides in response to increased turbidity and velocity, possibly to avoid being washed away. Several authors have recorded that seasonal movements of some invertebrate taxa to flow refugia may be a response to forthcoming seasonal flood events (Hauer and Stanford, 1982; Cobb *et al.,* 1992). However, it is unclear whether these are flood avoidance mechanisms, life-history behaviours or both. Microform bed clusters, organized stacks of stone in the stream bed, have also been predicted to act as stable refugia for invertebrates and periphyton during floods (Biggs *et al.*, 1997), but Matthaei and Huber (2002) found no evidence that they provided flood refugia for invertebrates in a German river.

The availability of refugia, in turn, determines the effect and subsequent recovery from flood events (Lake, 2000), although to what extent is unclear

(Lancaster and Belyea, 1997). Streams with more heterogeneous substrates composed of dead zones, debris dams, flood plains and stable surface stones provide more refugia and thus more colonists once high flows subside. In contrast, bedrock streams or those with homogeneous channels may be more affected by floods and slower to recover post flood (Fisher *et al.*, 1982; Angradi, 1997; Gjerløv *et al.*, 2003). Despite these studies, we still know very little about what happens to invertebrates immediately before and during floods: how and when the different refugia are used; what cues, if any, they use to avoid being washed away; and how taxon-specific responses to floods alter the recovery process.

How Quick is Recovery From Floods?

Although there are numerous potential refugia in many streams, floods generally result in a marked decline in both density and richness of resident invertebrates. However, one of the most characteristic phenomena of streams worldwide is the rapidity with which those communities recover (Resh *et al.*, 1988; Reice *et al.*, 1990; Lake, 2000). Small-scale, instream experimental disturbance studies have found invertebrate communities can recover within 4 days to 6 weeks (e.g. Boulton *et al.*, 1988; Brooks and Boulton, 1991; Death, 1996; Matthaei *et al.*, 1996). The number of taxa generally recovers more quickly than the density of animals (Mackay, 1992; Death, 1996; Matthaei *et al.*, 1996; but see Minshall *et al.*, 1983; Lake, 2000). However, mechanisms of recovery in these small-scale experiments may differ from those in larger floods (Fisher, 1987; Minshall, 1988; Lake, 1990). Smaller floods create mosaics of disturbed and undisturbed patches of substrate (Doeg *et al.*, 1989; Lancaster and Hildrew, 1993; Matthaei *et al.*, 1999) so these experiments are relevant to recovery from small disturbances, but may not be so for larger ones. Comparisons between natural floods and experimental disturbances are few and the results are dissimilar; Matthaei *et al.* (1997a) found similar responses between the two events in a Swiss river, but Brooks and Boulton (1991) found markedly different outcomes in an Australian temporary stream.

Different characteristics of the community (e.g. diversity, abundance, taxonomic composition) recover at differing rates. Furthermore, few authors have enough before-flood data, or evaluate recovery rates statistically. Recorded recovery rates from floods vary from 1 month in a Swiss river after a 200-fold increase in discharge (≈5-year recurrence interval) (Matthaei *et al.*, 1997a) to greater than 3 years after a 1 in 50-year rainfall event during summer in Ireland (Giller *et al.*, 1991) and a dam failure (and 3.5 months dewatering) in the Teton River, Idaho (Minshall *et al.*, 1983). However, changes in channel morphology and debris accumulation from severe floods (i.e. 1 in 2000 years) may have much longer lasting (>5 years) effects on invertebrate community density and productivity (Lamberti *et al.*, 1991; Snyder and Johnson, 2006). Recovery intervals from most floods seem to be about 2–4 months, although recovery is often incomplete before the study concludes or the next flood occurs (e.g. Fisher *et al.*, 1982; Scrimgeour *et al.*, 1988; Angradi, 1997).

Comparing recovery rates from floods in different rivers is extremely difficult, because no two floods will be of the same magnitude. Even for instream experimental manipulations there have been very few between-stream comparisons of recovery from disturbance (but see Yount and Niemi, 1990; Death, 1996; Gjerløv *et al.*, 2003; Melo *et al.*, 2003). Consequently, we know very little about whether, how or why recovery rates differ among streams. A greater rate of recovery would be expected in streams that experience more floods (Poff and Ward, 1990; Mackay, 1992). In northern hemisphere streams, flood recovery is more rapid in disturbed streams, but only when limited refugia are available (Matthaei *et al.,* 1996; Gjerløv *et al.,* 2003). In southern hemisphere streams, however, recovery rates are similar at sites that differ in disturbance history (Marchant *et al.,* 1991; Death, 1996).

Death and Zimmermann (2005) found the effects of floods on invertebrate diversity were less in the forested reaches of New Zealand mountain streams than in open reaches approximately 1 km downstream (Fig. 6.1). They argued that this occurred because the recovery of fauna post-flood in the forest reaches did not depend on recovery of the periphyton food base that delayed recovery in the downstream reaches. Therefore, recolonization of the invertebrate fauna may be more rapid where recovery of the stream food base is more rapid, as in some forest and high-nutrient streams (Gafner and Robinson, 2007). Recovery rates may also be influenced by the nature of any remnant populations that survive the flood (Ledger *et al.*, 2006) and/or whether a stream is perennial or intermittent (Fritz and Dodds, 2004).

Wallace (1990) argued that recovery from floods in warm desert streams (Gray and Fisher, 1981; Fisher *et al.*, 1982) was more rapid than in cooler

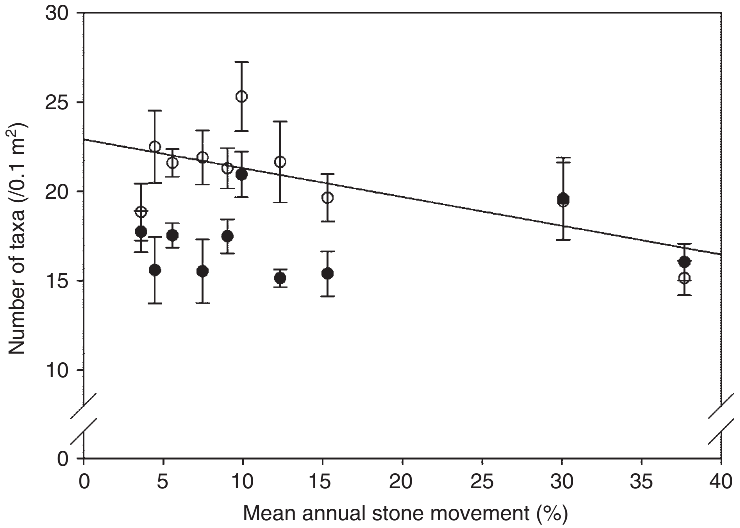

Fig. 6.1. Mean (± 1 SE) number of taxa as a function of stone movement at open (open symbols) and forested (closed symbols) sites on 10 Taranaki, New Zealand streams. Taxa number is unaffected by substrate movement at forest sites but declines with greater movement at open sites ($y = 22.92 - 0.16x$). Redrawn from Death and Zimmermann (2005).

temperate regions (Thorup, 1970; Giller *et al.*, 1991) because of flood-selected life-history traits in desert-stream invertebrates, such as rapid development, continuous emergence and diapausing eggs. However, it is difficult to judge the validity of this hypothesis from such a limited number of studies. Many New Zealand and Andean stream invertebrates have similar 'flood-adapted' traits (e.g. short life cycles, continuous emergence) and are characterized as being well-adapted to frequent flooding (Flecker and Feifarek, 1994; Winterbourn, 1997), but they recover at rates (Scrimgeour *et al.*, 1988; Flecker and Feifarek, 1994) similar to those of species in some northern hemisphere streams (Matthaei *et al.*, 1997a). There is also evidence that, in some regions, recovery rate depends on season: recovery from a flood in a tributary of the River Araglin, Ireland was much slower in summer than in winter, when flooding is more typical (Giller *et al.*, 1991). Again, although we know recovery is relatively rapid in streams following floods, we still do not have a clear understanding of how disturbance history, productivity, nature of stream food base and other factors affect the rate of this recovery.

Why is Recovery Quick?

A number of small-scale colonization and disturbance studies have found drift and movement over the stream substrate to be the main mechanism of (re)colonization (Williams and Hynes, 1976; Mackay, 1992; Downes *et al.*, 2005), although most studies have recorded only rates of colonization without examining colonization pathways (Downes and Keough, 1998). Colonization pathways also differ among taxa within a community. Downes *et al.* (2005) found some species of hydropsychid caddisflies colonized by drifting, whereas others used walking as well as drift. However, I am aware of only two studies that have examined colonization pathways following an actual flood: aerial recolonists dominated recovery of diversity following floods in a Sonoran desert stream, but drift and upstream movements provided the most individuals (Gray and Fisher 1981). Matthaei *et al.* (1997b) compared drift with movement within and over the substrate and found drift to be the principal mechanism of recolonization. Others have implied colonization from aerial sources (Siegfried and Knight, 1977; Flecker and Feifarek, 1994; Lytle, 2000) and walking along the substrate (Brooks and Boulton, 1991), based on the type and size of organisms found post-flood and knowledge of life-history patterns. Several authors (Wallace, 1990; Mackay, 1992) have also attributed differences in seasonal and regional recovery rates to the presence of adult insects for oviposition. Although there has been considerable speculation and investigation of refugia from flood events, corresponding studies have not been made of the relative contribution of recolonists from instream refugia compared with recolonization from more distant sources in adjoining catchments or upstream reaches. However, the use of molecular markers by Schmidt *et al.* (1995), Hughes (2007) and others to trace the ancestral streams of invertebrates is beginning to illuminate the relative contribution of those more distant colonization sources. The mobility of stream invertebrates through drift, walking or flying is a critical factor in the rapid recovery of invertebrate communities from dramatic losses. It has generally been assumed that drift is the principal mechanism of flood recovery (Minshall and Petersen, 1985; Townsend, 1989), but aerial (Gray and Fisher, 1981; Hughes, 2007) and within-stream (Matthaei *et al.*, 2000; Downes *et al.*, 2005) movement are equally important for some taxa and some streams.

How do Floods Affect Community Composition?

Disturbances from floods can have severe effects on invertebrate communities and occur during at least part of the year in most streams and rivers worldwide; it is therefore unsurprising that they have been considered one of the main driving forces of lotic community structure (Resh *et al.*, 1988; Lake, 1990, 2000). The effects of high flow events (Holomuzki and Biggs, 1999, 2000) and recovery from floods (e.g. Scrimgeour *et al.*, 1988; Downes and Lake, 1991; Mackay, 1992) depend greatly on the taxon. Ephemeroptera, Simuliidae and Chironomidae generally seem to characterize faunas soon after floods, whereas Mollusca, cased Trichoptera, Amphipoda, Platyhelminthes and some Hydropsychidae seem more susceptible to extirpation from floods (Mackay, 1992; Death, 1996; Townsend *et al.*, 1997a; Robinson *et al.*, 2003). Therefore, invertebrate faunas differ markedly between flood-prone and stable streams (Scarsbrook and Townsend, 1993; Death, 1995; Barquin and Death, 2004, 2006), although these differences are greater in open than in forested streams (Death, 2003; Death and Zimmermann, 2005). Taxa in flood-prone streams are also characterized as having small size, high adult mobility, generalist habitats, clinger habits, streamlined or flattened bodies, and two or more life stages outside the stream (Townsend *et al.,* 1997a).

Small floods create a patchy stream bed that maintains habitat heterogeneity and thus invertebrate diversity (Robinson *et al.*, 2003; Lepori and Hjerdt, 2006). However, inter-stream variability and regional diversity can be greater in streams less prone to floods (Death, 1995). All of the flood-prone streams in the study region had a remarkably similar fauna dominated by the mayfly *Deleatidum*, Simuliidae, Chironomidae and an oligochaete, presumably those taxa most able to recover from flood disturbances. However, there have been very few between-stream studies of flood effects on community composition on which to judge the generality of this finding. Potential changes to global rainfall patterns might lead to the homogenization of stream faunas with only taxa able to survive floods (or droughts) remaining abundant in some areas (Fowler and Hennessy, 1995; Lake *et al.*, 2000).

Changes in the abundance of taxa following substrate disturbance from floods have been proposed as examples of competitive exclusion along a successional pathway (Fisher *et al.*, 1982; Hart, 1983; Hemphill and Cooper, 1983). However, few studies show successional change in stream faunas following floods (Reice, 1985) and in other studies successional change was not detected (Scrimgeour *et al.*, 1988; Death, 2006; Ledger *et al.*, 2006). Some taxa dominate colonization processes following floods, but whether they are then replaced or simply joined by more slowly colonizing taxa remains unclear.

Diversity–Disturbance Relationships

The relationship between diversity and flood frequency or disturbance has been much studied in streams (Robinson and Minshall, 1986; Death and Winterbourn, 1995; Townsend *et al.*, 1997b; Death, 2002). From their study of Otago, New Zealand streams, Townsend *et al.* (1997b) claimed support for the idea that diversity is greatest at intermediate levels of disturbance (the intermediate disturbance hypothesis: Grime, 1973; Connell, 1978). However, Death and Winterbourn (1995) and Death (2002), in studies of other New Zealand streams, found no support for this intermediate disturbance hypothesis, nor a productivity-dependent, hump-shaped relationship (the dynamic equilibrium hypothesis: Huston, 1979). A review of stream diversity patterns by Vinson and Hawkins (1998) concluded that most studies showed a linear increase in diversity with decreasing disturbance.

Barquin and Death (2004, 2006) found that disturbance–diversity relationships differed between northern and southern hemisphere streams. Stable springbrooks in northern Spain had lower diversity than similar more flood-prone streams, whereas springbrooks in New Zealand had higher diversity than similar flood-prone streams (Fig. 6.2). Changes to the food base of a stream can also alter the relationship between disturbance and diversity. Diversity in open streams is reduced by floods, but not in forest streams (Death and Zimmermann, 2005), and low-nutrient alpine streams are affected by disturbance, but not when nutrients are added (Gafner and Robinson, 2007).

The wider ecological debate on neutral theory and metacommunities, suggesting that community structure is determined by colonization dynamics and not by niche partitioning (Hubbell, 2001; Leibold *et al.*, 2004), is particularly

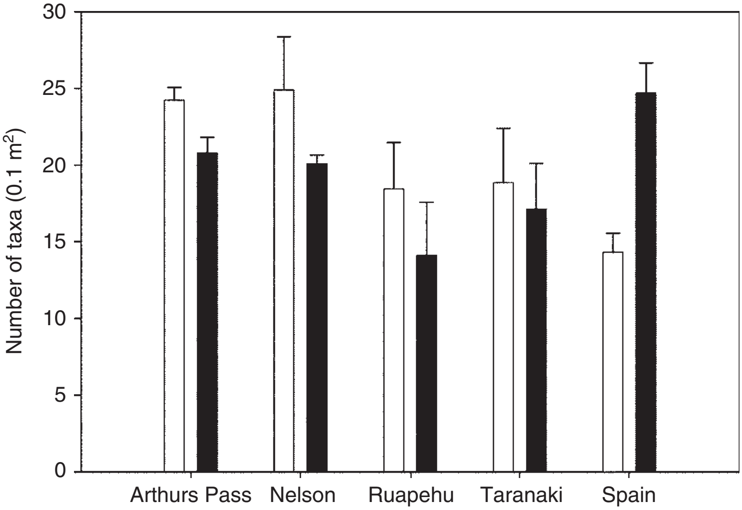

Fig. 6.2. Mean (± 1 SE) number of taxa in springbrooks (open bars) and rhithral springs (closed bars) in four regions of New Zealand and Spain. See Barquin and Death (2004, 2006) for more details.

appropriate for understanding the above patterns in stream communities (Heino, 2005; Thompson and Townsend, 2006). Colonization of small patches of stream substrate in several New Zealand streams is consistent with these ideas (Death, 2006).

Management Implications of Floods for Maintaining Ecosystem Integrity

Riverine habitats are increasingly under threat from flow manipulation (Poff *et al.*, 2003; Richter *et al.*, 2003; Poff *et al.*, 2007) and land-use intensification (Allan, 2004). Flow manipulations often involve water abstraction and/or dam construction that reduce the variability of flow, removing the structuring influence of floods on invertebrate communities. These changes can lead to dramatic, often deleterious, shifts in community composition (Poff *et al.*, 1997). For example, alteration of flow patterns in the Tongariro River, New Zealand have led to the proliferation of periphyton and a corresponding shift from an Ephemeroptera, Plecoptera and Trichoptera dominated fauna to one dominated by Chironomidae and Oligochaeta (Tonkin, 2006) (Fig. 6.3).

Adaptive management projects are under way around the world to better understand what level of flow variability is required to maintain some semblance of ecosystem integrity downstream of dams (Poff *et al.*, 1997; Patten and Stevens, 2001; Robinson *et al.*, 2003). For example, a regime of flushing flow discharges,

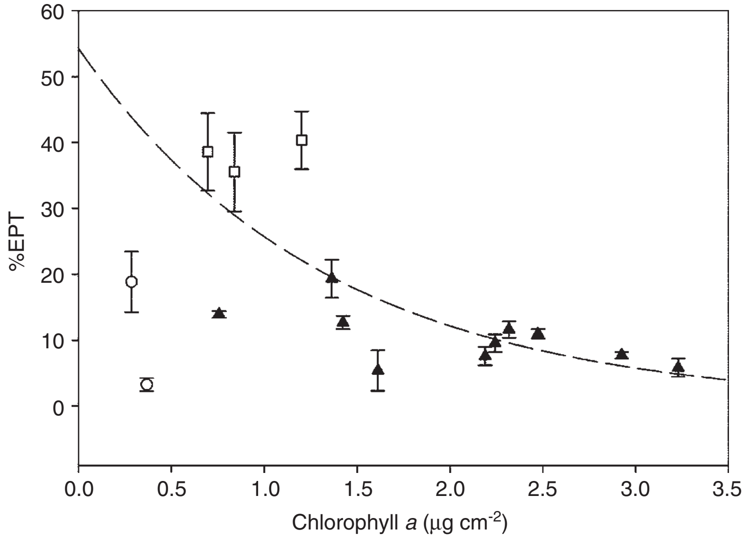

Fig. 6.3. Mean (± 1 SE) per cent Ephemeroptera, Plecoptera and Trichoptera in the drift as a function of chlorophyll *a* at 15 sites along the Tongariro River, New Zealand. Square symbols = sites above dams; circular symbols = sites below upper Rangipo dam; triangular symbols = sites below Rangipo dam and Poutu Intake.

triggered by periphyton cover, has been proposed to alleviate the effects of flow reduction in the Tongariro River, although the magnitude and frequency of the discharges required to restore an Ephemeroptera, Plecoptera and Trichoptera (EPT)-dominated community is still unclear.

One of the major anthropogenic influences on streams is modification of catchment land use, which tends to alter the flood regime so that floods are greater in magnitude and more flashy, changing the types of invertebrates present (Rowe *et al.*, 1997; Walsh *et al.*, 2005b). Changes in flood regime have been identified as one of the principal driving forces behind changes in the invertebrate communities of urban streams (Roy *et al.*, 2005; Walsh *et al.*, 2005a,b), but the effects of changes in flood regime that result from other land-use modifications have not been extensively investigated. Melo *et al.* (2003) subjected 90-m stream reaches to a standardized hydrological disturbance and found that recovery of invertebrate communities was similar in both native tussock streams and exotic pasture streams. However, their experiment did not mimic the changes in magnitude and flashiness of floods created by alteration to land-use patterns. Collier and Quinn's (2003) more realistic evaluation did find that communities in a pasture stream recovered from a 1 in 28-year flood event more slowly than those in a nearby forest stream. This finding confirms that major catchment modification, particularly deforestation, can alter the effects of flood events on stream invertebrates.

Conclusions

Disturbance from floods is one of the most important forces structuring stream invertebrate communities worldwide (Resh *et al.*, 1988; Lake, 2000). There have been numerous phenomenological studies of actual floods and experimental studies of small-scale substrate disturbances, and a few combining both approaches. However, we still have much to learn about what invertebrates do during floods, their relative use of potential refugia, local and regional factors controlling recovery rates and the relationship between disturbance regimes and diversity. Furthermore, we need to understand those effects in order to minimize changes in these ecosystems produced by modification of flow regimes by humans.

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7

Life-history and Behavioural Adaptations to Flow Regime in Aquatic Insects

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Abstract
Evolutionary history determines how aquatic insects cope with extreme flow events, both natural and anthropogenic. From a macroevolutionary point of view, aquatic insects possess different modes of adaptation (morphological, behavioural, or life history) to cope with flow events. For example, some Ephemeroptera, Plecoptera and Trichoptera are adapted to long-term average cycles of flood and drought via life-history timing, while other groups with aquatic adults (Hemiptera and Coleoptera) may use rain-triggered behavioural responses to escape floods on a per-event basis. From a microevolutionary point of view, populations may also evolve in response to flow regimes at very local scales. Models of life-history and behavioural evolution illustrate how disturbance regime characteristics (timing, frequency, predictability of events) and population structure (course- versus fine-grained, organism lifespan) determine how populations might evolve in response to different flood or drought regimes. All of these factors have implications for the structure of natural lotic insect communities, and for the effective management of dammed rivers and streams using ecological flows.

Introduction

Flood and drought disturbances are a fundamental part of most streams and rivers, and play a central role in the regulation of populations (Hemphill and Cooper, 1983; Holomuzki and Biggs, 2000), the structuring of communities (Fisher *et al.*, 1982; Wootton *et al.*, 1996; Townsend *et al.*, 1997), and the functioning of ecosystems (Grimm and Fisher, 1986; Townsend *et al.*, 1998). Aquatic insects, in particular, occupy the full spectrum of aquatic disturbance regimes, from the most stable headwater spring to the most dynamic desert wash. This diversity of habitats also means that aquatic insects experience a variety of selective pressures, and as such are a model system for understanding how aquatic organisms evolve in response to flood and drought disturbance. From a conservation point of view, as natural flow regimes are altered by human endeavours such as dams and

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water diversions (Graf, 1993; Bunn and Arthington, 2002; Nilsson *et al.*, 2005), we need to understand how aquatic organisms might evolve, or fail to evolve, in response to novel disturbance regimes. Some questions come immediately to mind: as flow regimes are changed, will organisms adapt to these novel environments or simply vanish from the system? What are the population-level characteristics that favour adaptation to local flood and drought regimes? To understand these conservation-oriented issues, a basic understanding of how aquatic insects evolve in response to flood and drought is required. This chapter seeks to identify some of the general biological processes that determine how aquatic insects evolve in response to flood and drought.

Most populations of organisms are under selective pressure to evolve in new directions and, at the same time, are constrained by their evolutionary past. Aquatic insects are typical in this respect. The variety of general body plans represented by the different insect orders presents an array of evolutionary constraints, while the varied habitats occupied by aquatic insects present a myriad of evolutionary challenges. This chapter will first outline how macroevolutionary patterns imposed by respiratory physiology and general life cycle considerations may favour different modes of adaptation (life history, behavioural or morphological) to flood or drought, with an emphasis on behavioural and life-history adaptations. The focus will then shift to microevolutionary patterns, with an emphasis on predictions derived from current models of life-history and behavioural evolution.

Modes of Adaptation

Major body plans can be a constraining factor on the evolution of strategies for coping with flood, drought, and flow variability in general. For aquatic insects, some a priori predictions about the mode of adaptation (life-history, behavioural, or morphological) can be made based on basic physiology and life cycle (Lytle and Poff, 2004). In general, life-history adaptations are expected in taxa that cannot respond immediately to disturbance events with behavioural avoidance, but may be able to anticipate disturbance from seasonal cues. Behavioural adaptations involve using environmental cues correlated with disturbance (rainfall, for example) as a signal to escape disturbance by moving within a stream or leaving the stream entirely. Movement out of the stream is especially important for mobile, air-breathing taxa that can respond to disturbances on a per-event basis. Morphological adaptations to flood and drought include traits such as streamlining to avoid shear stress during floods and drought-resistant life stages (Townsend and Hildrew, 1994; Poff *et al.*, 2006). This chapter focuses specifically on life-history and behavioural adaptations, and how these relate to flow regime components such as disturbance timing, frequency and predictability.

Life-history adaptations

Life-history adaptations include emergence strategies that are synchronized to avoid seasons when disturbances are likely (Gray, 1981; Gray and Fisher, 1981;

Lytle, 2002), or the use of proximate cues such as habitat drying to alter growth and development trajectories (De Block and Stoks, 2004, 2005; Danks, 2006). Life-history adaptations might be expected in taxa that cannot effectively escape disturbances on a per-event basis. In particular, taxa that require gill respiration as juveniles but have an aerial adult stage (Ephemeroptera, Plecoptera, Trichoptera, Odonata, Megaloptera and some Diptera) cannot exit the water immediately to avoid sudden flood events. However, they may be able to synchronize emergence into the adult stage to coincide with the long-term mean expected date of disturbance, thereby avoiding disturbance in most years. Life-history adapted taxa 'play the odds' over long timescales; although the strategy may fail occasionally if a disturbance is early or late (Lytle, 2003), this strategy maximizes long-term expected fitness given the constraints imposed by disturbance (Lytle, 2001).

Unlike floods, the onset of drought is often accompanied by proximate cues such as an increase in temperature and ionic concentrations, and a decrease in flow rate and water level. Particularly in the Trichoptera and Plecoptera, these cues may allow facultative entry into a drought-resistant stage (aerial adults or diapausing juveniles) (Wiggins, 1973; Hynes, 1976; Wiggins *et al.*, 1980; Delucchi and Peckarsky, 1989; Brock *et al.*, 2003), or provide a signal to adjust growth and development rates accordingly (Shama and Robinson, 2006; Robinson and Buser, 2007). In some cases, the transition to a drought-resistant stage occurs constitutively at a particular time, typically in synchrony with the expected date of drought occurrence (Wiggins *et al.*, 1980; Williams, 1996). However, some taxa apparently use asynchronous hatching of eggs as a way of 'bet-hedging' against the uncertainty of drought timing (Frutiger, 1996; Zwick, 1996). The presence or absence of these traits is sometimes responsible for determining species distributions along gradients of disturbance (Wissinger *et al.*, 2003).

Trichoptera may provide the most extreme example of an aquatic insect group that requires much advance notice that a disturbance will occur. The larvae of most Trichoptera species obtain dissolved oxygen via gills, and their aquatic pupal stage may last several weeks, during which time they may be exposed to mortality from flood or drought (Wiggins, 1973). This commitment to an aquatic environment precludes most behavioural strategies involving a temporary escape from flood by leaving the stream and subsequently returning to the water. In this instance a life-history strategy is favoured where emergence into the adult stage is synchronized with the expected occurrence date of flood events (Gray, 1981; Lytle, 2001).

Behavioural adaptations

Behaviours are context-dependent responses to different environmental cues. Although behaviours are often considered more evolutionarily labile than morphology or life history, studies have found a strong phylogenetic component to many insect behaviours such as nest building in Hymenoptera (Wenzel, 1992), web construction in spiders (Bond and Opell, 1998) and case construction in Trichoptera (Wiggins, 2004).

Many behavioural adaptations for disturbance avoidance rely on a proximate cue (rainfall, rising hydrograph, etc.) to signal a disturbance, which is then avoided by moving to safe zones within the stream or leaving the stream entirely. Behavioural strategies tend to take disturbances on a 'case by case' basis, rather than playing the long-run odds as in life-history strategies. For aquatic insects, behaviours may be subdivided into those facilitating within-stream survival during flood or drought, and those allowing escape from the stream during flood or drought. Instances of behavioural flood escape are best known in the Hemiptera and Coleoptera, possibly because their ability to breathe air allows them to persist out of water for relatively long time periods (Lytle and White, 2007). Other taxa that have the ability to persist out of water may possess similar behaviours (e.g. some Trichoptera and Megaloptera: Anderson, 1967; Erman, 1981; Contreras-Ramos, 1998), but more studies are needed to explore this. Within-stream behaviours for avoiding flood disturbance include the utilization of hydraulic refugia occurring in the substrate landscape, as well as adjustments to normal movement patterns that reduce the chance of displacement (Olden *et al.*, 2004; Lancaster *et al.*, 2006).

Flood escape behaviours include the use of proximate environmental cues as a signal to abandon streams. This has been well documented in the giant water bugs (Hemiptera: Belostomatidae), which use 'rainfall response behaviour' (RRB) to escape flash floods in desert streams. Individuals respond to some characteristic duration of strong rainfall by crawling out of the stream, moving perpendicularly away from the active channel over steep (sometimes vertical) stream banks, and not stopping until they have reached protected riparian areas (Lytle, 1999). The fitness benefit from RRB is substantial: the flightless belostomatid *Abedus herberti* experiences about 15% mortality from flash floods, while many other desert stream taxa endure mortality in excess of 95% (Grimm and Fisher, 1989; Lytle, 2000). Interestingly, RRB in belostomatids turns out to be an ancient, phylogenetically conserved trait that likely evolved to facilitate seasonal migration from perennial dry-season habitats to temporary rainy-season pools (Lytle and Smith, 2004). The co-opted use of RRB to escape flash floods is a more recent evolutionary event that has occurred separately in at least two distinct belostomatid lineages (an 'exaptation' *sensu* Gould and Vrba, 1982). The recent discovery of RRB in other aquatic Hemiptera suggests that flood escape behaviours may be the rule, rather than the exception, at least for taxa inhabiting desert streams where flash floods are commonplace (Lytle and White, 2007). Although rainfall cues are important for many taxa, in principle, other flood-associated cues such as changes in barometric pressure, turbidity, cloud cover or hydraulic pressure waves could be important as well.

For some taxa, behavioural escape from drought can be a viable strategy. Rivers and streams can experience sudden drops in flow caused by diel fluctuations in riparian plant evapotranspiration, lowering of the water table due to low rainfall inputs, and recession to baseflow following flood events (Stanley *et al.*, 1997). Aquatic Coleoptera adults seem particularly adept at drought escape, and the literature contains numerous accounts of beetle adults escaping drying habitats. For example, the dytiscid beetles *Rhantus gutticollis*, *R. binotatis* and *Eretes sticticus* have been observed taking flight en masse from drying desert ponds, and in some cases the emigration was preceded by loud, sustained vocalization (Zimmerman, 1959; Smith, 1973; Kingsley, 1985). Within-stream movement is also a mechanism for escaping the recession point of rapidly drying streams and rivers. Lytle *et al.* (in press) observed thousands of adults of the long-toed water beetle *Postelichus immsi* (Coleoptera: Dryopidae) crawling upstream concurrent with diel recession of surface water in a desert river. Larvae of the grey sand-dragon *Progomphus borealis* (Odonata: Gomphidae) were also observed burrowing upstream in high densities (690 larvae per m^2). Both taxa moved with sufficient speed to reach upstream perennial river reaches before being overtaken by drought. Given the proven ability of many aquatic insects to optimally relocate within streams in response to local fine-scale differences in flow (Lancaster and Hildrew, 1993; Lancaster, 1999; Wellnitz *et al.*, 2001), for many taxa, behavioural drought escape may be a special case of a more generalized ability to track sudden changes in flow.

When do Ecological Conditions Lead to Evolutionary Change?

While macroevolutionary considerations may determine the mode of adaptation to flood and drought, microevolutionary factors, such as ecological context and population structure, may influence the degree to which populations evolve in response to local differences in disturbance regime. From theory of evolution in fluctuating environments (Cohen, 1966; Iwasa and Levin, 1995; Lytle, 2001), we expect that selection for disturbance-escape strategies will be strongest when: (i) per-event mortality is high; (ii) predictability of events is high; (iii) frequency of events is high; (iv) events are 'coarse-grained' (synchronous over larger spatial scales); and (v) the organism's lifespan is long relative to the disturbance return interval. Several more predictions arise from basic population genetic considerations. Selection should be strongest when (vi) population-level additive genetic variance is high, and (vii) gene flow from differently adapted populations is small.

Mortality, Frequency and Predictability

Factors (i)–(iii) are fairly intuitive. If a lethal event occurs reliably on the same day each year, selection will favour life histories that are synchronized to escape this event. In most models of life-history evolution these three factors are multiplicative, in that a low value of one will cancel out high values of the other two (see Fig. 2 in Lytle and Poff, 2004). For example, selection may be weak for high-mortality events that are seasonally predictable but very infrequent, such as freezing events in tropical regions or hurricanes.

The notion of flood or drought 'predictability' deserves some discussion, as this has been defined variously in the literature (Resh *et al.*, 1988; Poff, 1992, 1996). For the purpose of understanding life-history or behavioural evolution, it is useful to define predictability as the degree of correlation between a disturbance and some environmental cue (*sensu* Lytle and Poff, 2004). For many types of flood and drought, it is possible to determine the mean Julian occurrence date of some flow event exceeding a given magnitude (timing) using long-term hydrograph data. The degree to which this date correlates with the actual date of disturbance across years (the variance) can thus be interpreted as a measure of predictability, in that it describes how reliably that date will predict an actual disturbance event from year to year. Proximately, many aquatic insects use day-length to estimate seasonal timing, and the literature is rich with examples of taxa that adjust growth and development in response to altered day-length (e.g. Johansson and Rowe, 1999; De Blok and Stoks, 2004). In certain cases predictability can be defined without respect to seasonal timing. Some organisms respond to rainfall events as a signal that a flood may soon occur (or a drought may be ending). Desert stream insects such as giant water bugs (Hemiptera: Belostomatidae), other Hemiptera and some Coleoptera use rainfall as a signal to escape flash floods by immediately abandoning the stream and moving into protected riparian areas (Lytle, 1999; Lytle and White, 2007). For these organisms, the degree to which rainfall events (the environmental cue) are correlated with floods (the disturbance) determines the predictability of the flood event. An example of how this kind of predictability can drive the evolution of behaviours in local populations is discussed below.

Coarse-grained versus fine-grained environments

Factor (iv) arises from theory related to measuring fitness in fluctuating environments. In fine-grained environments where disturbances occur independently across patches, and the breeding population is pooled from these patches, the arithmetic mean is the appropriate measure of fitness over time (Cohen, 1966; Gillespie, 1977). This is analogous to the ‘patch dynamics’ scale in stream ecology studies (Pringle *et al.*, 1988; Townsend, 1989; Downes *et al.*, 1998; Lake, 2000). By contrast, in coarse-grained environments where the entire population experiences the same disturbances in a synchronous manner, the geometric mean is the correct fitness measure. In fluctuating environments, geometric mean fitness is always lower than arithmetic mean fitness, especially when the fluctuations are large. The way this affects trait evolution can be understood heuristically by imagining two different populations of a mayfly, one composed of multiple subpopulations in adjacent streams that flood independently of each other, and another occupying streams that always flood simultaneously. In the former population, each subpopulation experiences the flood regime independently, and then the adults meet in a single swarm to mate and disperse. The population fitness is the arithmetic mean of all subpopulation fitnesses, and the population as a whole is buffered to some degree against a severe disturbance in any single stream (i.e. a zero value in the arithmetic mean will still result in a positive population-wide fitness). In the latter population, a severe flood event affects the entire breeding population simultaneously, producing a low or zero value for the geometric mean fitness. Because of these differences, when per-event mortality rates are high, selection is much stronger in coarse-grained than fine-grained environments (Iwasa and Levin, 1995; Lytle, 2001).

Two points arise from this discussion that are important to our understanding of disturbance in aquatic systems. First, large floods and droughts likely fall into the coarse-grained category as multiple stream reaches are affected simultaneously. Thus from an evolutionary point of view, disturbances that occur at the level of individual substrate particles or reaches are fundamentally different from disturbances that affect entire streams or rivers simultaneously – a point that may affect our interpretation of experiments that focus on disturbance acting at the level of individual rock particles. In other words, patch-dynamic disturbances may not scale up to full-stream flood or drought disturbances, because selection is acting in different ways at these two different scales. Second, the population genetic structure of aquatic insects may have a profound effect on how populations adapt to disturbance regimes, because it may determine whether the environment is coarse- or fine-grained. If a breeding population is drawn from a single stream, or groups of streams that experience simultaneous disturbance events, the coarse-grained fitness measures apply and selection may act more strongly to produce local adaptation. Although the predictions from theory are clear, the effect of environmental grain on aquatic insect evolution has yet to be examined empirically. The genetic structure of aquatic insect populations is an active area of research that should provide many insights concerning how organisms evolve in response to disturbance.

Lifespan

The lifespan of an insect relative to disturbance recurrence interval (v) determines to what degree selection can synchronize a life history with a disturbance regime. At one extreme, univoltine or semivoltine insects must pass through one or several disturbance seasons before emerging into the adult stage. For organisms in flood-prone environments, to use one example, selection might be strong for adult emergence that is synchronous with the expected date of flood disturbance, assuming that floods are sufficiently frequent, severe and predictable. For these taxa, the disturbance season entrains the population by restricting emergence to a specific pre-flood season. Individuals that emerge late risk being removed by floods, and individuals that emerge too early risk placing their offspring in harm's way. This life-history strategy has been observed in univoltine caddisflies inhabiting desert streams where severe flash floods occur during a fairly well-defined season (Lytle, 2002; see example below). At the other end of the spectrum, multivoltine taxa with very short lifespans may or may not face a disturbance season during their lifetime. This kind of multivoltinism has reached an extreme with the desert stream mayfly *Fallceon quilleri* (Ephemeroptera: Baetidae), which matures from egg to adult in an astounding 9–11 days (Gray, 1981). Although this short life cycle prevents the population from becoming synchronized with the seasonal flood regime, it is thought that a rapid life cycle may itself be an adaptation to flooding as it minimizes the time spent as a larva in a flood-prone habitat (Gray and Fisher, 1981).

Life-history strategies and environmental variability

The trade-offs faced by many aquatic insects inhabiting seasonally disturbed environments are typified by the sycamore caddis *Phylloicus mexicanus* (Trichoptera: Calamoceratidae). Sycamore caddis inhabit perennial streams in the desert south-western USA and northern Mexico, which are prone to flash floods during the July–September flash flood season. The flash flood season places limits on *P. mexicanus* emergence; individuals must balance the costs of remaining in the stream (flood mortality) against the benefits (opportunity to continue feeding as larvae and increase fecundity, as adults are non-feeding). Life-history models predict an optimal reaction norm strategy, where individuals are expected to emerge at a smaller body size (and thus lower fitness) as the risk of a flood increases (Rowe and Ludwig, 1991; Johannson and Rowe, 1999; Lytle, 2001).

As with many caddisflies, a large proportion of body mass increase in *P. mexicanus* occurs during the final instar, but the amount of growth varies substantially among individuals. Among-individual variation in body size can be due to genetic differences, environmental factors, or some combination of both. Figure 7.1 shows that fitness, as measured by the number of eggs produced, can vary substantially among females, in this case by a factor of 3 or more. These individuals inhabited a range of food conditions that ranged from scarce to abundant detritus [see Lytle (2002) for background and details]. The lower

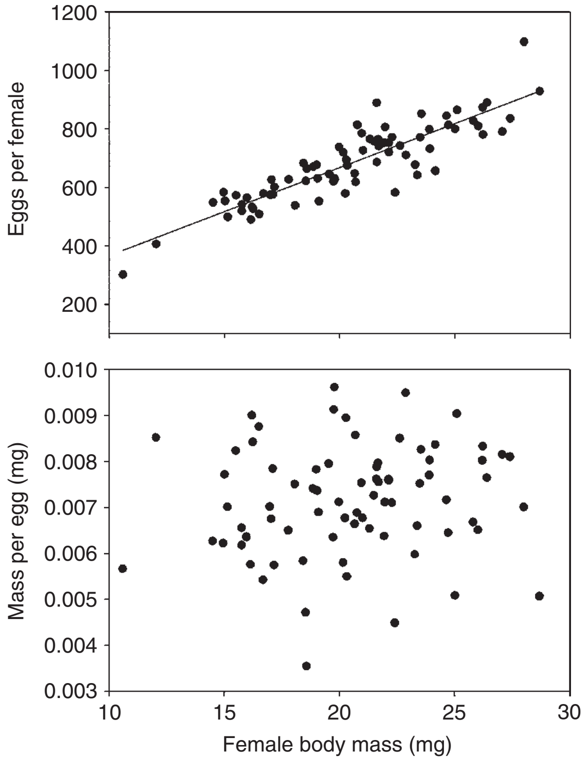

Fig. 7.1. Fitness gradient in a population of the caddisfly *Phylloicus mexicanus*. Fitness is increased by producing more eggs, rather than higher quality eggs. Top panel: larger females produce more eggs than smaller females (R^2 = 0.78). Bottom panel: egg mass does not vary systematically with female body mass.

panel of Fig. 7.1 shows that, for this species, there is no trade-off between egg quality and quantity, and so egg number is a reasonable predictor of fitness. This population-level variability in potential fitness represents a steep fitness gradient, where realized body mass determines the position of an individual along the gradient. The observed variability, which is typical of many aquatic insects (Statzner *et al*., 1997), has several implications for life-history evolution in flood-prone environments. First, there exists no single 'one-size-fits-all' optimal body size at emergence; rather, optimal body size at emergence is a reaction norm that changes through time as the costs and benefits of emergence change (in this case, mostly due to the increasing risk of a flood). Indeed, life-history models that incorporate a reaction norm of body size versus time perform substantially better than models that do not (Lytle, 2002). Similarly, the imposition of a disturbance is expected to increase within-population variability in fitness (Rowe and Ludwig, 1991; Lytle, 2001). To visualize this, imagine a population that is free from the time constraint of a disturbance. Even though there might be among-individual differences in growth rate due to genetics or microhabitat, individuals are free to grow until a maximum body size is reached, thereby reducing population-wide variability in egg number. Second, if the among-individual fitness variability is due mainly to environment and not genetics, individuals must be experiencing a large range of ecological conditions. Essentially, there is much latitude in the environment for individuals to do really well or really poorly. These differences could be due to microhabitat differences in ecological conditions (detritus as a food resource, predators, conspecific densities) or legacy effects (oviposition date, growth conditions during early development). If among-individual fitness variability is due to genetics, then fluctuating environmental conditions must maintain a large diversity of phenotypes within the population. In all likelihood, the observed variability is due to some combination of genetics and the environment.

In summary, the large within-population variability in aquatic insect egg production has implications for the evolution of life-history strategies in disturbed environments. A full understanding of these connections will require further studies, such as comparisons of populations of the same species inhabiting disturbed versus non-disturbed streams.

Local Adaptation of Populations

Flood and drought disturbance regimes can vary significantly at multiple spatial scales. Within a catchment, for example, floods may be less common in the headwaters due to small catchment area but commonplace in lower reaches that integrate many smaller drainages. Across catchments, flood and drought frequency, severity and predictability can vary due to differences in catchment area, underlying geology or even land use practices (Allan, 1995; Tague and Grant, 2004). Furthermore, anthropogenic factors such as dams, water diversions, revetments and alteration of flood plains can produce sudden changes (with respect to evolutionary timescales) in flood and drought dynamics (Poff *et al*., 1997; Bunn and Arthington, 2002). All of these factors raise the issue of the spatial scale at which aquatic insects can adapt to local differences in flood and drought disturbance regime.

Phenotypic plasticity versus local adaptation

The 'ideal' aquatic insect should be able to alter its life-history strategy or behavioural repertoire to match a range of disturbance regimes. For example, insects that inhabit streams prone to drought in some years and not others may benefit from a plastic strategy that allows different trajectories of growth and development (Johansson and Rowe, 1999; Johansson *et al.*, 2001; De Block and Stoks, 2004, 2005), assuming that sufficient proximate cues are present to signal the approach of different environmental outcomes (drought versus no drought, for example). For the aquatic insect populations that have been studied across disturbance regime types, phenotypic plasticity does appear to be common. Studies examining the proximate cues associated with the onset of drought (drying of pools, changes in photoperiod that are correlated with drought onset) have generally found evidence for plasticity – that is, individuals adjust rates of growth, development or both to compensate for different environments. In a common garden study of an alpine caddisfly, Shama and Robinson (2006) found that plasticity, rather than local adaptation, accounted for most observed differences between populations obtained from perennial versus temporary streams. Similarly, damselfly larvae from two habitats that differed in permanence showed no evidence for local adaptation in a common garden experiment, but responded to different treatments with phenotypic plasticity (De Block and Stoks, 2004).

Not all among-stream differences in disturbance regime are accompanied by useful proximate cues, however. For example, catchment size may determine the frequency and magnitude of flood events in some stream types (Gordon *et al.*, 1992), but there is no obvious way that an aquatic insect could determine catchment size from proximate cues. Local adaptation may be expected under these ecological conditions. Any population with sufficient heritable trait variation may evolve in response to local conditions, so long as selection is strong enough to counteract gene flow from nearby populations adapted to different optima.

Local adaptation to flood regime in giant water bugs

An example of local adaptation to different flood regimes is seen in populations of the giant water bug *Abedus herberti* that inhabit isolated, perennial streams in the arid south-western USA. Distinct populations of this flightless aquatic insect are confined to catchments that experience a large variety of flood regimes, which is dictated by catchment size. Floods are rare (<1 flood/year) or absent in smaller catchments, while larger catchments can experience multiple floods per year (Lytle, 2003). The predictability of floods from rainfall cues also varies according to catchment size (Fogel, 1969; Osborn and Laursen, 1973): predictability is highest in intermediate-sized catchments, where the correlation between rainfall and floods is strongest, but decreases as watersheds become smaller (strong rainfall events occur, but catchment area is too small to capture enough water for a flood) or larger (local rainfall is absorbed into alluvial fill, and floods are generated by storms occurring in distant parts of the catchment). The cost of encountering a flash flood is high because mortality rates of most insects caught in floods is near 95% (Grimm and Fisher, 1989; Lytle, 2000). As noted previously, *A. herberti* use flood escape behaviour to survive these events: individuals sense periods of heavy rainfall that often precede floods and use this as a cue to crawl out of the stream to protected riparian areas, then return to the stream post-flood (Lytle, 1999).

The problem faced by individual *A. herberti* is this: if it rains hard for, say, 30 min, does this mean that a flood will occur? How about 40 min? 50? It turns out that this is a classic problem in signal detection theory, a branch of information theory that is useful for understanding how animal behaviours evolve in response to noisy signals (in this case, rainfall events of a given duration that do or do not result in a flood) (Getty and Krebs, 1985; Reeve, 1989; Wiley, 1994; Getty, 2002). Essentially, each *A. herberti* individual must balance the cost of leaving the stream (predators in the terrestrial environment, desiccation) against the cost of remaining in the stream (mortality from a flood), in the context of flood predictability. Two types of mistakes can be made: an individual might abandon the stream when no flood occurs (a 'false alarm'), or an individual might choose to remain when a flood does occur (an 'incorrect rejection'). Rainfall cues provide information about the environment – in general, the longer the rainfall event, the more likely a flood. However, this information profile differs among catchments, because rainfall is a reliable predictor of floods in mid-sized catchments (≈ 10 km^2), but less so in smaller or larger catchments. Signal detection theory thus predicts that response time (the minutes of rainfall required to trigger RRB) should be fastest in the predictable mid-sized catchments, assuming that costs for incorrect rejections and false alarms are similar across catchments.

Behavioural experiments across 15 *A. herberti* populations inhabiting catchments ranging in size from 4 to >400 km^2 revealed local adaptation to different local flood regimes: individuals from mid-sized catchments did, in fact, require the shortest durations of rainfall to trigger flood escape behaviour (Lytle *et al.*, 2008). In an extreme case, individuals from the smallest catchment (4 km^2), where floods rarely if ever occur, 'refused' to leave the stream at all – for these individuals, there is simply no benefit to leaving the stream, only a cost.

In a sense, the *A. herberti* populations encompass the ideal conditions for local adaptation to different flood regimes. They are flightless and so local adaptation is not counteracted by gene flow from differently adapted populations, i.e. factor (vi) in the section above is satisfied. Phylogeographic analysis of mitochondrial data suggests that at least some of these populations may have been isolated since the Pleistocene (Finn *et al.*, 2007), allowing plenty of time for natural selection to adapt populations to local flood regime characteristics. Furthermore, high haplotype diversity in many populations suggests that there may be, or have recently been, much heritable trait variation on which selection can act [factor (vii) in the section above]. Flash floods are also a very strong selective pressure, as the cost of making a mistake approaches 100%. Thus, the *Abedus herberti* system provides a baseline against which we can evaluate local adaptation to flood or drought in other aquatic insect taxa. We now know that given sufficient time, sufficient isolation of populations and sufficiently strong selective pressures, that aquatic insect populations can adapt locally to a range of disturbance regimes.

Further Research and Management Implications

The examples given above show that aquatic insect populations can evolve in response to local flow regimes, at least under conditions where isolated populations are experiencing strong local selection. Next, we need to determine how common local adaptation is: Do most aquatic insect populations show some degree of local adaptation to flood or drought regime, or does this only happen in 'extreme' cases (i.e. fragmented populations with strong, divergent local selective pressures)? Also, many of the empirical examples come from desert systems where flood and drought are significant in both magnitude and frequency, and thus strong selective pressures – are adaptations to flood and drought as common in temperate and tropical systems? General disturbance theory predicts that traits such as life histories will evolve most quickly when disturbances are sufficiently frequent, strong in magnitude, and predictable (e.g. Lytle and Poff, 2004). The answers to these questions await further studies across different stream types.

Human-caused alteration of natural disturbance regimes is becoming ubiquitous in fluvial ecosystems, especially in the larger rivers (Nilsson *et al*., 2005), and so an understanding of how organisms might evolve in response to this, or fail to evolve, is needed immediately. For example, anthropogenic changes to flow timing, magnitude, and frequency have increased disturbance predictability in some cases, e.g. by homogenizing flow regimes below hydropower dams (Poff *et al*., 1997), and decreased disturbance predictability in other cases, e.g. irregular drought occurrence due to water diversion (Rader and Belish, 1999). Some aquatic populations have been observed to adapt rapidly to novel conditions if heritable genetic variation is available for selection (Hendry *et al*., 2000), so it is possible that aquatic insect populations may respond rapidly to novel changes in flow regime.

A growing body of research is demonstrating that behavioural adaptations to flooding and drought involving rainfall cues may be commonplace, and this has implications for the management of regulated rivers and streams. A number of river restoration projects are employing ecological flows from dam releases to manage downstream habitats, with the intent of enhancing habitat for flood-dependent organisms (Patten *et al*., 2001; Richter *et al*., 2003; Shafroth and Beauchamp, 2006). Because dam releases will often occur without prior rainfall or other cues associated with natural flood events (increased turbidity, cloud cover, lowered barometric pressure), aquatic insects that rely on these cues might suffer excess mortality from artificial floods that occur without warning.

In summary, macroevolutionary patterns appear to determine the mode of adaptation (behavioural, life-history, morphological) that aquatic insects may possess to cope with floods or droughts. In certain aquatic insect groups, respiratory requirements and life cycle constraints cause some modes to be favoured over others. As behavioural adaptations involving rainfall cues are widespread in some taxonomic groups, the implications of this for ecological flow events (which seldom have appropriate rainfall cues) needs to be explored. At microevolutionary scales, populations may adapt locally to natural differences in disturbance regime, especially when certain evolutionary criteria are met (factors pertaining to disturbance mortality, frequency and predictability; organism lifespan; environmental gain; heritable variation for trait; population isolation). Whether populations are evolving in response to anthropogenic changes to flood and drought regimes remains an open question.

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8

Movement and Dispersion of Insects in Stream Channels: What Role does Flow Play?

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Abstract

The interplay between landscape and movement can have far-reaching consequences for populations, so an understanding of movement (or lack of) is fundamental. Flow forces create heterogeneity within stream channels – the movement and spatial distribution of insects is related to this flow and topographic heterogeneity. No stream insects are sessile, all are mobile. Researchers often describe large-scale distribution patterns (e.g. abundance in riffles versus pools), but these may arise from small-scale movements and the insect's perception of the environment is only ever small-scale. The crawling behaviour of at least some insects (e.g. cased caddisflies) is influenced by microscale hydraulics and microtopography, and these movements are context-sensitive as they change with larger-scale flows. Thus, it is critical that movement studies are carried out on realistic topographies and near-bed flows. Drift is frequently assumed to dominate insect movement in streams, but this view may be biased by colonization studies that are ill-suited to this purpose and because other forms of movement are under-studied. Movement is multi-phasic and a full understanding requires integrating all forms. Various methods and approaches to studying movement are reviewed, with particular reference to their application to stream insects. Movement may play a key role in producing common distribution patterns and tests are required to discriminate between alternative mechanisms.

Introduction

Animal movements are individualistic events and the movements of many individuals combine to produce spatial distribution patterns. Large-scale patterns, therefore, are the accumulation of movements at smaller scales and movement behaviours may be scale-dependent. Movement plays a major part in determining the fate of individuals, thus linking behaviour with population dynamics. Studies of movement are often approached from one of two main perspectives: studies that target the behaviours and paths of individual animals, and those that examine the redistribution patterns of many animals. These perspectives are

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obviously linked, as the latter depends upon the former, but the approaches, methods and scales of investigation differ. Ultimately, movement studies seek to understand how patterns arise from movements and the consequences for population structure and dynamics.

For organisms with complex life cycles, such as insects with aquatic and terrestrial stages, research questions will vary with the organism's life stage and movement mode, and also the scale of examination. At large scales, landscapes with multiple habitat patches surrounded by territory unsuitable for habitation (e.g. multiple streams or catchments) are appropriate for studies of between-habitat dispersal (usually by adults) and multi-generation, multi-population phenomena (Bilton *et al.*, 2001; Malmqvist, 2002). This chapter focuses on smaller scales, the movement of individuals (usually juveniles) within streams and within one generation, but juvenile and adult movements are equally important for population dynamics. For example, a common assumption is that connectivity within streams is high, but empirical tests are rare and there is evidence to the contrary (below). Such assumptions influence our perception of population structure (Melbourne and Chesson, 2005; Downes and Reich, Chapter 10, this volume) and, from an applied perspective, are important for stream restoration targets (Lake *et al.*, 2007).

Environmental heterogeneity strongly influences movement and recognizing the importance of this interaction has led to a more spatially-explicit view of ecosystems. The heterogeneous nature of landscapes, the ability of individuals to track changes in patch quality and move between patches may influence population persistence, especially in temporally variable environments. The largely unidirectional flow of water is characteristic of streams and flow is often considered the 'master' variable dominating ecological process. While this may be true generally, flow can affect movement and dispersion in diverse ways, e.g. directly by influencing movement mode, speed and direction, or indirectly by creating the physical heterogeneity and topography of channels, which, in turn, influences movement. This chapter considers movements over landscapes large enough to contain multiple particles, not micro-scale movements on individual clasts. I use 'flow' in a generic sense to describe a suite of hydraulic variables (often correlated), including velocity, turbulence and shear stress. There is a rich literature in hydrology, hydraulics and fluvial geomorphology for those who wish detail. For a general review of physical–biological coupling in streams, see Hart and Finelli (1999).

Despite the ecological importance of movement, few studies have *directly* examined movement of invertebrates in streams and considered the implications for distribution patterns or population processes. Observing movements of individuals is difficult but, without appropriate empirical data, even the best inferences may hinge upon dubious assumptions. This chapter aims to stimulate interest in studying invertebrate movement and, to start, a conceptual example illustrates gaps in our understanding. This is followed by a review of the ways that stream insects move, with particular emphasis on how invertebrates perceive and respond to the stream environment. The approaches and numerical methods used in movement studies are reviewed, along with their suitability for stream studies. Spatial distribution and movement are inextricably linked. Some recurring patterns in streams are described along with the role that movement and flow may play in producing those patterns.

Received Wisdom and Knowledge Gaps

A wide ranging review of the literature gives the impression that drift is the dominant form of invertebrate movement, flow patterns largely determine movement (because drift is advective) and drift results in a net downstream displacement of individuals over the aquatic stage of the life cycle. Numerous studies illustrate the context-sensitivity of drift (differences in motivation or physical environment), but few generalizations arise about context-sensitivity. Invertebrates move around a lot within stream channels (the 'continuous redistribution' term coined by Townsend and Hildrew, 1976) and this movement may obscure spatial patterns at some scales. The spatial distribution of invertebrates in streams is heterogeneous at most scales, heterogeneity that is routinely attributed to species' resource and habitat requirements, which are patchily distributed themselves. As the master variable, flow is considered integral in driving insects' distributions by influencing the distribution of resources and habitats. Curiously, the role of movement in producing spatial patterns is rarely considered, yet animals must move in order to find resources. Overall, our understanding of movement in streams is weak and, consequently, 'knowledge gaps' underlie some fundamental aspects of stream ecology.

As an example of the link between movement and spatial distribution, consider a stream that is an alternating series of two patch types, such as riffles and pools. Benthic invertebrate assemblages typically differ between riffles and pools (Hynes, 1970), and invertebrates move around a lot. From these two observations follow two corollaries: First, invertebrates in their resident patch must move in such a way that they stay within that patch (local journeys) and do not cross patch boundaries (Fig. 8.1: A). Thus, movement behaviour in resident patches must ensure high patch residency. Second, individuals must move only infrequently between patches (distance travel). For distance travel to occur at all,

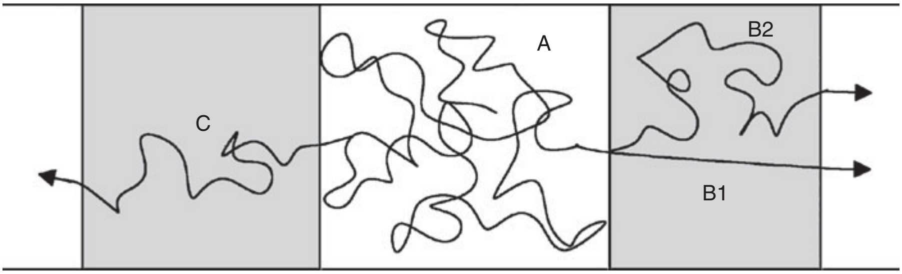

Fig. 8.1. Schematic of stream with series of riffle and pool patches (shaded versus open areas). Lines indicate hypothetical movement paths of an individual that is normally resident in open patches, but occasionally crosses shaded patches. See text for further description.

movement behaviour must allow individuals to cross patch boundaries on some occasions. Once a boundary has been crossed, movements in adjacent patches could be different (Fig. 8.1: A versus B1) or superficially similar to those in resident patches (Fig. 8.1: A versus B2), with the exception that patch residency must be low. Given the unidirectional flow of water, is movement during distance travel directionally reciprocal? i.e. the same in upstream versus downstream directions (Fig. 8.1: B1 and B2 versus C). Thus, we see that movement is multiphasic and context-sensitive, i.e. invertebrates switch between behaviours that produce local or distance travel. Each movement phase is also likely to differ in motivation and the interactive effects of environmental factors.

This example is conceptually simple, but, for virtually no stream invertebrate is there adequate empirical data about how movement behaviour produces or contributes to these riffle–pool patterns. This is surprising given the importance of riffle–pool patterns to many aspects of stream ecology. To pursue this problem further would require information on the characteristics of riffles and pools (e.g. velocity, particle size, food resources) and how those factors influence movement. We need to know how animals move (walk, swim, etc.), characterize their paths across the topographic landscape (around or over rocks?) and the flow landscape (along or across flow isovels?), determine what motivates movement (especially cross-boundary movement), movement speed and frequency.

It is often presumed that stream insects occur in places that are beneficial and avoid places that incur costs of some sort. Insects do have physiological limitations, resident patches may be places of high food resources (examples below) and insects may avoid places of high predation risk, as do some fishes (Power *et al.,* 1989). Importantly, we need to know how, or whether, aquatic insects balance these costs and benefits through movement, as do terrestrial vertebrates for example (Fortin *et al.,* 2005). Equally, costs/benefits cannot be assumed from distribution patterns as other processes may be more important determinants of distribution (Fonseca and Hart, 2001).

Modes of Movement (or not) in Streams

Invertebrate movements in streams are almost as diverse as the species. Movement mode may change ontogenetically with body size and Reynolds' number (Kutash and Craig, 1998), and individuals of any particular size may employ multiple modes (Olden *et al.*, 2004). There are two main modes of movement: self-propelled (crawling, swimming, looping, etc.) and advective or fluid-assisted (drift, saltation). Truly passive movement is uncommon as insects rarely behave like inanimate particles or have no control over their movement. Passive movement includes rafting of larvae attached to floating debris or algal mats (Gore, 1979), and at the egg stage if eggs are broadcast or masses laid on hard substrates that float and drift, such as bark and wood (personal observation; Reich and Downes, 2004). Broadcast eggs may have an attachment disc or other adhesive structures that allow eggs to stick to the stream bed (Koss and Edmunds, 1974; Rosciszewska, 1991), but eggs may travel considerable distances before touching the bed. Passive transport also occurs for insects attached to other animals in commensal, parasitic or epibiontic relationships (Disney, 1971; Tokeshi, 1993). Perhaps equally important to studying movement is understanding when invertebrates do not move. Many species go through prolonged periods of little or no movement during pupation, diapause or as eggs and early instars. Where they go during these periods (resource and environmental requirements) can influence dispersion patterns and population dynamics (Marchant and Hehir, 1999).

The bug's-eye view

Research questions may focus on how movements are played out over large scales, but the perception of invertebrates is invariably small scale, they are unlikely to perceive the larger landscape and movements are conditioned by the immediate environment. Thus, all movements are context-dependent and there may be apparent contradictions in the nature of these dependencies, e.g. drift density can be increased by reducing or increasing flow (Poff and Ward, 1991). In the bug's-eye view, stream beds are complex, three-dimensional landscapes with multiple particles packed together, and overlain by equally complex flow fields that this surface creates. Movements are likely to be associated with bed topography (particle size, size distribution, packing imbrication) and with near-bed flow, and these factors are closely related. For drifting invertebrates, the impact of bed topography on flow structures in the water column decreases with increased distance above the bed, but is still important as drift events start and finish at the bed surface.

Observations of animal movements in natural streams or faithful replicas of stream environments are required to understand how the physical environment influences small-scale movements. Unnatural or over-simplified experimental arenas may produce abnormal behaviour, observations and inferences that differ from patterns in real systems. Flume studies routinely use simplified substrates or randomly arranged stones, but these do not replicate the water-worked surfaces of stream channels. For example, the frequency distribution of bed elevations in streams are typically log-normally distributed with a positive skew, whereas those of random or unworked beds are negatively skewed due to differences in packing geometry (Kirchner *et al.*, 1990; Nikora *et al.*, 1998). With fundamentally different surface topographies, near-bed flow fields will also differ. A few flume studies have recreated natural gravel substrates for hydraulic (Young, 1992; Buffin-Bélanger *et al.*, 2006) and ecological studies (Lancaster *et al.*, 2006; Rice *et al.*, 2008). These are challenging technically, but provide unprecedented opportunities to record movements in fine detail and map movements on to landscapes with equally fine physical descriptions.

Evidence indicates that the micro-topography and micro-scale hydraulic patchiness of streams strongly influences the movement and distribution of benthic invertebrates. A good example is a study in which a cast replicating a large patch (≈ 2 m^2) of water-worked river gravels (Buffin-Bélanger *et al.*, 2003) was placed in a flume where the microtopography and near-bed flow field was described in detail (Buffin-Bélanger *et al.*, 2006). The short-term (<30 min) movements of cased caddisflies (Limnephilidae: *Potamophylax latipennis*) across the cast was described in equally fine detail (Lancaster *et al.*, 2006; Rice *et al.*, 2008). These observations were carried out without food or predators and, thus, the results reflected responses to the physical environment only. Near-bed flows were modest and similar to those in glides or slow riffles, and maximum flow was below the threshold for entrainment of the framework particles (details in Buffin-Bélanger *et al.,* 2006). Crawling was the dominant form of movement for cased caddisflies on this cast and only at high discharge was advective movement (saltation) significant. Crawling paths were non-random and closely related to local micro-topography and hydraulics (Fig. 8.2). Animals tended to crawl around particles rather than over the top, and crawling activity was concentrated on certain pathways, especially corridors on the lee side of imbricated particle clusters (e.g. behind particles at top-middle of Fig 8.2). Indeed, caddis crawled most frequently in low-lying areas where velocities and turbulent kinetic energies were relatively low (Rice *et al.*, 2008), suggesting that these caddis tracked velocity gradients. Overall, the animals appeared to exploit hydraulically sheltered pathways, possibly to minimize the energetic costs of fluid drag and the risk of entrainment, as might be expected (Vogel, 1981).

Context-sensitive movements were recorded in the studies described above, as in many others. First, movement behaviour was contingent upon discharge. Crawling caddis selected areas of relatively low velocities and turbulent kinetic energies, and the strength of this discrimination increased with discharge and overall near-bed flow (Rice *et al.*, 2008). Caddis crawled more slowly and shorter distances at high discharge (Lancaster *et al.*, 2006) and there was a corresponding decrease in population spread (Fig. 8.3a), as indicated by random walk models

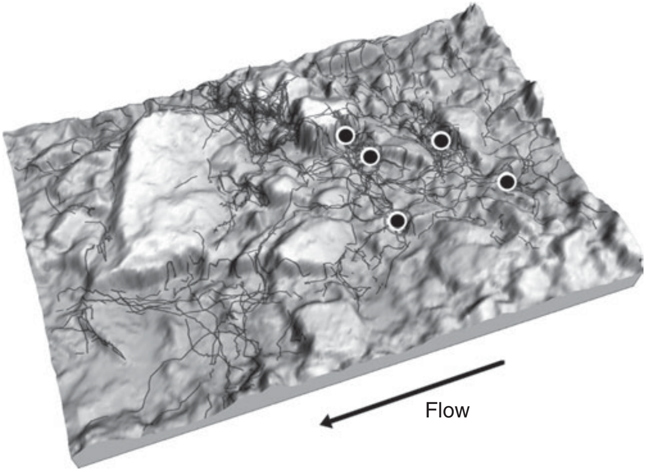

Fig. 8.2. Topography of a section of cast stream bed (0.8 × 1.1 m) based on an oblique view of the digital elevation model. High elevations are white; low-lying areas are dark. Lines are crawling paths followed by cased caddisflies cumulated over three flow treatments. Black circles are seeding locations where animals began crawling. (For details see Lancaster *et al.*, 2006; Rice *et al.*, 2008.)

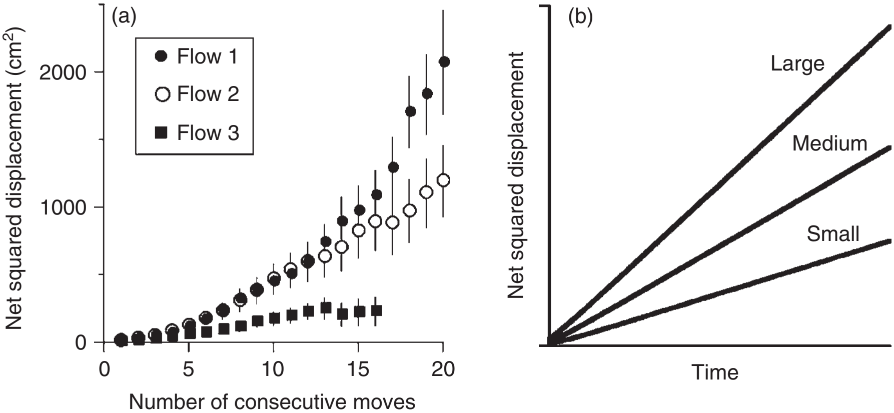

Fig. 8.3. (a) Rate of population spread (mean ± 1 SE) estimated by random walk models for cased caddisflies *Potamophylax latipennis* crawling on a replica gravel bed at three discharges. (Redrawn from Lancaster *et al.*, 2006.) (b) Illustration of how an increase in substrate particle size can increase rate of population spread, if animals walk around particles.

(discussed below). That caddisflies crawl ineffectively at high flow may be unsurprising, but empirical data to demonstrate this phenomenon are scarce. The second interesting contingency was the tendency for caddis to crawl around rocks, not over the top (Lancaster *et al.*, 2006), with the consequence that animals will disperse farther and faster as rock size increases (Fig. 8.3b). Given that particles are usually bigger in riffles than pools, this topographic control on movement would result in caddis spending more time in pools than riffles and, thus, could contribute to the commonly observed predominance of heavily cased caddis, such as *P. latipennis*, in pools (Scott, 1958).

This set of studies is illuminating, and more such studies in realistic environments are now required to characterize the behaviour of different taxa and under a range of environmental conditions. For example, does the movement of these caddis alter in the presence of food and predators? Are other crawling or swimming taxa subject to topographic control?

Advective movement

Drift is the iconic form of advective movement (e.g. reviews by Waters, 1972; Brittain and Eikeland, 1988) and many drift studies focus on active or intentional drift (Kohler, 1985). Accidental or disturbance-related drift may be rare over a life cycle, although the population-level consequences could be significant if disturbances are large. During spates, instead of drifting, animals may tumble at the bed surface in a manner akin to saltating particles (Lancaster *et al.*, 2006). The fate of saltating particles differs from that of particles fully entrained in the drift, e.g. the direction, distance and pathways of current-assisted particles will differ in association with difference in flow patterns at the bed surface (saltation) and in the water column (drift). This distinction between drift and saltation may be important when considering the effects of floods on populations. Saltating insects risk physical damage from being bumped against stationary objects and risk burial during bedload transport (Dobson *et al.*, 2000); drifting insects risk being stranded on stream banks when flood waters recede (personal observation).

Knowing when and where invertebrates stop moving may be as important as movement itself. In particular, the factors determining where drifting individuals regain the substrate are vital when estimating drift distance and destination (similar questions apply to saltation, but studies are scarce). Ambient flow conditions obviously influence drift distance, but drift distances also vary among species in the same stream (Elliott, 1971; Lancaster *et al.*, 1996) and these variations can be attributed to body morphology, behavioural changes in body posture (Blum, 1989; Oldmeadow, 2005) and swimming (Campbell, 1985; Allan and Feifarek, 1989). If turbulence is high, animals may tumble in the water column, unable to swim or maintain body posture, and may have difficulty contacting the bed (Oldmeadow, 2005). Some insects, such as larval Simuliidae, use adhesive filaments (threads of mucus or silk), which enhance the effective size of larvae and increase their ability to make contact with the bed (Fonseca, 1999; Fingerut *et al.*, 2006). Where they contact the substrate depends on local hydraulics and current direction (Fonseca and Hart, 2001). Once animals regain the substrate, whether they remain (settle) or return to the drift may depend upon the microenvironment, habitat requirements and ability to assess patch quality (Walton, 1978).

Drift is often considered the dominant form of movement in streams, a perception likely to be influenced by research biases and, more importantly, by studies using unsuitable methods. In terms of research bias, movement studies have focused overwhelmingly on drift and other movement modes receive much less attention. But most, perhaps all, invertebrates are capable of self-propelled movement and some taxa rarely drift. Further, most drift studies target only a few taxa, namely mayflies of the family Baetidae and some crustacean amphipods, especially *Gammarus*. Baetid nymphs are unique with regards to dispersal ability (Rader, 1997) and, as Hynes (1970) stated nearly 40 years ago, ‘what applies to them [Baetidae and *Gammarus*] may not be true of stream invertebrates generally.’ Baetids are also adept swimmers (Craig, 1990), but their swimming movements are rarely incorporated into movement models. Methodologically, the relative importance of different movement modes is often inferred from colonization studies, but colonization methods are poorly suited for this purpose. Most colonization studies are unable to separate drift from swimming, so estimates of drift are likely to be conflated. Travel distance cannot be estimated, yet the distance travelled in each mode may be more important than the last few centimetres of the journey. Colonization studies are also sensitive to variations in settlement behaviour and colonization substrates may create significant biases between movement modes. Settlement on denuded or disturbed substrates (typical of colonization methods) may differ from settlement on substrates with intact assemblages or with natural topographies (see *The bug’s-eye view*). Further, hydraulic patterns around substrates raised above the bed (to exclude walkers) will alter settlement rates relative to the bed itself (Fingerut *et al.*, 2006). Finally, if drift is the major form of movement, then evidence of net downstream displacement of juveniles over the life cycle should be common, but it is rare. Indeed, some species have high patch residency (Hart and Resh, 1980; Hancock and Hughes, 1999; Jackson *et al.*, 1999) and some occupy only short lengths of stream (Williams and Williams, 1993; Bogan and Lytle, 2007).

On balance, this assumption of drift dominance requires scrutiny. Similarly, alternative methods (not colonization studies) are required to assess the relative importance of movement modes – methods that permit estimates of the time and distance travelled in each mode. It is perhaps overly simplistic to expect one mode of movement to dominate. At the very least, variations among species and developmental stages are likely and, given that movement is multi-phasic, different modes may dominate different phases. A more pluralistic approach would be enlightening.

Study Approaches

Studying movement of any animal is challenging, but benthic invertebrates and the streams they inhabit present particular difficulties and approaches need to match the research questions. Here I briefly outline the main practical and numerical approaches to studying movement of stream insects.

Movement of individuals versus population redistribution

Movement data comes in two main forms depending on whether investigations target the behaviour of individuals or the spatial redistribution of an assemblage or population. Direct observation of movement behaviours and paths is perhaps the most powerful source of inference, but difficult in streams. Continuous observation, either recorded on video (Lancaster *et al.*, 2006) or live (Poff and Ward, 1992; Olden *et al.*, 2004), allows fine-scale documentation of paths and factors influencing those paths. This data acquisition is labour-intensive, and the spatial and temporal scales of study are necessarily short. Larger-scale studies usually involve uniquely marked individuals and recording their spatial position at longer time steps, a series of capture–recaptures. Animals can be marked in diverse ways (Hart and Resh, 1980; Freilich, 1991) or radio transmitters used to follow their movement (Hayashi and Nakane, 1989; Bubb *et al.*, 2006). If the time step between recaptures is large relative to the distance moved, the data can provide information on the overall displacement of individuals between recapture points, but the movement mode, path and interacting environmental factors are largely unknown. Because recapture rates are typically low (Freilich, 1991), inferences may be based on small subsamples and distinguishing between movement and death can be difficult.

Mass mark–recapture methods are often used to examine the spatial redistribution of populations. For stream invertebrates, mass marking techniques include physical marks (Erman, 1986; Jackson *et al.*, 1999) and chemical marks, such as stable isotopes (Hershey *et al.*, 1993; Macneale *et al.*, 2005), but these studies also suffer low recaptures (Jackson *et al.*, 1999). As chemicals are transported downstream and individuals could acquire chemical marks anywhere within a large area, the release point and distance travelled becomes uncertain

(Macneale *et al.*, 2005). Genetic markers are commonly used to assess genetic differentiation among populations and infer dispersal processes (Hughes, 2007), but translocating genetically distinct individuals can facilitate direct observations of movement (Hancock and Hughes, 1999).

An indirect approach is to examine temporal differences in local densities. This avoids the risk that marking or observation methods might influence behaviours (Gallepp and Hasler, 1975; Barmuta *et al.*, 2001), but they tell us little about movement modes or pathways. Often, these are colonization studies where habitat patches are denuded initially and the presence of animals at a later date implies movement. Inferences about movement based on colonization studies requires caution (discussed above) as the origin of colonists is unknown and the relative colonization speed of different taxa may be confounded by variations in their relative abundance (Lancaster *et al.*, 1990; Winterbottom *et al.*, 1997). Carefully designed colonization studies can, however, provide insight into how movement influences spatial distribution (Fonseca and Hart, 2001).

Modelling movement, scales and scaling-up

Different kinds of movement data require particular kinds of analysis and a substantial body of theory describes animal movement patterns (review in Turchin, 1998). Random walk models are powerful tools for analysing movement paths, diffusion models are more appropriate for data on spatial redistribution, and simulation models can scale up the effects of many small-scale movements.

Random walk models translate individual movement data into a measure of dispersal or population spread over a two-dimensional area. Animal movement is rarely random but, in homogeneous environments, movement is often described by a correlated random walk. Here, correlation refers to the tendency for individuals to move in the same direction as the previous move. A biased random walk may be appropriate if there is a directional bias in movement, e.g. downstream or along velocity isovels. Random walk models often fail to predict empirical patterns over large scales (Bergman *et al.*, 2000), but are reasonable null models for small scales. Lancaster *et al.* (2006) tested various random walk models against movement paths of cased caddisflies and their results suggested that flow-related changes in dispersal (Fig. 8.3a) could increase patch residency of caddis during high flows. This provided insight into how this species exploits flow refugia and populations persist during floods (Lancaster and Belyea, 1997).

Density–distance curves (the relationship between drift or benthic density and distance from a release point) commonly describe data about population redistribution. Most organisms tend to settle and few travel far, a pattern typical of diffusion processes and testable using diffusion models. If dispersal is biased along an environmental gradient, then advection–diffusion models may be appropriate. Model relationships fit to density–distance data may reveal something about the dispersal process provided the models are mechanistic rather than phenomenological but, in the stream literature, phenomenological curve fitting is more common than mechanistic models. To simplify models, streams are often treated as one-dimensional linear landscapes and this is inappropriate for small-scale studies – even drift has a lateral component (Ciborowski, 1983). Most diffusion models assume further that the environment is homogeneous or quasi-homogeneous (the spatial scale of heterogeneity is much smaller than the scale of dispersal). These assumptions, coupled with the shortage of empirical data to parameterize most diffusion models, limit their usefulness. Perhaps the biggest weakness of density–distance curves is the lack of information about the movement mode or path, e.g. the occurrence of an animal in the drift reveals nothing about movement modes used between release and capture points. Was that one drift event? Or a hop, skip and jump?

Elegantly, Fonseca (1999) used computer simulations of a *mechanistic* individual based movement model to demonstrate how *phenomenological* density–drift relationships observed in the field could arise from the drift and settlement behaviours of individual black fly larvae. Importantly, this work unravelled why the relationship between larval abundance in the drift and distance from the release point is linear in the smooth flow of flumes, but fits a negative exponential relationship in the heterogeneous environment of streams channels. Individual based movement models assume that each action in the movement process can be described empirically or probabilistically and, likewise, that influences of the local environmental can be characterized. Computer simulations of individual based movement models can then generate redistribution patterns of populations if paths cannot be traced but movement behaviours are known. The real power of simulation models lies in generating specific predictions and comparing these predictions to independent, empirical measures in real landscapes, an approach under-exploited by stream researchers.

Distribution Patterns Within Streams: Roles of Movement

The heterogeneous distribution of invertebrates in streams is legendary and aggregated distributions occur at most scales. The usual presumption is that these patterns are driven by the location of resources and habitats. But, insects must move to locate resources and the role of movement (or not) in producing spatial patterns is largely unknown. Resource and habitat distributions are not necessarily correlated, however, and the actual distribution of animals may reflect complex trade-offs and interactions among gradients. The important point is that patterns could arise via multiple routes, movement may be integral to many, and these movements warrant attention.

Congregative movements and distributions

The consequences of congregative or gregarious movement for population dynamics may be profound (Turchin, 1989), but are rare (or rarely reported) among stream insects. Stream invertebrates are commonly assumed to be independent entities that react to the environment but not to one another. Congregations (gathering of conspecifics in response to one another) do occur, however, as illustrated by congregations of caddisflies when pupating or in late instar diapause

(Gotceitas and Clifford, 1983; Marchant and Hehir, 1999) and which arise without physical stimuli (Gotceitas, 1985). Some larvae are clearly capable of tactile or visual recognition of conspecifics (chemical cues have not been detected, Martin and Barton, 1987), but the cues and movements that underlie these congregations are unknown. The paucity of information makes it difficult to determine whether congregation is unimportant to stream insects, or simply under-studied.

Prey, predators and distribution patterns

Food resource patches are often aggregation centres for consumers, be they aggregations of predators and prey (Malmqvist and Sjöström, 1984; Lancaster, 1996), detritivores and leaves (Dobson and Hildrew, 1992; Murphy *et al.*, 1998), or grazers and algae (Feminella and Hawkins, 1995). Many such aggregations result from preytaxis, in which animals condition their movement on an assessment of patch quality or consumption rates to increase residence time in high food patches (Hart, 1981; Kohler, 1984; Olden *et al.*, 2004). Flow can also contribute to these aggregations as depositional areas may accumulate detritus and advectively dispersing consumers. Consumer–resource aggregations are not ubiquitous, especially for predator–prey associations, and exceptions may result from mutual aggression among predators (Peckarsky and Penton, 1985), presence of larger predators (Peckarsky, 1991), or high prey mobility and escape behaviours (Lancaster *et al.*, 1991; Sih and Wooster, 1994). Thus, movement can break down consumer–resource aggregations. Species-specific differences in habitat or flow requirements can also preclude aggregative patterns as flow may provide predator refuges for some prey taxa (Hansen *et al.*, 1991; Hart and Merz, 1998).

Food resource exploitation can also result in uniform distributions, usually only at very small scales (<0.01 m^2). Filter-feeding larvae of black flies and hydropsychid caddisflies often form parallel bands aligned perpendicular to the flow and these reflect a complex interaction between behaviour, food concentration and flow pattern (Ciborowski and Craig, 1989; Thomson *et al.*, 2004). These larvae depend on flow to deliver food, but the larvae themselves alter fine-scale flow patterns to facilitate feeding efficiency among side-by-side neighbours and interfere with upstream and downstream neighbours. The existence of these patterns, however, is contingent upon larvae moving into these sites and patterns can vanish if feeding sites are abandoned (Sharpe and Downes, 2006). Intraspecific competition also results in regular spacing of semi-sessile grazing caddis (McAuliffe, 1984a; Hart, 1985) and interspecific competition can result in negative spatial associations between species (McAuliffe, 1984b; Hemphill, 1988). Many of these small-scale patterns are transient, however, and often disrupted by flow disturbances and associated animal movements (McAuliffe, 1984a; Hemphill, 1991).

Flow and distribution patterns

That invertebrate density is influenced by flow is widely accepted, but close associations between local density and flow are rare at small scales, given the confounding effects of movement and other factors (Lancaster and Belyea, 2006). The mechanisms underlying these associations are diverse and include oxygen uptake, feeding behaviours and maintaining the position in shearing flows (Vogel, 1981; Lancaster and Belyea, 2006). Invertebrates encounter and tolerate a range of flow conditions as they move across stream beds and the flow range encountered may vary spatially and temporally (Rice *et al.*, 2008). Conversely, movement constraints may make some flow environments and channel areas inaccessible and animals may be absent from seemingly optimal environments (Fonseca and Hart, 2001). Thus, while species may be broadly categorized as fast or slow flow specialists, these designations are of limited use when trying to locate animals or elucidate the mechanisms underlying distribution patterns.

At larger scales, channel units (riffles, pools, etc.) and subunits (steps, bars, etc.) typically differ in flow regime, invertebrate distributions often reflect these flows, and patterns could arise in multiple ways. The example at the beginning of this chapter illustrates how movement behaviours could be important in maintaining riffle–pool distribution patterns. Those multi-phasic movements could arise from preytaxis (if food is abundant in resident patches) or, given the differences in flow regime among channel units, by flowtaxis (movements conditioned on an assessment of the flow), as described by Rice *et al.* (2008). Additionally, patch-specific particle sizes and topographic control of movement could also contribute to riffle–pool patterns, as described above. Alternatively, the initial distribution of juveniles may be related to the distribution of oviposition sites across channel units and the behaviour of ovipositing females (Hoffman and Resh, 2003; Lancaster *et al.*, 2003; Reich and Downes, 2004). Such patterns could persist if movement is limited, i.e. contrary to the assumptions of continuous redistribution and high connectivity. Similarly, the distribution of late instars may be related to the requirements of pupae and emerging adults (Otto, 1971; Marchant and Hehir, 1999), not the requirements of juveniles. Invertebrate abundances in riffles (or pools) on the same stream can be more variable than riffles in different streams (references in Robson *et al.*, 2005). Such patterns could arise if the physical environment of each riffle is unique or, equally plausible, if invertebrates are unable to move between channel units or maintain residency in some patches.

Flow patterns in streams are dynamic, changing with hydrological disturbances (floods and droughts), and the distribution of stream insects is equally dynamic. Flow may be the ultimate driving variable behind some pattern changes, but the proximate movement behaviours are likely to be complex. Indeed, the persistence of populations in environments subject to these disturbances may be contingent upon the ability of individuals to move between habitat patches (Lancaster and Belyea, 1997; Lake, 2000), but these processes are poorly understood.

Spatial arrangement of resources and habitats

If movement behaviours are important in producing aggregations in resource and habitat patches, then we must also consider how the spatial arrangement of those patches influences movement. The movement paths of terrestrial insects across landscapes of patchily distributed resources is influenced by their spatial arrangement (Wiens *et al.*, 1997), and there are consequences for distribution patterns and population dynamics (Fahrig and Paloheimo, 1988). In streams, it has been suggested that any response of invertebrates to patch arrangements would be obscured by high movement rates (Sih and Wooster, 1994; Englund *et al.*, 2001), but recent studies indicate that patch arrangement can influence how individuals move through the landscape (Bond *et al.*, 2000; Olden *et al.*, 2004; Hoffman *et al.*, 2006), their distribution and abundance (Palmer *et al.*, 2000; Lancaster *et al.*, 2003), and life history (Silver *et al.*, 2000). Even if the precise arrangement of patches is unknown, spatial heterogeneity of resources, not just mean resource abundance, may influence the distribution and growth of invertebrates (Downes *et al.*, 1993; Palmer, 1995). So few studies examine the spatial arrangement of resources in streams that generalizations are not yet possible and more research is required.

Conclusions

Movement is of fundamental importance to many ecological phenomena and, despite a long-standing interest in invertebrate drift, invertebrate movement *in toto* and its consequences are poorly understood in streams. The literature is rife with assumptions about movement: some may be incorrect and most warrant scrutiny. Observing aquatic invertebrates directly is difficult, but indirect methods (e.g. colonization studies) and observations in artificial arenas are poor substitutes. Progress will depend on overcoming methodological difficulties and developing creative study designs. The context-sensitivity of movement is established and we now need to put movement studies into a context that will help elucidate population-level patterns and processes. There are alternative explanations for commonly observed distribution patterns and movement is integral to many, but few tests discriminate among the alternatives. Although the physical heterogeneity of stream channels is legendary, researchers have been slow to adopt a spatially-explicit perspective of these systems and to integrate movement studies with a landscape perspective.

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9

Population Responses of Drifting Stream Invertebrates to Spatial Environmental Variability: an Emerging Conceptual Framework

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Abstract

Stream communities are shaped by environmental influences at multiple spatial scales. The uncovering of general distributional patterns among benthic organisms and environmental parameters has, however, proven difficult. Empirical relationships tend to explain minor fractions of the variance in any given data set and are often inconsistent across data sets. A potential mechanism contributing to this weakness of empirical patterns is that drift behaviour creates downstream lags in population responses to local signals. We summarize recent theoretical developments describing how spatial environmental variation affects the distribution of drift-prone organisms, assuming a temporally constant environment. Typically, environmental variation affecting demographic rates is tracked by model populations if environmental conditions change over long distances, but averaged if the environment varies over short distances. Environmental variation affecting drift rates produces opposite patterns: the population tracks short-distance variation and averages long-distance variation. 'Long' versus 'short' are defined by the ratio L_E/L_R relating the spatial wavelength of environmental variation (L_E) to the population 'response length' (L_R), which is the average individual lifetime drift distance. Examples illustrate that expected correlations among local environmental conditions and local population densities are frequently weak. Moreover, the distributions of organisms with different response lengths may correlate only weakly with each other, even if they respond identically to the local environment. While theory suggests that the influence of spatial environmental variability on the distribution of drifting stream invertebrates cannot be inferred reliably from the

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resulting (lack of) empirical patterns, the reverse approach seems promising. Local responses to the environment as well as the response length can be estimated from small-scale experiments, which, in principle, allows the prediction of population responses to arbitrary patterns of spatial environmental variability.

Introduction

Streams are heterogeneous at scales ranging from millimetres to tens of km and the distribution of the organisms inhabiting them is believed to be shaped by physical, chemical and biological factors varying over a similarly wide range of scales (Pringle *et al.*, 1988; Cooper *et al.*, 1997, 1998; Thorp *et al.*, 2006). Linking general distributional relationships of benthic organisms to environmental parameters has, however, proven difficult. Empirical relationships tend to explain only minor fractions of the variance in any given data set and are often inconsistent across data sets (Heino, 2005; Murphy and Davy-Bowker, 2005; Mykrä *et al.*, 2007). This lack of explanatory power is, in part, due to biotic interactions and abiotic disturbances, both of which can superimpose considerable variance in the distribution of organisms on the environmental template (Hart, 1992; Crowl *et al.*, 1997; Matthaei and Townsend, 2000; Effenberger *et al.*, 2006). Here we focus on advective drift transport – common for many stream organisms (Müller, 1982; Lancaster *et al.*, 1996; Elliott 2002) – as yet another mechanism that can cause weak spatial associations of organisms with their environment.

Experimental manipulations at small spatial scales have shown that local dynamics of many mobile stream organisms are largely driven by migration processes (Cooper *et al.*, 1990; Forrester *et al.*, 1999; Englund, 2005; Roll *et al.*, 2005). Migration then obscures the demographic effects of the local environment by swamping local demographic processes. The latter are, however, responsible for the average population dynamics observed at larger scales to which migration *within* the larger spatial domain does not contribute. Considerable effort has therefore been devoted to identifying the spatial scales at which migration and demography, respectively, dominate dynamics and to the problem of 'scaling up' from small-scale experiments (Wiley *et al.*, 1997; Englund *et al.*, 2001; Melbourne and Chesson, 2006). This leaves still unanswered the important question of how spatial environmental variability *within* a large spatial domain is reflected in the population distribution.

We have recently proposed a framework for modelling the spatial dynamics of organisms that move exclusively by advection, and used it to derive insights into how such organisms would be expected to respond to multi-scale spatial environmental variability (Anderson *et al.*, 2005, 2006; Nisbet *et al.*, 2007). We showed that the degree to which spatial environmental variation is reflected in the distribution of a frequently drifting organism should depend on three attributes: (i) the spatial scale over which the environment varies; (ii) the kind of vital rate (demographic versus movement) that is affected by the environment; and (iii) the organism's lifetime movement activity. Collectively, these three attributes identify spatial domains over which environmental variation is either tracked or averaged by the population. The theory also provides a means for predicting spatial correlation patterns among organism distributions and the environment.

The purpose of this chapter is twofold. First, we review the assumptions and conclusions derived from the simplest possible case of our model, which describes the spatial population dynamics of a single, advectively moving stream organism in the absence of intra- and interspecific interactions. Second, we explore how the spatial covariance between the environment and the population distribution depends on the spatial scales of environmental variation. Throughout, this chapter is illustrated with numerical examples, which we hope will make the conclusions accessible and transparent to empiricists.

Model Description

We emphasize that our model considers general features of drift-prone stream organisms and should not be taken as a description of any specific organism or system. Instead, we chose to analyse a minimally detailed model that allows us to focus on general results and point to potential future directions as opposed to making system-specific predictions. We expect further insights from the future addition of temporal and hydrological complexity, detailed movement behaviour, and multi-species interactions to the model. Some of this work is in progress and we address it in the final section of the chapter.

The model describes the dynamics of a population of benthic organisms living in an idealized, one-dimensional stream with unidirectional flow. $N(x,t)$ denotes the population density at downstream location x and time t in units of individuals per length of stream bottom. Subsequently, we use the word ‘local’ whenever we refer to a point location x. Conditions are simplified by assuming a temporally constant environment, i.e. the environment affecting recruitment, death and/or movement rates may vary in space but is, at each location x, constant in time. Thus, individuals recruit locally to the population (e.g. from an egg bank) at rate $R(x)$ and die with per capita rate $m(x)$. They occasionally leave the bottom at per capita rate $e(x)$ and drift some distance before settling at a new downstream location. Neglecting short-distance movement by crawling, the rate of population change at location x is described as:

$$\frac{\partial N(x,t)}{\partial t} = R(x) - m(x)N(x,t) - e(x)N(x,t) + I(x,t) \tag{9.1}$$

All symbols are defined in Table 9.1. $I(x,t)$ is the local arrival rate of drift immigrants from upstream, calculated as the integral over the drift immigrants from all upstream locations y that settle at location x:

$$I(x,t) = \int_0^x e(y)N(y,t)h(x-y)dy \tag{9.2}$$

The settlement distribution $h(x - y)$ describes the average probability that an emigrant from an upstream location y settles at location x. If the probability of a drifting individual settling to the bottom is approximately constant per distance

Table 9.1. Definition of symbols [with units] and parameter values of example species 1 and 2.

Symbol	Definition
a_i	Scaled amplitude (= amplitude divided by mean) of a vital rate varying sinusoidally with spatial wavelength L_{E_i} [dimensionless]
b_i	Scaled amplitude (= amplitude divided by mean) of population density varying sinusoidally with spatial wavelength L_{E_i} [dimensionless]
$e(x)$	Per capita emigration rate at location x [1/time]
$\varepsilon(x)$	Proportional deviation of per capita emigration rate from its spatial average at location x [dimensionless]
e_H	Per capita emigration rate at the homogeneous space equilibrium [1/time]
$\bar{e}$	Spatially averaged per capita emigration rate [species 1: 0.29/day; species 2: 6.0/day]
$h(x-y)$	Probability of a drift emigrant from location y to settle at location x [dimensionless]
$I(x)$	Immigration rate at location x [individuals/length/time]
L_D	Average distance travelled in a single drift event [both species: 1.83 m]
L_{E_i}	Wavelength i of sinusoidal spatial variation in a vital rate [length]
L_{L_i}	Spatial lag in the population response to sinusoidal variation in a vital rate with spatial wavelength i [length]
L_R	Response length (approximate average lifetime drift distance) [species 1: 130 m; species 2: 2654 m]
$m(x)$	Per capita mortality rate at location x [1/time]
$\mu(x)$	Proportional deviation of per capita mortality rate from its spatial average at location x [dimensionless]
m_H	Per capita mortality rate at the homogeneous space equilibrium [1/time]
$\bar{m}$	Spatially averaged per capita mortality rate [both species: 0.00414/day]
$N(x)$	Population density at location x [individuals/length]
$n(x)$	Proportional deviation of population density from its spatial average at location x [dimensionless]
N_H	Population density at the homogeneous space equilibrium [individuals/length]
$\bar{N}$	Spatially averaged population density [individuals/length]
$R(x)$	Recruitment rate at location x [individuals/length/time]
$r(x)$	Proportional deviation of recruitment rate from its spatial average at location x [dimensionless]
R_H	Recruitment rate at the homogeneous space equilibrium [individuals/length/time]
$\bar{R}$	Spatially averaged recruitment rate [both species: 0.414 ind./m/day]
x	Spatial location in downstream direction [length]
x_d	Location of a spatially localized disturbance [length]

travelled, this yields the commonly observed exponential settlement distribution (Waters, 1965; Elliott, 1971). Thus, the probability that a drift emigrant from location y settles at location x is an exponentially decaying function of the downstream distance $x - y$:

$$h(x-y) = \frac{1}{L_D}\exp\left[-\frac{x-y}{L_D}\right] \tag{9.3}$$

Here, L_D is the average distance travelled during a single drift event, assuming no mortality during drift. The simplifying assumptions of no drift mortality and a constant drift distance are not crucial to our conclusions, if time spent in the drift is short (Appendix C in Anderson *et al.*, 2005). When spatial variability in stream flow and/or drift mortality are very high, a version of the model needs to be used where benthic and drifting organisms are modelled separately (Lutscher *et al.*, 2006).

Local and Regional Equilibrium States and the Concept of the Response Length

Equation 9.1 can be solved for the *local* equilibrium density at any location x:

$$N(x) = \frac{R(x) + I(x)}{e(x) + m(x)}, \tag{9.4}$$

which depends on both demographic and movement rates. In contrast, if the population is considered over a sufficiently large spatial domain, most migration occurs *within* that domain. Immigration and emigration within the larger spatial domain therefore cancel and the *regional* equilibrium density is determined solely by the balance of regionally averaged recruitment and mortality, $\overline{R} = \overline{mN}$, where bars denote spatial averages. If spatial variation in m and N is small, $\overline{mN} \approx \overline{m}\,\overline{N}$ and the *regional* equilibrium density is approximated by

$$\overline{N} = \frac{\overline{R}}{\overline{m}}. \tag{9.5}$$

When drift rates are high compared with demographic rates [$I(x) >> R(x)$ and $e(x) >> m(x)$], the sensitivities of local and regional equilibrium densities to changes in these rates differ strikingly (Nisbet *et al.*, 2007). For example, if $e(x) >> m(x)$, a twofold increase in local emigration rate will almost halve the local population density (Eqn 9.4), whereas a twofold increase in emigration rate everywhere in the stream has no effect on the regional population (Eqn 9.5).

The above analyses highlight two extremes, a change in a rate parameter at a single location or a uniform parameter change along an entire stream. In reality, environmental conditions affecting vital rates vary continuously at multiple spatial scales and the resulting population distributions are non-uniform. Before addressing population responses to such more realistic scenarios, we first review the concept of the *population response length* introduced by Anderson *et al.* (2005). We then demonstrate how the response length can be used to understand population responses to continuous environmental variation.

Consider a temporally constant, spatially homogeneous environment where the recruitment, death and emigration parameters assume fixed values R_H, e_H and m_H everywhere except at a single location x_d, where one of these parameters persistently deviates. We call this a 'localized disturbance' in space, which must not be confounded with the common notion of disturbance as a temporal event (recall that we assume a temporally constant environment). Upstream of the disturbance there is a balance of emigration and immigration and, analogous to Eqn 9.5, the resulting homogeneous space equilibrium density N_H is set by recruitment and mortality alone, as given by

$$N_H = \frac{R_H}{m_H}. \tag{9.6}$$

In general terms, a localized disturbance represents an 'impulse' and the system's downstream behaviour is called 'impulse response' (see Appendix 9.1 for mathematical and ecological interpretations). Figure 9.1 illustrates this for two species. Species 1 was parameterized for the stonefly *Leuctra niger* in Broadstone Stream (details in Anderson *et al.,* 2005), which is compared with a hypothetical species 2 with identical parameters, except for a 20.7-fold higher per capita emigration rate. Both species, therefore, have identical homogeneous space equilibria upstream of the disturbance (at $x < 0$). At location $x_d = 0$ a vital rate parameter deviates abruptly from its upstream value, which produces a discrete change in population density at x_d. Now, although the rate parameter returns to its upstream value immediately downstream of the localized disturbance (at $x > 0$), the population density may return much more slowly. This can be intuitively understood from Fig. 9.1a. When the disturbance causes an increase in per capita mortality, the equilibrium population density at the disturbed site $N(x_d = 0)$ will decrease compared with its upstream value. As a result, the number of emigrants from that location also decreases. Downstream locations will then receive fewer immigrants and thus have reduced population densities, the biggest reduction occurring immediately downstream of the disturbance. Reduced population density implies, however, also a reduction in total mortality $m(x)N(x)$, which is the ultimate reason for the gradual return of the population to its homogeneous space equilibrium. The exact converse holds if a disturbance affects recruitment, because a local increase in R produces an *increase* in population density (Anderson *et al*., 2005).

In conclusion, if the localized disturbance affects a *demographic* rate parameter [$m(x_d)$ or $R(x_d)$], drift migration creates a carry-over effect in downstream direction that decays exponentially with distance. This decay can be expressed as a return to the homogeneous space equilibrium density N_H, approximated by

$$N(x) = N_H\left[1 + n(x)\right] = N_H\left[1 + n(x_d)\exp\left(-\frac{x - x_d}{L_R}\right)\right]. \tag{9.7}$$

Here $n(x)$ is the *population response*, i.e. the *proportional* deviation in population density from the upstream, homogeneous space equilibrium N_{H}, and

$$L_R = L_D\left(1 + \frac{\bar{e}}{\bar{m}}\right) \approx L_D\frac{\bar{e}}{\bar{m}} \quad \text{if} \quad \bar{e} >> \bar{m}. \tag{9.8}$$

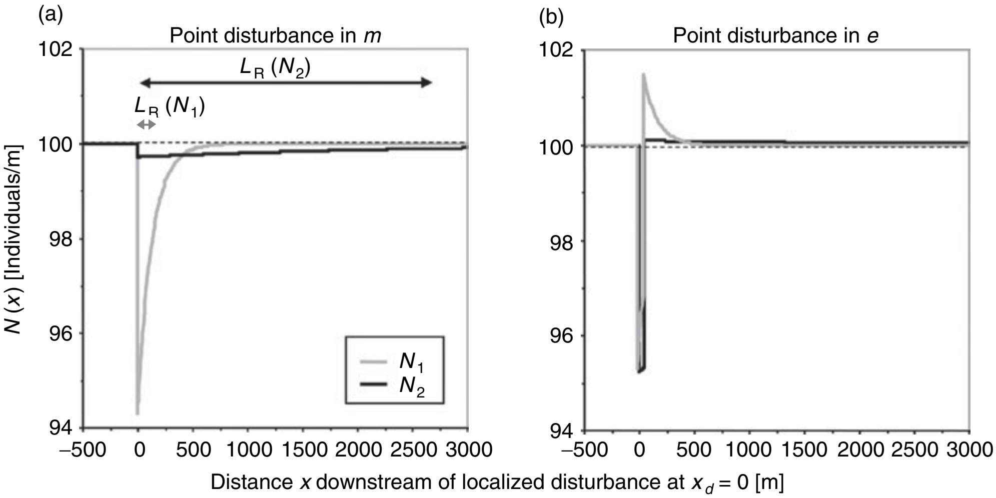

Fig. 9.1. Population responses of species N_1 and N_2 to a spatially localized increase in (a) per capita mortality rate *m* by a factor 4 and (b) per capita emigration rate *e* by a factor 0.05 at location $x_d = 0$ in an otherwise spatially homogeneous environment. Stream flow is from left to right. The dashed horizontal line indicates the homogeneous space equilibrium $N_H = 100$. Arrows indicate the response lengths $L_R(N_i)$. The calculations of population density at the site of the localized disturbance and of the return to equilibrium are described in Appendix 9.1.

L_R is the *response length* of the system, which is the distance required for the population response to decay to exp[−1] or ≈37% of its value $n(x_d)$ immediately downstream of the disturbed site (Fig. 9.1a). Equation 9.8 is written in its general form using spatially averaged values of per capita mortality $\overline{m}$ and emigration $\overline{e}$. In the examples in Fig. 9.1, the contribution of the disturbance to these regional averages is negligible and the spatially averaged rates correspond to their homogeneous space values, i.e. $\overline{m} \approx m_H$ and $\overline{e} \approx e_H$.

For organisms that drift often during their lifetime ($\overline{e} >> \overline{m}$) the response length L_R has an intuitive interpretation. Because $1/\overline{m}$ is the average individual lifetime and $1/\overline{e}$ is the average time between drift events, the response length corresponds roughly to the average number of drift events per lifetime multiplied by the average travel distance per drift event L_D. The response length L_R is thus approximately the average lifetime drift distance for organisms that drift often (Anderson *et al.*, 2005).

The return to equilibrium after a localized disturbance in *emigration* rate is also governed by the response length, but the return pattern differs strikingly from the response to a disturbance in *mortality* rate (Fig. 9.1b). While the equilibrium population density is also depressed at the site of increased per capita emigration $e(x_d)$, it bounces back with an overshoot immediately downstream. This rebound arises because, contrary to a localized increase in mortality, the absolute number of emigrants $e(x_d)N(x_d)$ from the disturbed site is not reduced compared with the homogeneous space situation (the increase in per capita emigration $e(x_d)$ approximately compensates for the decrease in $N(x_d)$). To be exact, the number of emigrants at the disturbed site (which are the downstream immigrants) is even slightly elevated, causing the overshoot at downstream sites $x > x_d$. The downstream decay of this overshoot is again largely governed by the response length L_R, but its calculation involves an additional term in Eqn 9.7 when the disturbance in emigration rate occurs over a finite length of stream (see Appendix 9.1 for details).

Figure 9.1 illustrates two patterns that characterize the responses of a population to a localized disturbance in a demographic or migration rate parameter for organisms that drift often ($\overline{e} >> \overline{m}$). First, the higher an organism's drift activity (the larger the ratio $\overline{e}/\overline{m}$), the longer it takes for a localized disturbance to decay, i.e. the longer the response length L_R. For organisms that drift often, L_R is almost directly proportional to drift activity. For example, species 2 has a 20.7-fold higher per capita emigration rate and a 20.4-fold longer response length (2654 m versus 130 m) than species 1. Note that the emigration rate of species 2 was chosen this high to produce contrasting response lengths with species differing in a single trait. Although data needed for rigorous calculations of response lengths are sorely lacking, crude empirical estimates suggest that response lengths of several hundred metres may be common in organisms that drift often (Table 9.2). The response length estimates in Table 9.2 come from small, shallow streams with relatively low current speed. Longer response lengths seem plausible in faster and deeper streams, where the travel distance during each drift event is much larger (Elliott, 1971). For example, Hershey *et al.* (1993) estimated the lifetime drift distance of *Baetis* mayflies in an Alaska river to 1900 m, almost two orders of magnitude longer than our response length estimate for *Baetis* from the small streams (Table 9.2).

Second, the magnitude of the immediate population response to a localized disturbance in a demographic rate is very weak and almost inversely related to the response length. A fourfold increase in m decreases the densities of species 1 and 2 at the disturbed site by only 5.6% and 0.28%, respectively (Fig. 9.1a). In contrast, the immediate population response to a localized disturbance in per capita emigration rate e is strong (almost proportional to the fractional change in e) and nearly independent of the response length. For example, a 5% increase in e decreases the densities of species 1 and 2 at the disturbed site by 4.7% and 4.8%, respectively (Fig. 9.1b). Much of this strong initial response vanishes, however, immediately downstream of the disturbed site, and the residual deviation from the homogeneous space equilibrium (which can still be substantial compared with the weak responses to disturbances in demographic rates) switches sign.

These results already suggest that the population density of a frequently drifting organism responds sensitively to small-scale environmental variation affecting *movement* rates, but rather insensitively to small-scale environmental variation affecting *demographic* rates. That this is indeed the case will be shown in the next sections, which extend the numerical examples to environments of increasingly complex spatial heterogeneity.

Table 9.2. Estimates of response lengths L_R of taxa from Convict Creek belonging to five insect orders (see Appendix 9.2 for details). Species identifications are based on Leland *et al*. (1986).

Taxon	L_R [m]
Ephemeroptera	
Baetis spp.	44
Epeorus dulciana	3
Paraleptophlebia pallipes	5
Plecoptera	
Malenka californica	54
Sweltsa pacifica	2
Trichoptera	
Polycentropus sp.	1
Rhyacophila spp.	89
Wormaldia gabriella	9
Ceratophsyche oslari	58
Hydroptilidae (approximately 60% *Oxyethira* sp., 40% *Hydroptila* sp.)	161
Brachycentrus americanus	133
Micrasema sp.	35
Lepidostoma spp.	1
Coleoptera	
Optioservus divergens	5
Diptera	
Simulium spp.	218
Chironomidae	42

Population Responses to Continuous Spatial Environmental Variability

Spatial variation in demographic rates

We first consider spatial variation in an environmental factor influencing the local mortality rate $m(x)$. We initially make the simplifying assumption that this environmental variation follows a single sinusoid with spatial wavelength L_E such that

$$m(x) = \bar{m}\left[1 + \mu(x)\right] = \bar{m}\left[1 + a\cos\left(\frac{2\pi x}{L_E}\right)\right]. \tag{9.9}$$

While no natural environmental variation follows such a simple pattern, this assumption is useful, because any pattern of spatial environmental variation can be written as a sum of sinusoids (Table 9.3). Here $\bar{m}$ represents the spatial mean value of per capita mortality, averaged over multiples of the wavelength L_E of spatial environmental variation. The magnitude of this variation is characterized

Table 9.3. Summary of the algebraic relationships between driving spatial variability in demographic and migration rates and the resulting equilibrium population responses.

Environmentally affected rate	Recruitment [*R*(x)]	Per capita mortality [*m*(x)]	Per capita emigration [*e*(x)]
Driving variability	$R(x)=\bar{R}[1+r(x)]=\bar{R}\left[1+\sum_i^k a_i\cos\left(\frac{2\pi x}{L_{E_i}}\right)\right]$	$m(x)=\bar{m}[1+\mu(x)]=\bar{m}\left[1+\sum_i^k a_i\cos\left(\frac{2\pi x}{L_{E_i}}\right)\right]$	$e(x)=\bar{e}[1+\varepsilon(x)]=\bar{e}\left[1+\sum_i^k a_i\cos\left(\frac{2\pi x}{L_{E_i}}\right)\right]$
Population response	$N(x)=\bar{N}\left[1+\sum_i^k b_i\cos\left(\frac{2\pi(x-L_{L_i})}{L_{E_i}}\right)\right]$	$N(x)=\bar{N}\left[1-\sum_i^k b_i\cos\left(\frac{2\pi(x-L_{L_i})}{L_{E_i}}\right)\right]$	$N(x)=\bar{N}\left[1-\sum_i^k b_i\cos\left(\frac{2\pi(x-L_{L_i})}{L_{E_i}}\right)\right]$
Amplitude of the response	$b_i=a_i\sqrt{\frac{L_{E_i}^2+4\pi^2L_D^2}{L_{E_i}^2+4\pi^2L_R^2}}$	$b_i=a_i\sqrt{\frac{L_{E_i}^2+4\pi^2L_D^2}{L_{E_i}^2+4\pi^2L_R^2}}$	$b_i=a_i\frac{2\pi(L_R-L_D)}{\sqrt{L_E^2+4\pi^2L_R^2}}$
Spatial lag of the response	$L_{L_i}=\frac{L_{E_i}}{2\pi}\tan^{-1}\left[\frac{2\pi L_{E_i}(L_R-L_D)}{(L_{E_i}^2+4\pi^2L_DL_R)}\right]$	$L_{L_i}=\frac{L_{E_i}}{2\pi}\tan^{-1}\left[\frac{2\pi L_{E_i}(L_R-L_D)}{(L_{E_i}^2+4\pi^2L_DL_R)}\right]$	$L_{L_i}=L_{E_i}-\frac{L_{E_i}}{2\pi}\tan^{-1}\left(\frac{L_{E_i}}{2\pi L_R}\right)$

$\tan^{-1}$ = arctangent.

by its scaled amplitude a, which is the maximum proportional deviation $\mu(x)$ from the mean $\overline{m}$. We use this scaling because the scaled amplitude of the driving variability in m can be directly compared with the similarly scaled amplitude of the resulting population response (see Eqn 9.10). In Fig. 9.2a–c, $a = 0.1$, which means that mortality deviates up to ±10% from its spatial mean.

The population response to sinusoidal spatial variation in per capita mortality yields a similarly sinusoidal equilibrium population distribution:

$$N(x) = \bar{N}\left[1 + n(x)\right] = \bar{N}\left[1 - b\cos\left(\frac{2\pi(x - L_L)}{L_E}\right)\right], \tag{9.10}$$

where $\overline{N}$ is the spatial mean value of population density, the scaled amplitude b is the maximum proportional deviation $n(x)$ from this mean value, and L_L is a downstream lag in the population response caused by downstream drift.

Figure 9.2a–c illustrate equilibrium population distributions resulting from sinusoidal spatial variation in per capita mortality at three wavelengths L_E. Similar to a localized disturbance, a spatially continuous change in mortality produces an opposite change in population density (a and b in Eqns 9.9 and 9.10 have opposite signs). If the two species were perfectly tracking the spatial variation in mortality, their distributions should be mirror images of the driving environmental variability, i.e. population density and mortality should be exactly out of phase and their relative amplitudes a and b should be equal. However, we already know that the relative magnitudes of a *localized* disturbance and the resulting population response may differ greatly and that a localized disturbance produces a carry-over effect of the population response in downstream direction (Fig. 9.1a). Similarly, perfect tracking of continuous spatial variation by the population is never attained. Instead, the population response is often considerably weaker than the amplitude of the driving variability in mortality and occurs with a downstream lag.

This yields the following patterns. First, the magnitude of the population response is always smaller than the magnitude of the driving environmental variability ($b < a$). The magnitude of the population response increases, however, with increasing spatial scale L_E of the driving variability in m and the ratio b/a approaches one at the largest scales of environmental variability (Fig. 9.2a–c).

Second, the population response has a downstream lag L_L caused by the same mechanisms that produce the downstream tail in the population response to a *localized* disturbance (Fig. 9.1a). With increasing spatial scale L_E of the environmental variability, this downstream lag approaches an asymptote of approximately one response length (Anderson *et al.*, 2005). Therefore, as L_E increases, the population response is *relatively* less displaced in downstream direction (L_L/L_E in Eqn 9.10 decreases) and the population distribution gets closer to being perfectly out of phase with the driving variability in m (Fig. 9.2a–c). An exception from this pattern occurs at very small scales of environmental variability not considered here, because the absolute lag L_L approaches zero as L_E becomes very small (see Fig. 3c in Anderson *et al.*, 2005).

Finally, a longer response length L_R reduces the above effects of increasing L_E. In particular, the amplitude of the population response to variation in m is more strongly dampened (the ratio b/a is reduced) and the spatial lag of the

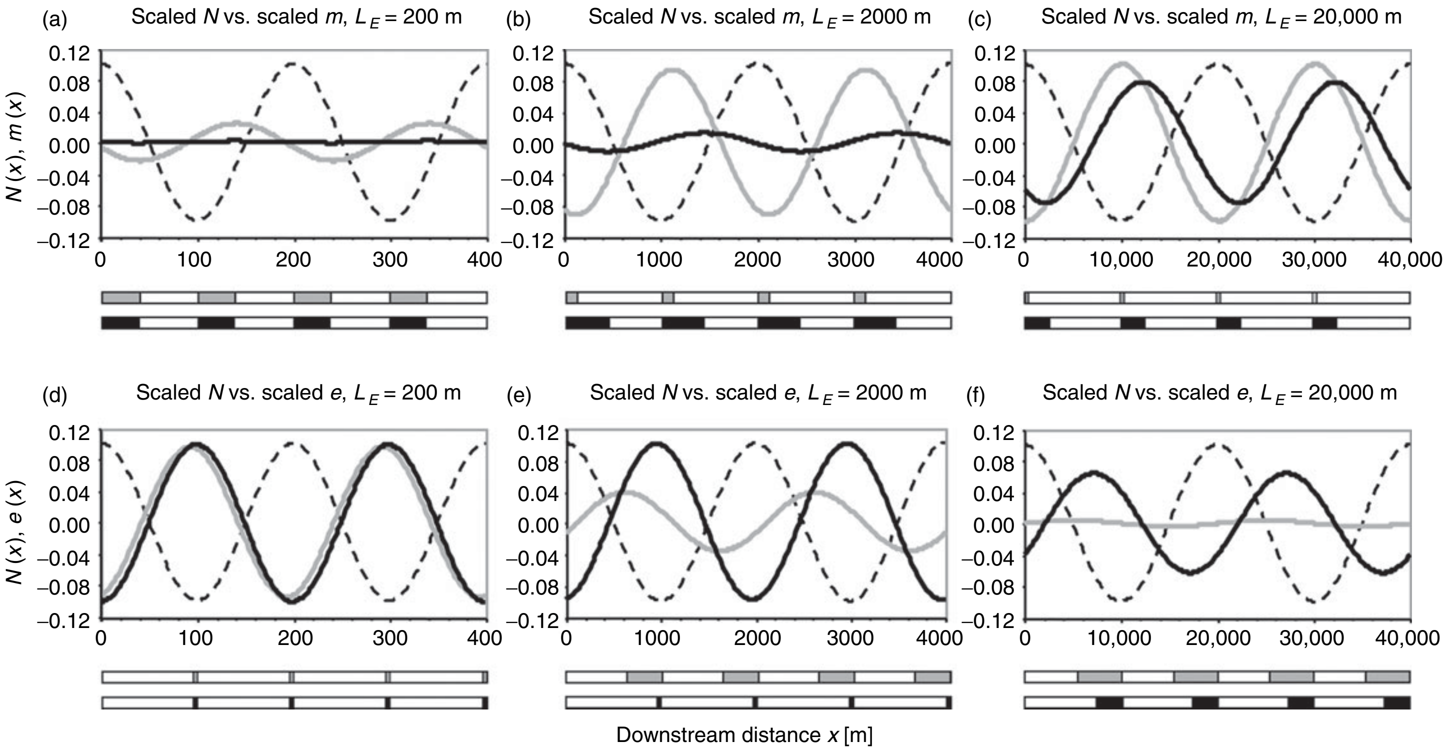

Fig. 9.2. Population responses of species N_1 and N_2 to sinusoidally varying spatial variation in per capita mortality rate (upper panels) or per captita emigration rate (lower panels) at three different length scales L_E of environmental variability. Dashed lines = scaled per capita mortality rate μ (a)–(c) or scaled per capita emigration rate ε (d)–(f); grey solid lines = scaled density of N_1 (L_R = 130 m); black solid lines = scaled density of N_2 (L_R = 2654 m). Horizontal bars mark regions where population densities correlate negatively (open) or positively (filled) with changes in μ and ε, respectively.

response increases for a species with a longer response length (species 2). This highlights the crucial role of the response length in determining a population's response to spatial environmental variability. The longer the response length, the longer the spatial scale over which advection links upstream and downstream dynamics, thus dampening the influence of local demography.

Sinusoidal spatial variation in recruitment R can be described with an analogue of Eqn 9.9, where $\overline{m}$ is replaced by $\overline{R}$ (see Table 9.3). The population response to recruitment variation has the same amplitude and spatial lag as the response to identical spatial variation in mortality (Eqn 9.10) but the sign of the response is reversed (b is positive, Table 9.3), because an increase in R produces an *increase* in population density. Consequently, spatial variation in R and the resulting population distribution become increasingly synchronized with increasing scale of the environmental variability L_E (see Fig. 2 of Anderson *et al.*, 2005).

Spatial variation in migration rates

Sinusoidal spatial variation in the emigration rate e can also be described with an analogue of Eqn 9.9 (Table 9.3). Similar to variation in m, a spatially extended increase in e results in a decrease in the population density (b and a have opposite signs) and the magnitude of the population response is always smaller than the magnitude of the driving variability ($b < a$). Otherwise, population responses to spatial variation in e show strikingly opposite patterns compared with population responses to variation in demographic rates (Fig. 9.2d–f). First, the magnitude of the population response is largest for variation in e occurring at the *smallest* spatial scales (Fig. 9.2d–f). Second, the spatial distributions of a population and the driving per capita emigration are closest to being exactly out of phase for variation in e occurring at the *smallest* spatial scales (Fig. 9.2d). Finally, the longer a species' response length L_R, the more *closely* it tracks environmental variation in e, i.e. the larger is the amplitude of its response and the closer is its population to being exactly out of phase with the driving variation in e (cf. species 1 and 2 in Fig. 9.2d–f). These results can be understood as follows.

When $\overline{e} >> \overline{m}$, local population dynamics are dominated overwhelmingly by migration. At equilibrium, local immigration and emigration are then in almost complete balance everywhere along the stream. At a location x where per capita emigration e decreases *very sharply* in downstream direction (L_E is small), local immigrants come from upstream sites with much higher per capita emigration rates. Population densities in those upstream sites must therefore be considerably smaller than in the receiving downstream site x to achieve a balance of immigration and emigration at site x. A steep spatial gradient in e therefore results in a steep gradient in N and a strong tendency for e and N to fluctuate out of phase.

Conversely, the larger the scale L_E of spatial variation in per capita emigration, the flatter the gradient in e. A local balance of immigration and emigration is then only achieved if the population sizes at neighbouring sites are also similar, resulting in an increasingly weaker population response and a downstream lag of three-fourths of a period as the spatial scale of variation in e increases (Anderson *et al.*, 2005). When the response length is larger, local immigrants are emigrants from a longer upstream source section. Consequently, at a given spatial scale of variation in e, the magnitude of the population response is greater and the distributions of e and N are closer to being in complete anti-phase the longer a species' response length.

Transfer Functions Relating Population Distributions to the Environment

We now ask how populations of frequently drifting organisms respond to more realistic patterns of spatial environmental variation. To answer this we make use of two mathematical relationships. First, any spatial pattern in a driving environmental parameter and in the resulting population distribution can be represented as a sum of sine and cosine functions with different amplitudes a_i and wavelengths L_{E_i}. This sum is conveniently represented using a mathematical operation known as the Fourier transform. For example, the pattern of environmental variation in the upper panel of Fig. 9.3a is the sum of seven cosines with different wavelengths L_{E_i} (ranging from 87 to 20,000 m) and identical amplitudes (all $a_i = 0.06$). Second, when the environment deviates nowhere too strongly from its spatial average, it is possible to establish algebraic relationships ('transfer functions') between the Fourier transforms of the driving environmental variability and the resulting population distribution from our population model.

While Fourier analysis is unfamiliar to many ecologists (for an introduction, see Nisbet and Gurney, 2003), the resulting algebraic relationships (Table 9.3) are easy to handle and interpret. As discussed above, each component cosine (with amplitude a_i and wavelength L_{E_i}) of the driving environmental variation produces a sinusoidal population response with identical wavelength L_{E_i} but different amplitude b_i and a downstream lag L_{L_i} (Fig. 9.2). The total population response is the sum of the responses to all component wavelengths of the driving environmental variation (Table 9.3). Furthermore, the responses to mild spatial variation in recruitment, mortality and emigration are *additive*, i.e. the total population response is the sum of the responses to each of the spatially varying parameters R, m and e (Nisbet *et al.*, 2007).

The calculations of b_i and L_{L_i} for a given population (listed in rows 3 and 4 of Table 9.3) all involve the population response length L_R, the average distance travelled during a drift event L_D, and the component wavelengths L_{E_i} of the driving environmental variability. As discussed in the previous section, these expressions identify a common response pattern to spatial variation in *demographic* rates (the responses to variation in R and m have opposite signs but are otherwise identical), but a very different response pattern to spatial variation in per capita *emigration* rate.

Tracking Versus Averaging of Spatial Environmental Variability

We used the term *tracking* to characterize a situation where spatial environmental variation is strongly reflected in the population response, i.e. spatial variation

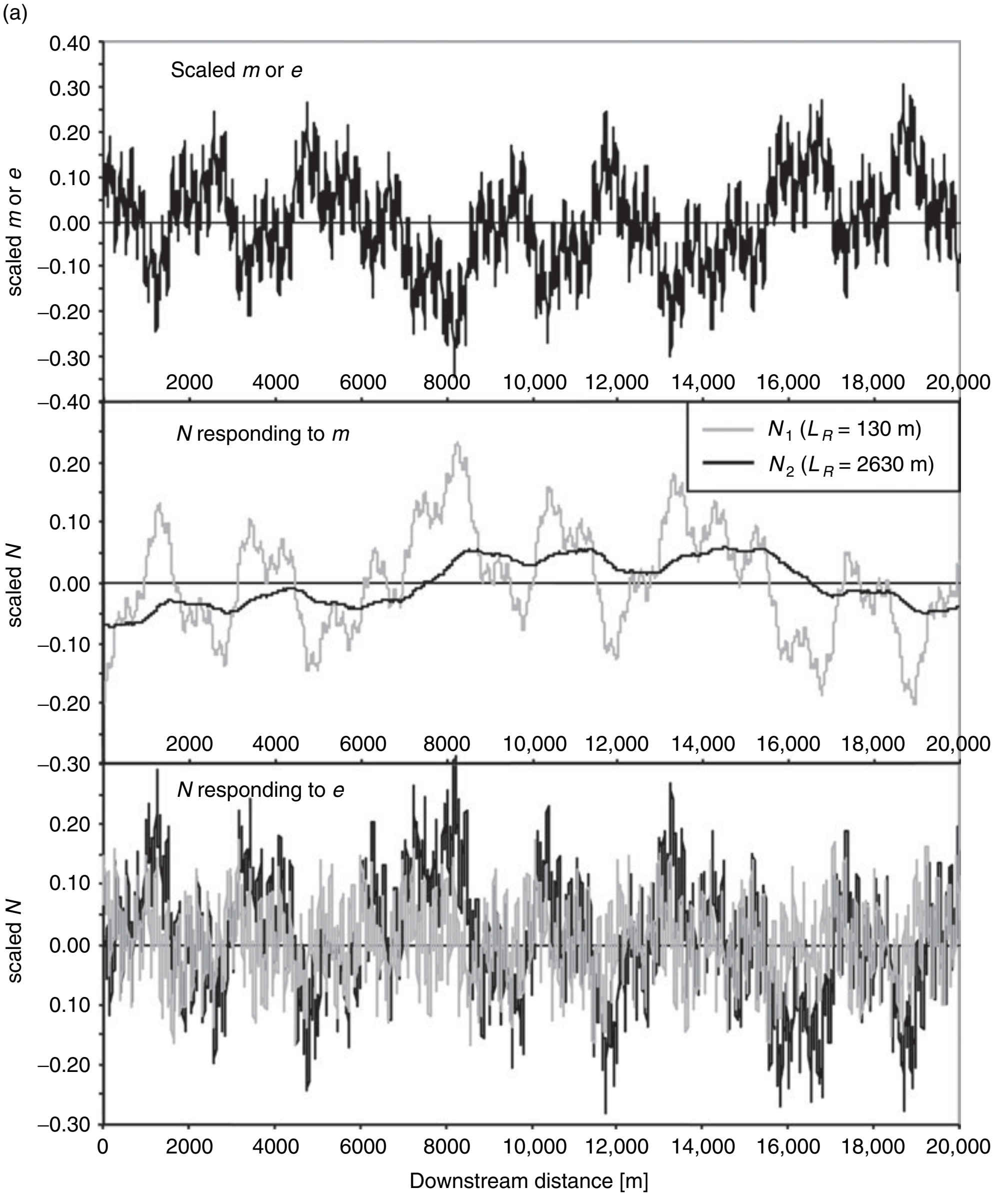

Fig. 9.3. Tracking versus averaging of identical spatial variation in *m* (upper versus middle panels) or *e* (upper versus lower panels) by populations of species N_1 and N_2. (a) No single scale of environmental variability dominates. (b) Environmental variability at large scales dominates (e.g. fish predators are present only downstream of a waterfall at $x = 10{,}000$ m). (c) environmental variability at short scales dominates (e.g. pool–riffle sequence with fish predators only in pools).

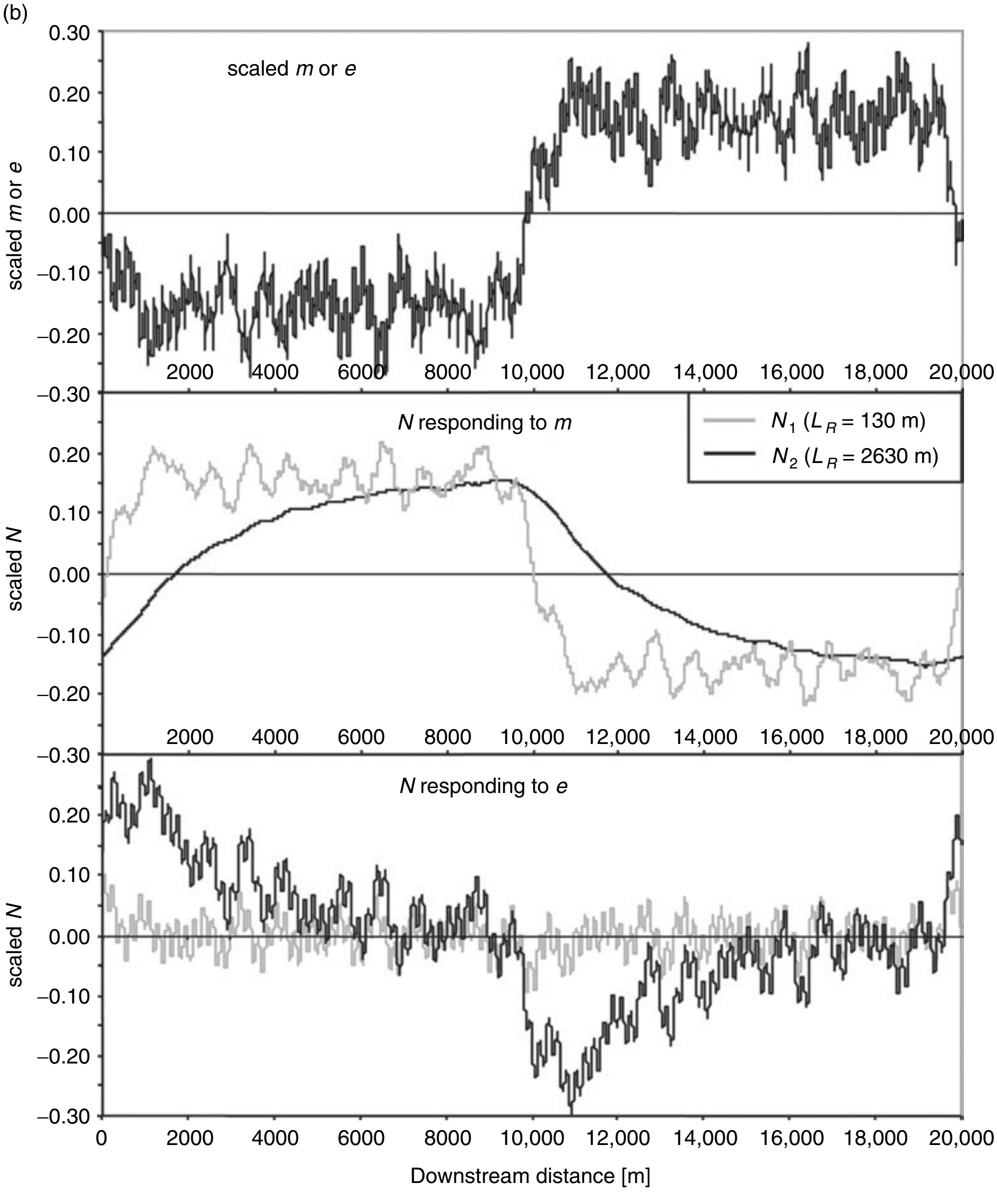

Fig. 9.3. *continued*

in the population and the driving environment have similar amplitudes and are either in phase (variation in R) or in anti-phase (variation in m or e). Correspondingly, we use the term *averaging* to describe a situation where the amplitude of environmental variation is strongly dampened in the population response (e.g. Fig. 9.2a). Using our example species, we now illustrate how populations track or average different components of more complex environmental variability.

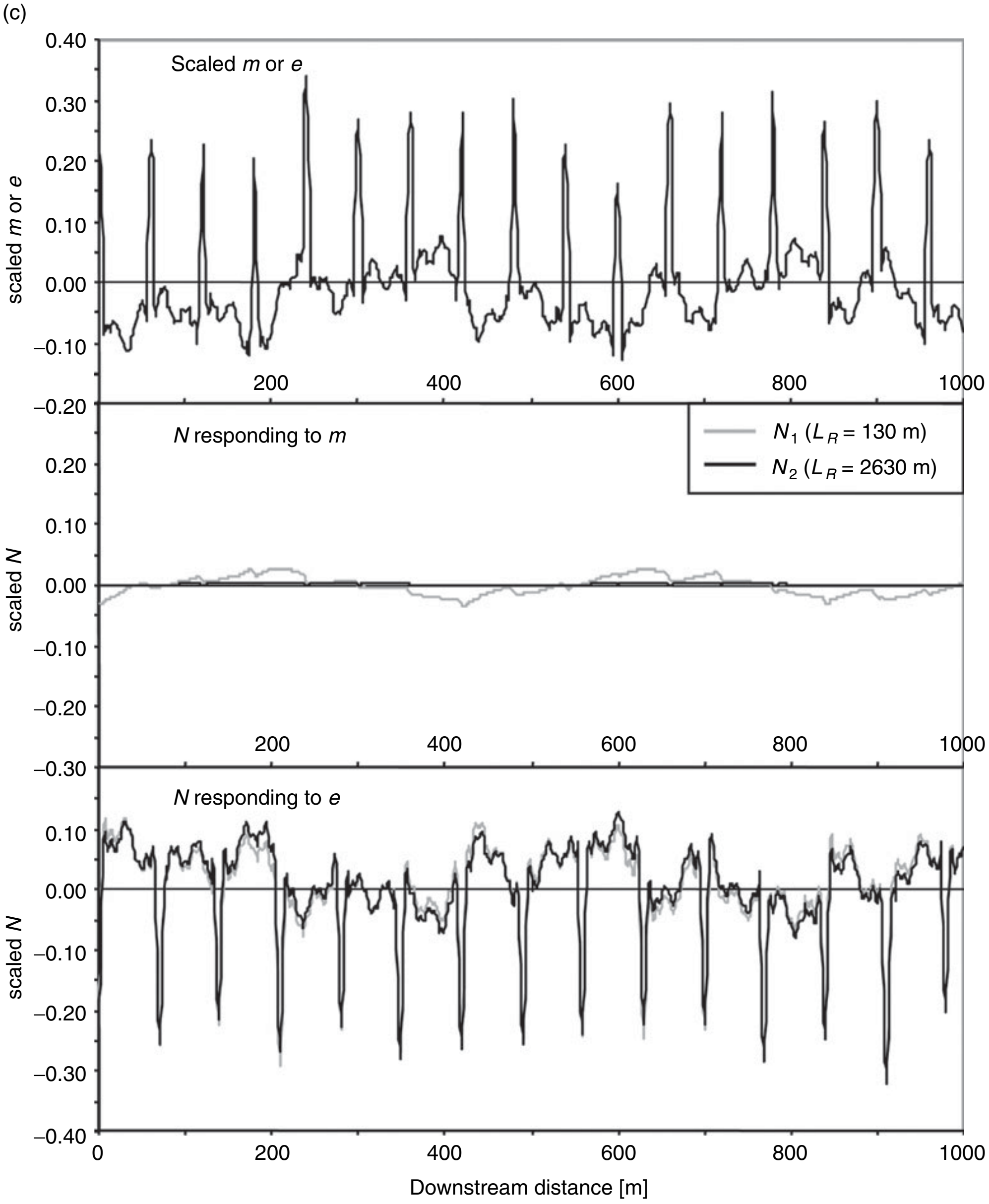

Fig. 9.3. *continued*

We use identical patterns of spatial variation in *m* and *e* as environmental drivers (Fig. 9.3, upper panels) to highlight their contrasting effects on the resulting population distributions (Fig. 9.3, middle versus bottom panels). As previously, we assume that the driving environment affects either *m* or *e*, but not both simultaneously.

The environment in our examples can be thought of as the distribution of predatory fishes to which our target populations respond. In the first example, no single spatial wavelength dominates environmental variation (Fig. 9.3a). This could be a situation where the distribution of fishes is driven by random, stationary variation in in-stream cover. In the second example, mild background variation is superimposed by variation at a very large scale (Fig. 9.3b). This could be a situation where upstream dispersal of fishes is prevented by a waterfall, yielding much lower mortality or emigration in a fish-free region upstream of $x = 10{,}000$ m. In the third example, mortality or emigration are dominated by high-amplitude, small-scale variation mimicking a pool–riffle sequence, where fish are only present in the pools (Fig. 9.3c).

When comparing the responses of species 1 and 2 to these patterns of environmental variability, we retrieve the same results as in the examples of simple sinusoidal variation (Fig. 9.2). First, variation in per capita mortality m at small spatial scales is completely averaged (Fig. 9.3c, middle panel), whereas variation in m at larger spatial scales is increasingly tracked (species 1 in Fig. 9.3a,b, middle panels). Second, the degree of tracking of spatial variation in m is the larger the shorter the response length. Thus, species 1 ($L_R = 130$ m) tracks (with a short downstream lag) components of the variation in m that have wavelengths of hundreds of metres or more; in contrast, species 2 ($L_R = 2654$ m) responds (with a considerable downstream lag) only to variation in m occurring over several thousands of metres or more (Fig. 9.3a,b, middle panels). The response of species 2 to variation at even the largest scale ($L_E = 20{,}000$) is still visibly dampened (Fig. 9.3b, middle panel). Third, variation in per capita emigration e at small spatial scales is completely tracked (Fig. 9.3c, bottom panel), whereas variation in e at larger spatial scales is increasingly averaged (note the different x-axis scales in Fig. 9.3a–c). For example, the largest-scale variation in e ($L_E = 20{,}000$) leaves no trace in the distribution of species 1 (Fig. 9.3b, bottom panel). Finally, the degree of tracking of spatial variation in e is larger, the longer the response length. Thus, most medium-scale variation in e is tracked by species 2 with almost no lag but averaged by species 1 (Fig. 9.3a, bottom panel).

Correlations of Local Population Densities with Local Environmental Conditions

Figures 9.2 and 9.3 yield intriguing insights into expected correlational patterns among driving environmental variability and resulting population distributions of frequent drifters. First, a given magnitude of spatial environmental variability (the amplitude of the dashed lines in Fig. 9.2) can produce anything from a population response of similar magnitude to no measurable response at all, depending solely on the spatial scale of the environmental variation. This is remarkable, because the *local* responses to the environment are equal in all examples.

Second, the horizontal bars in Fig. 9.2 indicate stream sections along which population densities correlate positively (filled sections) or negatively (open sections) with spatial variation in m or e. As the immediate response to a local increase in per capita mortality or emigration would be a population *decline*

(Fig. 9.1), *positive* correlations obscure the ‘true’ local impact of the driving environment. Positive correlations occur in up to 50% of a stream when the phase shift between the driving environment and the (negative) population response approaches one-quarter of a period (species 1 in Fig. 9.2f). A descriptive study might then detect a positive, negative or no relationship between the driving environment and the population distribution, depending on the sampling scheme. Note that most stream sections yielding positive correlations in Fig. 9.2 exceed the length of an average riffle (a common study unit). Note also, that the amplitude of the population response is smallest when the proportion of stream yielding positive correlations is largest (Fig. 9.2a,f).

These considerations suggest that scale dependence in the magnitude and spatial lag of population responses could explain why empirical relationships among environmental factors and local population densities are often weak or inconsistent among different streams or different sections within a stream. To explore this further, we quantified the degree of covariance between environment and population density in the spatially complex scenarios of Fig. 9.3. Perfect tracking of the environment by a population would imply that a linear regression of scaled population density on scaled variation in m or e has a slope of –1 and no scatter. Relationships between population density and the driving environment may, however, be so weak as to become undetectable, if environmental variation is dominated by component wavelengths that are averaged (Fig. 9.4c, right pair of bars; Fig. 9.4d, left pair of bars). Conversely, strong relationships arise if environmental variation is dominated by component wavelengths that are tracked (Fig. 9.4c, left pair of bars; Fig. 9.4d, right pair of bars). Relationships of intermediate strength arise if variation at scales longer and shorter than a species’ response length contribute equally to overall environmental variation (Fig. 9.4a,b; Fig. 9.4c,d, central bars).

Overall, covariance between environment and population density increases with the dominant spatial scale (period) of variation in m and decreases with the spatial scale of variation in e (Fig. 9.4c,d). Covariance also depends on a species’ response length with, all else being equal, a species with a longer response length showing higher covariance with e and lower covariance with m. Thus, although species 1 and 2 respond *identically* to local environmental variation (i.e. show the exact same relative changes in per capita mortality or emigration along the stream), their spatial distributions need not be strongly correlated (Fig. 9.5). Note also that *strength* (slope) and *tightness* (R^2) of relationships between environment and population density are of similar magnitude (Fig. 9.4a,b). Thus, if a spatially variable environmental factor affects a vital rate of a target species, the statistical power of detecting the *mere existence* of this relationship by means of correlation with the resulting population distribution will depend on the spatial scale of the environmental variability relative to the species’ response length. This statistical power will frequently be weak, given that the number of data points (benthic samples) is usually low and that sampling error will further weaken the relationships (compare left and right panels in Fig. 9.5).

Correlations between environment and population density predicted by our model are frequently weak, in spite of the model’s deterministic nature and the (unrealistic) assumption of a temporally constant environment. Ubiquitous temporal

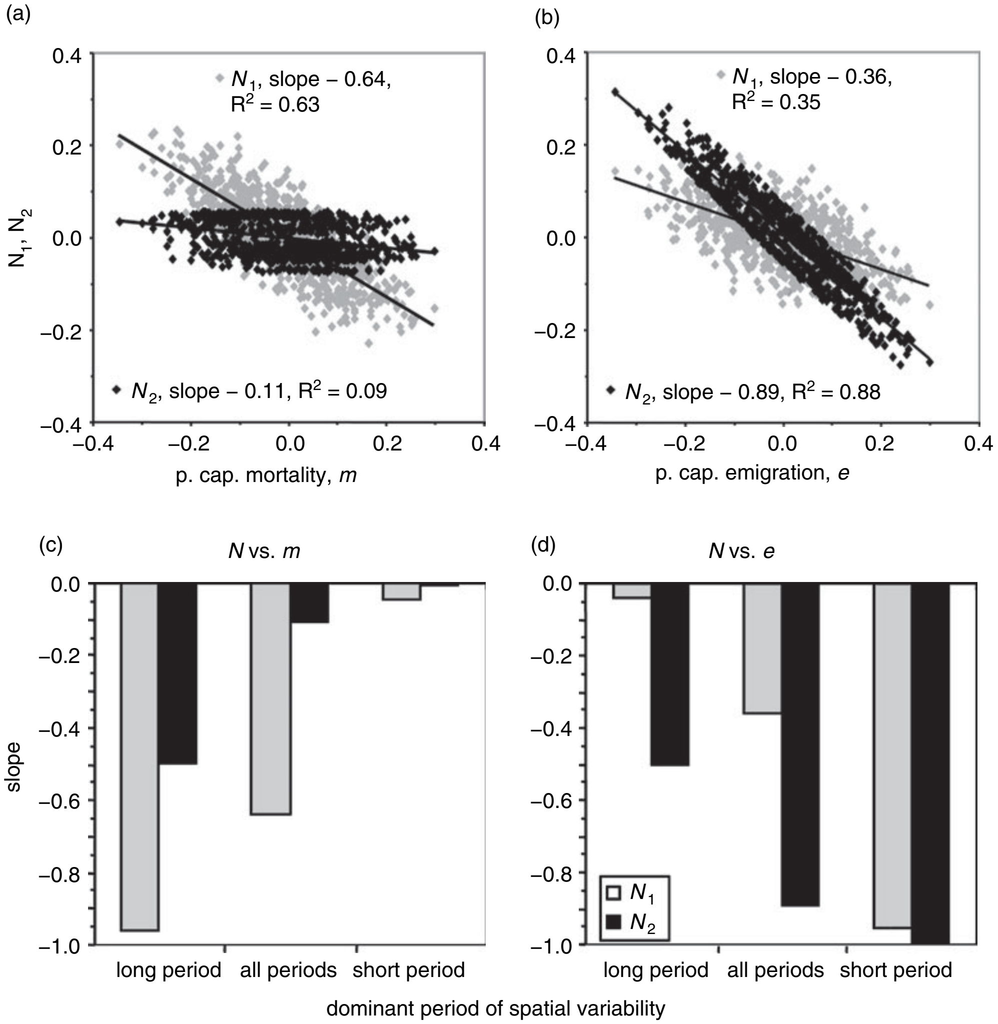

Fig. 9.4. Upper panels: regressions of scaled population density N_1 (grey diamonds) and N_2 (black diamonds) against (a) scaled mortality rate *m* and (b) scaled emigration rate *e* for the scenario depicted in Fig. 9.3a. Lower panels: slopes of linear regressions of scaled population densities of species N_1 and N_2 versus (c) scaled mortality rate *m* and (d) scaled emigration rate *e*. Left pairs of bars: scenario of Fig. 9.3b; middle pairs of bars: scenario of Fig. 9.3a; right pairs of bars: scenario of Fig. 9.3c. Grey bars = species 1; black bars = species 2.

variability and sampling error should further weaken these correlations. Moreover, we characterized environmental variation directly as spatial variation in vital rates, bypassing the tedious and error-prone step of establishing functional relationships between environmental parameters (e.g. canopy shading, fish density) and vital rates of target populations. Thus, empirically derived correlations between environment and population density may be weak even where our deterministic model predicts strong relationships.

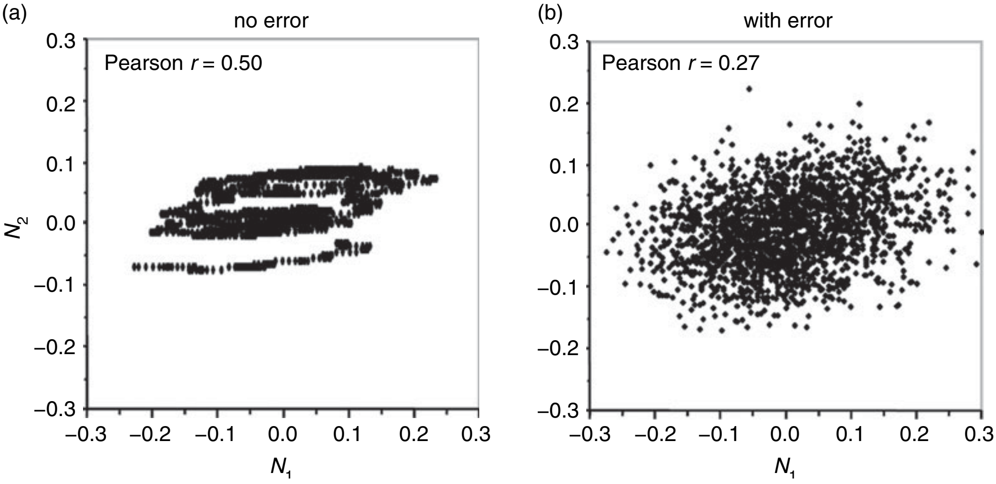

Fig. 9.5. Examples of correlations of scaled population densities N_1 and N_2 against each other: (a) plots the (deterministic) data from Fig. 9.4a, and (b) assumes an additional average random sampling error (uncorrelated between the two species) of ± 4%.

While these conclusions may appear sobering, our model also offers exciting perspectives for the development of a predictive theory of population dynamics of stream organisms, including the prediction of population responses to multiscale spatial environmental variability. In the final section, we briefly discuss some theoretical and empirical issues that need to be addressed in this endeavour.

Outlook

There are obvious extensions to the model, several of which have been explored. First, many real stream populations experience density dependence in vital rates. While the response of a population to spatial environmental variability is always governed by its response length, density dependence may alter its magnitude. Specifically, negative density dependence in demographic rates ($\partial R/\partial N < 0$, $\partial m/\partial N > 0$) will shorten the response length, whereas negative density dependence in emigration rate ($\partial e/\partial N > 0$) will lengthen it (for details, see Anderson *et al.*, 2005). Density dependence often results from interspecific interactions. Using coupled resource–consumer models, we have demonstrated the generality of the response length concept as a means to characterize the spatial scales over which environmental variation is tracked versus averaged (Anderson *et al.*, 2006). When spatial environmental variability affects only one of the interacting species directly, both species will usually respond in a spatially synchronized way (in or out of phase), demonstrating that the response length is a system – rather than population – property (for details, see Anderson *et al.*, 2006).

Second, the contribution of random bi-directional movement has been studied with advection–diffusion models (Speirs and Gurney, 2001; Pachepsky *et al.*, 2005;

Lutscher *et al.* 2006). While these authors focused on persistence problems (how much local reproduction and random movement is needed to compensate downstream drift?), Roughgarden (1974) explored the influence of spatial heterogeneity on a purely randomly moving organism. Extrapolating from Roughgarden (1974), random bi-directional movement from sources such as benthic crawling or hydrodynamic turbulence should contribute to the averaging of demographic heterogeneity and the amplification of emigration heterogeneity in our model, but not qualitatively change the results.

Finally, while our model analyses assumed temporal constancy of the environment, streams are notorious for high flow variability and occasional flood disturbances (Poff and Ward, 1989; Matthaei *et al.*, 1999). Consequences of floods can be traced in population distributions long after the disturbance (Matthaei and Townsend, 2000; Effenberger *et al.*, 2006). Developing theory for the description of such transient dynamics in advective systems is an area of active research. It is straightforward to extend Fourier transforms across spatial *and* temporal dimensions (Nisbet and Gurney, 2003), which enables the analysis of spatial population responses to temporal perturbations. While this approach is most appropriate for the analysis of mild perturbations, the dynamics following extreme disturbances (such as scouring floods) are better understood using persistence criteria and invasion wave speeds (Pachepsky *et al.*, 2005; Lutscher *et al.*, 2006).

The emerging theory of spatial population dynamics in advective systems produces predictions that are empirically testable (discussions in Anderson *et al.*, 2005, 2006). The functional dependencies of many demographic rates on environmental conditions can be estimated from small-scale experiments. Estimation of per capita emigration rates requires knowledge of travel distances per drift event, which are less commonly reported in the literature (Englund and Hambäck, 2004). What is sorely missing, however, are data on longitudinal patterns of population densities and environmental drivers similar to Fig. 9.3.

In this context, it must be pointed out that there is a minimum spatial scale over which our model predictions can apply. Below this scale, which should be on the order of a few drift distances L_D, spatial patterns in the population distribution are caused by directed movement in response to microhabitat conditions such as flow or food patches. While such small-scale environmental variability can contribute substantially to the variance in organismal densities (Downes *et al.*, 1993, 2000; Cooper *et al.*, 1997), our model cannot address spatial variation at the scale of microhabitats. This has important implications for the empirical examination of model predictions, which requires extensive longitudinal estimates of *average* population densities and environmental conditions with a spatial resolution of several L_D. One way of accomplishing this could be the use of a relatively fine-grained sampling scheme followed by the calculation of running means across adjacent samples.

We conclude by noting that the theory outlined in this chapter may contribute to the development of new statistical approaches that help tease out relationships when faced with weak correlations. Transfer functions are routinely used to characterize lagged relationships in time series analyses and there are well-documented methods for their estimation (Priestley, 1981). Two challenging issues for applying the methodology to stream invertebrates are (i) the limited number of spatial locations used in even the most ambitious studies (e.g. seven stations in the Lotic Intersite Nitrogen Experiment in North America, http://www.biol.vt.edu/faculty/webster/linx/), and (ii) the universal occurrence of temporal variation. Both call for further theoretical developments that will require close collaboration between theorists and empiricists.

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Appendix 9.1 Mathematical and Ecological Interpretation of a Localized Disturbance

Localized disturbances are conveniently represented by the Dirac delta function (Nisbet and Gurney 2003; appendix D), a formal construct that represents a very large perturbation, concentrated in an infinitesimally small space or time. The function is widely used in physics and engineering to describe an ‘impulse’ such as a hammer blow (a large force applied for a very short time). The behaviour of a system following an impulse is called the ‘impulse response’ (McGillem and Cooper, 1991).

The impulse response is readily interpreted when applied to demographic rates. There is then a discontinuity in the density $N(x)$ at the point x_d. This represents addition or removal of a large number of individuals in a very small stretch of stream corresponding to recruitment of organisms from a tributary or mortality from some localized obstacle as in Fig. 9.1a. The population density at the site of the localized disturbance in per capita mortality in Fig. 9.1a was calculated as

$$N(x_d) = \frac{R_H + I(x_d)}{e_H + m(x_d)} \text{ where } I(x_d) = e_H N_H,$$

because the immigration rate at xd is equal to the immigration rate at upstream sites where immigration and emigration balance. The return to equilibrium in Fig. 9.1a follows Eqn 9.7.

Interpretation of the impulse response concept is trickier for movement rates. Eqn 15 in Nisbet *et al.* (2007) shows that the response to an impulse is the sum of two terms, one of which is itself an impulse. Because this result is of little help to an ecologist intent on relating models to data, we calculated the plots in Fig. 9.1b making the more reasonable assumption that the emigration rate was increased by a finite amount over a fixed region of length a. Thus we assumed

$$\varepsilon(x) = \begin{cases} b & \text{for } x \le a \\ 0 & \text{for } x > a \end{cases}, \tag{A1}$$

where *b* is a constant. Eqns 10–14 of Nisbet *et al.* (2007) provide a recipe for calculating a good approximation to the resulting density distribution, valid for all but the smallest spatial scales. The calculations may appear intimidating, as they require the use of 'Laplace transforms' (McGillem and Cooper, 1991). However, this is not hard in practice as the MATHEMATICA software (Wolfram Research Inc.) provides appropriate routines. The result of the calculation is that downstream of the disturbance, the population response is given by

$$n(x) = \begin{cases} -b\exp\left(-(x - x_d)/L_R\right) & \text{for } x \le a \\ -b\exp\left(-(x - x_d)/L_R\right)\left(1 - \exp\left(a/L_R\right)\right) & \text{for } x > a \end{cases}. \tag{A2}$$

In the example of Fig. 9.1b the population size at the site of the localized disturbance in e is

$$N(x_d) = \frac{R_H + e_H N_H}{e(x_d) + m_H}.$$

We used a finite disturbance in e over a length a = 50 m and calculated the return to equilibrium with b set to [NH – N(xd)]/100.

Appendix 9.2 Estimation of response lengths

The response length estimates in Table 9.2 are based on extensive sampling in the stream research facility at the Sierra Nevada Aquatic Research Laboratories, which consists of nine 50 m long, natural-like stream channels (mean water depth 0.14 m, discharge 30 l/s, mean current speed 0.21 m/s) fed by Convict Creek. Drift nets blocking entire cross-sections were deployed simultaneously at the up- and downstream ends of all channels during five 1-h intervals over a 24-h cycle in late September 1994. On the following day, six benthic samples were taken in each channel (for details, see Diehl *et al.*, 2000). Downstream drift and benthic data were combined to calculate an average per capita emigration rate per channel (e_C) for each taxon. Note that the product of e_C and channel length L_C (= 50 m) is equal to the product of the spatially averaged instantaneous per capita emigration rate $\bar{e}$ times the length of an average drift bout L_D. Because few insects emerge from Convict Creek during winter (October–April), we assumed a lifespan of 200 days until emergence. Estimates of mortality rates are lacking, so spatially averaged mortality rate $\bar{m}$ was arbitrarily set to 0.01 per day for all taxa (yielding a 13% survival probability after 200 days). For each taxon, the response length was then calculated as

$$L_R \approx \frac{\bar{e}L_D}{\bar{m}} = \frac{e_C L_C}{\bar{m}}.$$

10 What is the Spatial Structure of Stream Insect Populations? Dispersal Behaviour at Different Life-history Stages

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Abstract

Populations are shaped by the collective rates of four fundamental processes: births, deaths, emigration and immigration. For stream insects, the focus has largely targeted just mortality and even this has only been examined via indirect measures, whereby high densities are assumed to reflect low death rates. Additionally, the bulk of information is restricted to relatively mature juveniles; almost nothing is known about other stages. We believe a 'classical view' of stream insect distributions has led to an implicit presumption that populations extend over entire catchments, with lots of dispersal up- and downstream, and across catchments. However, there is a profound lack of data on dispersal, even though measuring the rates of movement by individuals between patches of suitable juvenile or adult habitat is necessary to resolve the spatial boundaries of populations and critical for interpreting results from typical surveys on benthic densities. We explore some of the implications of different spatial population structures for stream insect populations and present approaches to test between these alternatives. We suggest researchers need to re-think the ways in which streams are sampled and better address survey design to improve the inferences that can be drawn about dispersal distances and frequencies.

Introduction

Sorting out how populations are regulated is a big question in ecology. Exactly what regulation per se entails is a contentious debate (Berryman, 2002) we do not wish to enter, noting simply that density-dependent mortality, birth or dispersal rates are likely to sit centre stage (Chesson, 1998; Hixon *et al.*, 2002). Demonstrating exactly how and where density dependence acts is difficult, because species are not distributed uniformly or continuously throughout their ranges, but

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inhabit variously sized patches of suitable habitat that are distributed across landscapes. This habitat patchiness imposes a problem: are individuals in different patches all part of one, breeding population or not? The answer depends on the frequency of movement between patches (Harrison and Hastings, 1996; Thomas and Kunin, 1999). Without knowing the frequency, timing and direction of dispersal, we cannot assess what role density dependence in one or more patches plays overall (Chesson, 1998).

Before setting out our specific aims, we emphasize first that, in this chapter, dispersal refers to the successful movement of individuals from one breeding population into another breeding population over time periods reflecting separate generations, i.e. immigration and emigration in the classic demographic sense. Populations where immigration and emigration are important sources and losses of individuals are described as 'open' (Hixon *et al.*, 2002). While this term is sometimes used simply to mean movement by individuals into and out of a study area, we define openness analogously to Hixon *et al.* (2002), as one minus the mean probability that a dispersing individual was produced from the same population of breeding adults (i.e. within the same population bounds) as individuals already present in the area. Thus, arrival into a study site of drifting larvae does not make that site 'open' (i.e. constitute immigration *per se*) unless the majority of drifters were produced from a separate population of inter-breeding adults to the larvae already present.

An alternative view (see Diehl *et al.*, Chapter 9, this volume) emphasizes that dispersal occurs over a continuum of frequent, short distance to infrequent, long distance movements. Consequently, the effects of dispersal on demography should itself be viewed along a continuum rather than as producing discrete types of populations, like 'open' or 'closed' (Thomas and Kunin, 1999). The point about artificial classification is well taken, but there is a danger of repeating mistakes made in the late 1970s, where failing to differentiate different sorts of movement produced specious outcomes. The movement of individuals among patches of food, for example, can look superficially equivalent to the movement of individuals between breeding populations, and can even be modelled with the same equations, but the results may have few implications for population-level processes (Hanski, 2001). A classic example was the failure to differentiate true migrants from transients that led to misleading conclusions about how much empirical evidence supported the theory of island biogeography (Simberloff, 1976). Such outcomes can be avoided by using clear definitions of terms and ensuring that they are applied in a meaningful way given the biology of the species at hand.

In this chapter, we pose the following questions: (i) how might aquatic insect populations be structured within catchments? (ii) How might these different spatial structures arise? (iii) How can we test between alternative models of structure and their causes?

This chapter is not a review on the dispersal of aquatic invertebrates. We believe that the state of knowledge about stream insects is somewhat poor and we set out some suggestions for how progress might be made. We start first by describing briefly a 'classical view' of aquatic insect populations, and then describe how research over the last couple of decades has seen this model falter in the face of evidence with which it is inconsistent. We then go on to describe four general steps we believe researchers need to tackle in order to begin sorting out the spatial structure of populations, make suggestions for how to solve some of the more intractable logistical problems and finally consider where we might seek generality among species and systems.

Background to the Problem

The classical view of stream insect populations

We think much of our current understanding about stream insect populations (which for simplicity we term 'the classical view') has been shaped by the phenomenon of drift dispersal. This occurs primarily during the juvenile stage (either larva or nymph) for some species, which have terrestrial and usually winged adults, but many species are fully aquatic, e.g. many beetles and bugs. Although juveniles are able to move relatively short distances by crawling (Freilich, 1991), drift is thought to represent the principal mode of long distance movement for most taxa and a major means by which larvae are redistributed and are able to re-colonize bare habitat following a disturbance (see Mackay, 1992). Drift has been reviewed repeatedly, so we will comment only that the ubiquity of drift and the sheer density of drifters appears to have convinced many researchers that populations must encompass long lengths of stream channels, with juvenile forms drifting considerable distances downstream. Müller (1982) proposed the Colonization Cycle whereby adults emerge from locations along the stream and fly upstream to lay their eggs, thus re-colonizing stream sections experiencing a continual loss of individuals via the drift. Despite the fact that it was well known many species did not drift, the overall picture created was largely that of frequent dispersal along (and probably between) channels within catchments.

Another traditional focus of limnologists has been how the physical nature of catchments determines the density and identity of aquatic fauna. These sorts of studies (when done on insects) have almost all focused again on the aquatic juvenile forms and produced classifications of channels into types (reviewed by Hynes, 1970), with the expectation that different types of river environments have distinct faunae. More recent versions of this approach focus on the way in which catchments determine the identity of fauna hierarchically from larger to smaller spatial scales (e.g. Frissell *et al.*, 1986). Although often implicit, these classifications usually presume that the *cause* of associations between types of physical environments and fauna is adaptive habitat preference. This approach has sprung from limnology's traditionally strong interactions with the disciplines of geomorphology, hydrology and chemistry, rather than with ecology per se (McIntosh, 1985).

Since the early 1950s, we have gained a body of work on insects that tends to presume that:

- frequent dispersal up and down channel occurs (often upstream by adults and downstream by juveniles), with some cross-catchment movement between channels by adults;

- events during the juvenile stage are critical to setting numbers and distribution (i.e. adults and other stages may be safely ignored);
- it is the physical nature of the channel that sets overall limits to density and distribution of species via adaptive habitat preferences;
- large-scale physical drivers are of most importance; small-scale variation is of little consequence.

We suggest that a collective outcome of these assumptions is an implicit presumption that conspecific individuals in catchments of the size typically studied by researchers comprise a single population, with densities largely constrained by physico-chemical gradients acting on juveniles. Our evidence for this contention lies not in stated claims within most studies, but within common approaches to study designs. A typical study design uses benthic samples of juveniles and correlations with physico-chemical variables, both collected from a single site, to draw conclusions about the drivers of insect densities over an entire catchment (Townsend *et al.*, 2004). To warrant such conclusions, we typically make most of the four assumptions above. Thus, drawing inferences about species' densities, when we only have data on juveniles, explicitly presumes that nothing that adults do impacts on densities or distribution. Additionally, if most researchers thought dispersal was highly restricted between sites along the same channel, we think they would be much less comfortable assuming routinely that information garnered from single sites can be extrapolated beyond site boundaries.

We intend no criticism of this work, which is often done for reasons unrelated to questions about populations *per se* (indeed, the senior author has published such studies herself!). We acknowledge also that many recent papers take different views about insect populations (e.g. Peckarsky *et al.*, 2000). Our purpose here is simply to highlight this: there are unspoken assumptions that sit behind the common ways in which people sample streams. These assumptions, in turn, have established the above expectation about stream insect populations, even though it is rarely explicitly enunciated.

The wheels come off

Over the last couple of decades, the classical view has collided with modern population biology. Evidence of strong connectivity via dispersal along and between channels still remains scant. There are still few studies that have tested the actual (as opposed to presumed) role of drift in driving benthic densities along channels (Downes and Lancaster, unpublished results). Studies on adults have found mixed results. While some species show evidence of strong dispersal and longitudinal connectivity (most notably the mayfly *Baetis*: Hershey *et al.*, 1993; Peckarsky *et al.*, 2000), other studies have demonstrated little movement, no upstream or downstream bias (as might be expected), or movement sideways into the vegetation (Jackson and Resh, 1989). The direction and extent to which adults move varies between species and locations, and does not obviously comply with a generalized theory, such as the Colonization Cycle. Either way, convincing evidence of strong or frequent dispersal along or between channels is still largely lacking for most species. Over this same period, increasing numbers of genetic studies have found startlingly high levels of genetic differentiation between individuals collected in different places along channels or within subcatchments (Bunn and Hughes, 1997). There are several explanations for this finding, but these data do not suggest even occasional dispersal over even moderate spatial scales. In fact, in some cases the results have raised the prospect of isolated populations within catchments (see Hughes, 2007).

Another source of disquiet has been the repeated finding that benthic densities of channel units, such as riffles, can be as different as samples collected from different catchments or tributaries, even when the riffles are in close, spatial proximity (Heino *et al.*, 2004; Townsend *et al.*, 2004). Such results are inconsistent with a model where distributions are constrained largely by the physical environment, because variation among replicate, proximate channel units ought to be trivial relative to differences between much larger spatial units, such as catchments. Finally, an increasing number of experimental studies have demonstrated that simple models of habitat preference do not explain the distribution of species (e.g. Fonseca and Hart, 2001; Sharpe and Downes, 2006). The freshwater literature seems to be slowly mirroring the general ecological literature, where 1950s (and earlier) models proposing that the distributions of species are determined by species' preferences for particular physical habitats were overturned once experimental tests were applied (Underwood *et al.*, 1983). Perhaps there is insufficient cross-citation between the general and freshwater literature. Regardless, we are now at the point where it is clear that simple classifications of physical environments alone cannot predict the distribution and abundance of species, nor can we *assume* that conspecific individuals in the same catchment or channel comprise one population.

How can we Sort Out the Spatial Structure of Stream Insect Populations?

We begin by describing briefly the broad types of spatial structures that have been recognized and how they might fit within individual catchments (Fig. 10.1; see Thomas and Kunin, 1999). We do this in the spirit of summarizing theoretical possibilities that have markedly different implications for the sorts of inferences that can be drawn given particular data. We do not suggest that classification, in of itself, is an end point or that all populations should fit neatly into one of these categories. Our purpose is to start with a 'clean slate' and no presumptions about the spatial structure of stream insect populations and then to ask how we might collect data to address the possibilities.

In the first model, all individuals within a catchment spring from the same breeding population (Fig. 10.1a), as discussed earlier. There is lots of dispersal within the catchment by juveniles and adults, but that does not constitute immigration or emigration per se. There is no dispersal to or from neighbouring catchments, so the population is closed (i.e. bounded) at this scale and, while there may be spatial differences in mortality or birth rates in different habitat patches, the catchment is best viewed as one population (Hixon *et al.*, 2002). Alternatively, if individuals are distributed patchily within catchments and dispersal

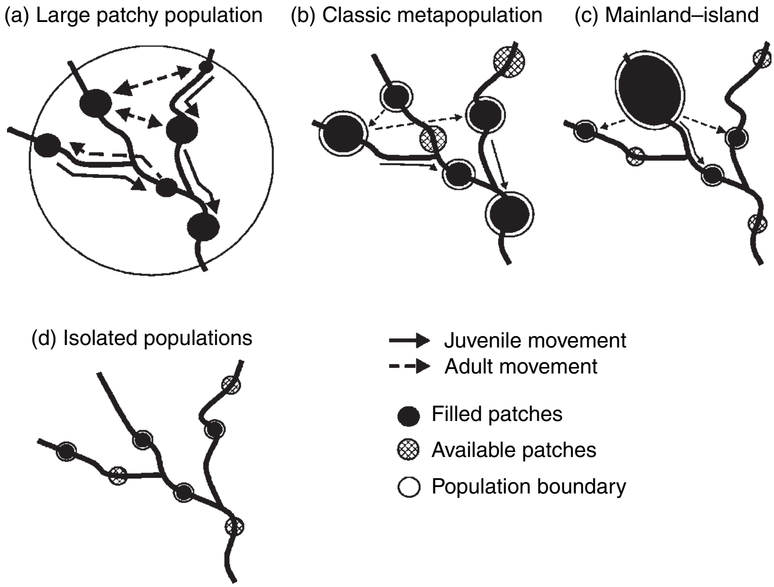

Fig. 10.1. Types of population structures in catchments. (a) Large, patchy population, where individuals occupying patches of habitat on different channels comprise one population because of frequent dispersal during the juvenile and adult stage; (b) classic metapopulation where individuals on different patches are in different local populations of roughly equal size and connected by some dispersal; (c) metapopulation where local populations are of different sizes creating so-called mainland–island dynamics; (d) isolated populations where no dispersal between patches occurs. There is no scale on this figure because we do not know, as yet, the distances over which individuals can and do disperse. Thick arrows indicate high movement frequency while thin arrows indicate infrequent movement, leading to local populations situated in habitat patches. (Figure modelled after Harrison and Hastings, 1996.)

between such habitat patches is restricted, we can have multiple local populations that are somewhat isolated but still linked by dispersal in some places and times (Fig. 10.1b,c). The frequency and direction of successful dispersal means that local populations can have different local dynamics. It is also possible that some suitable patches of habitat are unoccupied, possibly because a local population has gone extinct. The final possibility is that habitat patches are fully isolated with no dispersal between them (Fig. 10.1d), in which case their dynamics are completely independent, and a population that goes extinct cannot be ‘rescued’ by immigrants from elsewhere.

Obviously, ‘large, patchy populations’, ‘metapopulations’ and ‘isolated populations’ simply occupy different points along a gradient of dispersal frequency (Thomas and Kunin, 1999). Ergo, we can re-pose our question to ask: at what spatial scale are populations demographically closed? That is, is the catchment depicted in Fig. 10.1a 10,000s, 1000s, 100s or 10s of km^2 in area? Then, the challenges become clear. If Fig. 10.1a covers many thousands of km^2, then it is impossible to draw population-level conclusions from data collected from just one catchment of a few hundred km^2. There is so much movement into and out of that area that there is no way to gauge its demographic significance to the whole. This situation is analogous to studies of barnacle and mussel settlement on to rocky intertidal reefs along the west coast of North America. It took scores of small-scale studies and some 30+ years of work coupled with oceanographic modelling of advective dispersal of larvae before a picture emerged (Connolly *et al.*, 2001). Alternatively, if Fig. 10.1a covers only 10s or 100s of km in area, then individual studies could potentially draw conclusions about populations. Unless we know the scales over which immigration and emigration occur – and, most critically, the spatial scales over which they never, rarely or only episodically occur – it is impossible for us to link empirical data to theory.

How then might we go about sorting out the spatial structure of riverine insect populations? We suggest a series of steps or research priorities. These steps are: 1 – thinking about the spatial scales of study; 2 – measuring dispersal distances and frequencies; 3 – examining birth and death rates at different life-history stages; and 4 – looking for generalities among species (Table 10.1). The logic of this approach is addressed below. Some steps may seem pedantically self-evident, but we argue that some traditional approaches to data collection may be leading researchers down potentially erroneous pathways.

Before we continue, there are three issues we would like to emphasize and which will appear as themes below. First, if we hope to understand what regulates aquatic insect populations, we need to take a focus that encompasses examining events across all life-history stages. The mortality of juveniles, for example, cannot be assessed in isolation from examining mortality rates of other stages, because events during the juvenile stage may have little repercussion for populations (e.g. Marchant and Hehir, 1999). Second, rather than looking at taxa individually, we suggest that comparing groups of species differing systematically in significant aspects of their biology or ecology seems likely to be a useful way of strengthening inference. We explain and describe this further below. Third, experiments can provide strong inference to answer some questions (e.g. examining oviposition choices of females: Reich and Downes, 2003b), but some questions might also be tackled by improving survey design. A blend of both survey and experimental work seems likely to provide the most powerful form of enquiry. We make suggestions below about how we think surveys might be better designed to tease out cause-and-effect associations and strengthen inference.

Step 1: What are the ‘right’ spatial scales?

The first step to quantifying densities and distribution is to ask about the spatial (and temporal) scales over which resources of food and habitable living space are distributed throughout the study area (here, a catchment). The patchiness of resources and habitable space then dictates the initial spatial scales of sampling, in terms of both sample resolution (e.g. quadrat size) and range (e.g. boundaries

Table 10.1. The steps required to sort out the spatial structure of populations, with some suggested approaches and examples, which are discussed further in the text. Note that although we are suggesting an order in which research tasks need to be tackled, this order should not be interpreted literally. We anticipate that researchers will need to revisit steps multiple times. For example, information about dispersal distances and frequencies will likely mean re-thinking ideas about the appropriate spatial (and temporal) scales at which to pose questions.

Approach	Examples
Step 1: Define scale	
• focus on resources and specific gradients	• detritus loadings and retentive structures
• match spatial scale with biology	• spatial decoupling of adult and larval resources
• design surveys that are appropriately scaled	• spatial 'scoping', e.g. semi-variograms
• consider timing of data collection	• disturbances, e.g. floods, mediate the spatial arrangement of resources
Step 2: Dispersal frequency	
• how is dispersal related to patches?	• oviposition and pupation site selection
• targeted correlative studies	• correlative data on drift and benthic settlement
• behavioural ecology of organisms	• sexual bias of movement
• incorporate dispersal at multiple LHS	• adult flight and larval drift
• incorporate between-species contrasts	• good versus poor dispersers at various LHS
• consideration of timing of study?	• flood-mediated dispersal
• integrate genetic studies with direct data	• dispersal kernels of adults linked to genetic distance
Step 3: Births and deaths	
• establish fecundity	• egg or adult rearing, field observations
• determine mortality at multiple LHS	• life tables, field observations
• incorporate between-species contrasts	• good versus poor dispersers at various LHS
Step 4: Sources of variation	
• targeted contrasts between local and regional factors of interest	• stream architecture, land use, hydrology
• testing of theory	• Recruitment Limitation Hypothesis
• evaluate response of population structure to restoration	• restore connectivity and/or spatial arrangement of resources
• modelling	• alter spatial/temporal distribution of resources

LHS, life-history stages.

of sites where samples are collected) (Schneider, 1994). So how is this scaling approached in stream studies?

Traditionally, stream studies use hydrological or geomorphological units, such as 'reaches' or 'riffles', within which samples are collected. This is because hydrological or geomorphological factors create the large-scale physical gradients that, in turn, are expected (assumed) to drive the distribution of species in streams. In reality of course, insects do not 'care' about geomorphology or hydrology; they respond to physical or resource gradients, but often over quite small spatial scales. Gradients at small scales do not necessarily relate consistently, strongly or at all to gradients measured over large scales. Mismatches between the spatial scales of important gradients and the spatial scales of sampling produces noisy data and weak correlations between densities and environmental variables. The result is quite literally a misleading, blurry picture of both species' distributions and the variables to which they are responding.

We can illustrate this point using a brief example. Some female caddisflies use large boulders that are emergent from the water's surface as places to lay eggs, and some species select specific boulders according to water velocities or depths (Reich and Downes, 2003a). Over large spatial scales, the position and average density of boulders will be driven by hydrological and geomorphological features of the catchment (e.g. geology, slopes, discharge), but if females are selecting boulders using small-scale hydraulic conditions, then they are responding to the environment at scales far smaller than units like reaches. The positions and densities of suitable boulders may map only coarsely on to reaches, and a study that averages densities over such scales would end up obscuring the underlying pattern (Fig. 10.2a). Another problem occurs where boulders have different

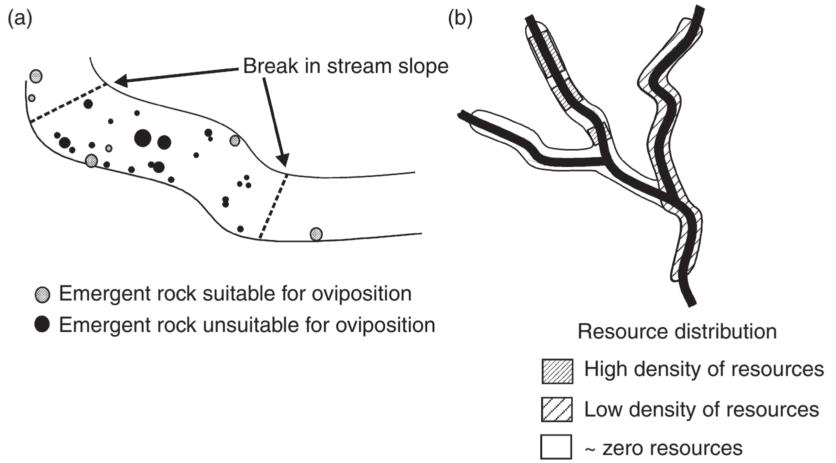

Fig. 10.2. The distribution of an essential resource – in this case, large, emergent boulders sought by female caddisflies ovipositing eggs – illustrated over two spatial scales. (a) Emergent boulders distributed along a length of channel, with a local increase in average density of emergent boulders caused by breaks in stream slope. Females, however, use only boulders occurring in specific conditions of velocity and depth; these boulders are not more common in places where the overall density of emergent boulders is high. (b) High variation in distribution and density of emergent rocks in three separate channels within a catchment. The thick black line indicates the working channel.

densities and distributions in different channels, necessitating a varied sampling approach (Fig. 10.2b). A fixed sampling design for all channels will produce estimates of poor quality.

A lot of our knowledge about insect distribution in streams is based on use of geomorphological or hydrological sampling units. This is because assumptions about hydrology or geomorphology underpin our sampling designs, even if we just use riffles because they are shallow and easy to sample, but few studies ever link the specific choices or ranges of sampling sites to the conclusions drawn from the data. We suggest that researchers may wish to start afresh in thinking about distributions and approaches to sampling. Detritus, for example, is deposited in slowly flowing areas but also trapped around objects such as logs and rocks in fast flows. The distribution of such food patches may not map on to channel units in useful ways. Some recent examples (e.g. Lancaster *et al.*, 2003; Ganio *et al.*, 2005) illustrate alternative means for mapping – and scaling – the distribution of essential resources.

It follows, of course, that considerations about appropriately scaled sampling designs apply to all life-history stages. Adults and juveniles are likely to have different scales of distribution precisely because they respond to different physical gradients and have different resource needs. Although that sounds self-evident, it is rare for researchers to consider the implications when different life-history stages have different spatial distributions. In a typical case, a single 'representative' site is used to sample aquatic larvae and to draw conclusions about densities of species in a catchment. That single location could fail to produce any larvae of some species if they were highly patchily distributed throughout the catchment and we were unlucky. Likewise, we could fail to collect larvae of some species if they are annuals and adults have only recently laid eggs in some places, meaning that the distribution of larvae still largely reflect the adult distribution, not specifically the habitat needs of larvae. It is rare for either of those explanations to be considered explicitly in interpretations drawn from simple benthic samples.

Step 2: Measuring the scales and frequencies of dispersal

By definition, frequent movement between habitat patches is simply inter-patch movement conducted during feeding bouts or mate searching (Bowler and Benton, 2005), not emigration or immigration as we defined it earlier, but distinguishing the two forms of movement is difficult.

One solution is offered by behavioural studies (Van Dyck and Baguette, 2005), because the motivation underlying dispersal movements may be quite different to those leading to routine movements during foraging or mate searching. Factors such as an organism's perceptual range will interact with the strength of cues and landscape features and ultimately determine dispersal success (Lima and Zollner, 1996). While dispersal is often treated as a fixed strategy with a constant fraction leaving each generation, mobility is not a static trait. For instance, emigration is usually initiated at high densities by competition for resources, however, at very low population densities, Allee effects can induce individuals to leave (Roland *et al.*, 2000). We need only look to the wealth of behavioural studies on terrestrial invertebrates to appreciate the benefits of this knowledge when placed in a population context (Cappuccino, 1995; see Lancaster, Chapter 8, this volume). A greater understanding of the behavioural basis underlying dispersal decisions would aid predictions of movement within streams. There are relatively few such studies in the stream literature, although one by Resh *et al.* (1987), demonstrating the role of sex pheromones in Trichoptera movement, and another by Coupland (1991), examining the effect of conspecifics on movement behaviour and dispersal success, provide nice examples of what is possible.

Another suggestion is that studies of dispersal need to be designed specifically to demonstrate how movements relate to densities within study areas or habitat patches. For those taxa that drift, we can make use of drift's unidirectional nature to ask questions about the role of new arrivals in driving benthic densities in habitat patches. Thus, if benthic juveniles come usually from the drift (i.e. are not individuals produced from eggs hatched in that patch), then we should expect to get strong, consistent associations between drift numbers and densities of newly settled individuals across habitat patches. It is feasible with species that are sedentary (such as many of the filter-feeders) to quantify new arrivals into habitat patches over short time frames – because they will accumulate on cleared, hard substrata that supply filtering spots – and compare these numbers to the numbers of drifters arriving into patches. In a recent study, we used this approach with two species of hydropsychids drifting into riffles and found strong correlations between drift from upstream and benthic settlement for *Smicrophylax*, but not for *Asmicridea* (Fig. 10.3). Individuals of the latter species may move only short distances within riffles, suggesting that the population structure of this species could be quite different from the more drift-prone *Smicrophylax*. It is theoretically possible to take this approach with species searching for other kinds of resources, as we would expect patches of abundant resources (such as detritus, epilithon) to retain and accumulate individuals over short periods of time.

Another correlative approach is to look for strong, consistent associations between numbers of individuals found in sequential life-history stages, which can provide some indication of whether individuals disperse out of habitat patches or not. For example, consistent, high correlation between the numbers of eggs and benthic densities of neonates in patches – time lagged to allow for development – suggests that neonates do not disperse immediately away (Willis and Hendricks, 1992; Reich and Downes, 2004). If we also found consistently few neonates exiting patches using the drift or walking between patches, this improves our confidence that neonates are not moving immediately out of patches. Another approach is to manipulate the number of propagules by directly removing eggs or suitable oviposition sites, and exploring whether knock-on effects are manifest in subsequent life-history stages (Hildrew *et al.*, 2004; Speirs *et al.*, 2000). Where dispersal is limited, we would expect to see a drop in benthic densities because there would be no compensatory migration from other locales.

Theoretically, similar approaches can be pursued with adults, although these stages are less tractable because dispersal is typically not unidirectional. Nevertheless, if we gained consistently high correlations between local numbers of

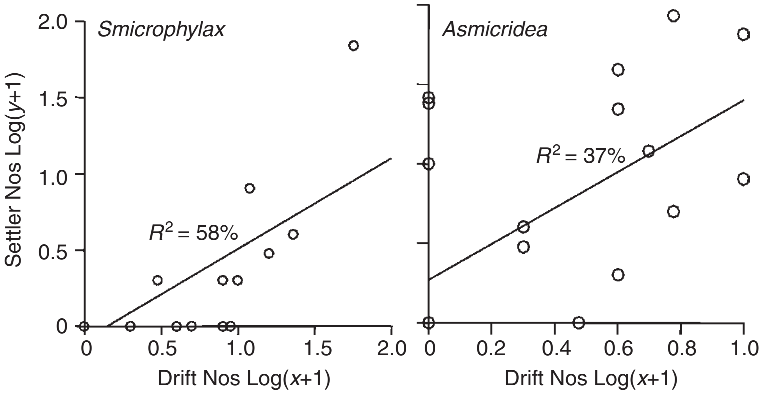

Fig. 10.3. The total number of second instar hydropsychids *Smicrophylax* sp. AV2 (left) and *Asmicridea* sp. AV1 (right) settlers on settlement substrata (plain bricks) accumulating over a week plotted versus the total numbers of that instar collected in the drift, over the space of the same week, into 24 separate riffles sampled over 2 years; each point is one riffle/time combination. The lines are least square regression lines, and we expect a strong positive slope and y-intercept equal to zero where all setters come from drift from upstream. For *Smicrophylax*, the highly significant slope ($P < 0.001$), a y-intercept not different from zero ($P > 0.05$) and a relatively high r^2 suggests that settlement arose from individuals drifting into sites from upstream. For *Asmicridea* though, while the slope is significant ($P < 0.05$), the relatively low r^2 and scatter about the line suggest settlement and drift are poorly related. Additionally, the y-intercept is significantly greater than zero ($P < 0.001$), suggesting that many settlers came from local sources, not from upstream. Additionally, settlement numbers were far higher than for *Smicrophylax* even though drift numbers were typically low, suggesting poor association was not caused by low sampling efficacy and further bolstering the argument that drift is not an important source of settlers for *Asmicridea*. (From Downes and Lancaster, unpublished results.)

pupae and numbers of adults and if few adults are found in traps placed between habitat patches, then we might conclude that adult dispersal is limited. These sorts of approaches have rarely been explored in streams.

In each of these approaches, the evidence is circumstantial because it is correlative, but a lack of correlation provides poor information. Low correlations can be caused by poor sampling efficacy and that tells us nothing about population structure. A way of strengthening inference is to examine multiple species simultaneously and to make a priori predictions about outcomes on the basis of biology. For example, if a group of species frequently found in the drift is matched taxonomically with a group of species that are rare in the drift, then we can make a series of specific a priori predictions about which species should show strong correlations between drift and benthic density and which should not. Strong inference comes from predicting both the presence *and* absence of correlations; this comparative approach also helps with issues about whether low correlations are caused by poor sampling efficacy (Fig. 10.3). Other forms of inference can include genetically based studies when available (see Hughes *et al.*, Chapter 14,

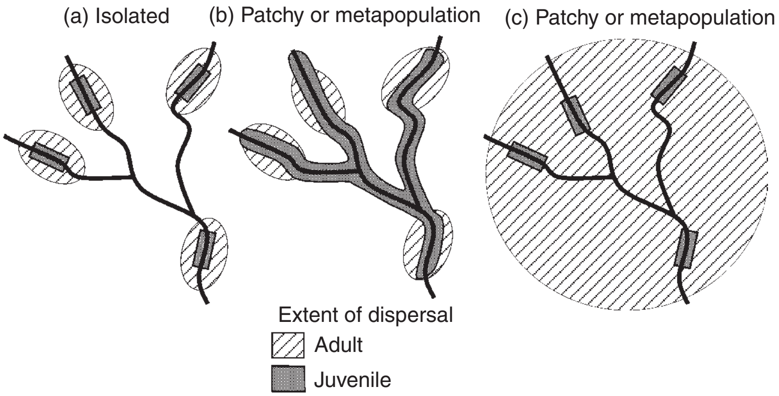

Fig. 10.4. Scenarios of dispersal extent by adult and juvenile stages in a catchment. (a) Both adults and juveniles have very limited dispersal ability, leading to a series of isolated populations on different channels or locations along channels. (b,c) These illustrate situations where there are markedly different dispersal abilities by different life-history stages, which may result in patchy populations or metapopulations depending on the exact dispersal frequencies at different life-history stages.

this volume) and modelling approaches (e.g. Anholt, 1995; Anderson *et al.*, 2005; Melbourne and Chesson, 2005) where germane.

Finally, individual studies are unlikely to provide a comprehensive picture in their own right. We suggest the aim is to build that picture gradually, using multiple pieces of evidence to determine which of the spatial structures depicted in Fig. 10.1 might be the most correct for the catchment at hand. Isolated populations (Fig. 10.4a) are starkly different from how most ecologists probably think about stream populations, but patchy populations or metapopulations caused by markedly different dispersal abilities during different life-history stages (Fig. 10.4b,c) also offer some intriguing possibilities. In Fig. 10.4b, juveniles disperse long distances along channels while adults have very restricted movement. Adult distribution could be set largely by the locales where pupae or mature nymphs enjoy highest success. In Fig. 10.4c, we have the reverse situation of limited dispersal by juveniles and wide dispersal by adults. Juvenile distribution and location may be determined by mating and oviposition success of females.

Step 3: How and where does density dependence occur?

We can now ask questions about the significance of variation in birth, death and dispersal rates of different life-history stages in different places. In effect, we have placed a scale bar on Fig. 10.1a, and we understand whether our study area encompasses whole populations or just one patch. What we do next largely depends on the size of that scale bar. If it represents many 1000s of km^2, we need to collect information from many different places if we hope to tackle questions about populations per se. If the scale bar only represents 10s to 100s of km, asking population-level questions becomes more feasible – although still a significant task! The type of questions we ask depends on whether we have isolated populations or ones that are linked sometimes or in some places by dispersal. In the former case, it is feasible to quantify birth and death rates in multiple populations to contrast their dynamics. In the latter case, it would make sense to assess immigration and emigration rates relative to birth and death rates in different populations (Harrison and Hastings, 1996; Thomas and Kunin, 1999). Finally we note that births, deaths and dispersal rates should be assessed relative to densities of individuals, so we can assess what role, if any, density dependence plays (Hixon *et al.*, 2002).

Many of the correlative approaches described above can be used also to ask questions about birth and death rates in habitat patches, using a wealth of examples from the literature. Habitat patch selection by adults can be critical in determining larval densities within different habitat types (Resetarits, 1996). Oviposition site selection can specifically affect offspring distribution, survival and eventual reproductive success (e.g. Rausher, 1979; Craig *et al.*, 1989). The way in which eggs are packaged, intra- and interspecific variations in fecundity and developmental times, and neonate behaviour and survivorship are all parameters that have profound effects on distribution and abundance (Bernardo, 1996). There is obvious scope for stream ecologists to explore further the influence of all these factors. Jackson and Sweeney's (1995) account of the egg masses of 35 lotic species from a tropical stream in Costa Rica illustrates the level of detail needed. Pupal stages remain a complete mystery for most species and yet could be critically important. Much of this discussion is a simple reminder that basic life-table analysis (e.g. Embree, 1965) is critically important. Life-table analyses might be considered dull and old hat, but those sorts of data supply the foundations for understanding populations. We cannot build sophisticated models when a lot of basic information is missing.

Step 4: Looking for generality

Based on the types of data generated by undertaking the above steps, can we begin to generalize across stream types, latitudinal gradients and species or their traits? These sorts of questions are crucial, because we can notionally get the same spatial structure for different reasons or different outcomes for the same species in different places or times. For example, if there are significant barriers to dispersal in a particular stream system, we might conclude a species has poor dispersal capacity and tends to have isolated populations, when in other systems the lack of such barriers means the species has a different population structure. The key though is: How can we solve the logistical problems of distinguishing between these situations?

We can think of at least three, over-arching suites of factors that might affect frequencies of dispersal: the physical nature of streams and the catchment; the dispersal traits of particular species; and interactions with other organisms. In the material above, we have largely focused upon the dispersal traits of species, and there is scope to consider further whether species vary geographically or between different generations (e.g. effects of differing voltinism). Nevertheless, the physical architecture of streams provides an obvious framework for examining variation in the spatial distribution of resources and the dispersal of individuals (Grant *et al.*, 2007). There may be characteristics related to stream networks that affect frequency of dispersal by adults between channels (Wishart and Hughes, 2003) or the propensity of larvae to drift (Fagan, 2002). Likewise at smaller spatial scales, the distribution of a particular resource may be mediated by broader-scale phenomena. As mentioned above, the distribution of potential oviposition sites, such as large emergent boulders (Reich, 2004), may reflect the distribution of geological formations longitudinally along a stream or between streams. The potential for widespread or patchy sedimentation to inundate potential oviposition sites and thus alter the spatial arrangement of these resources may also modify dispersal behaviour and ultimately population spatial structure. Similarly, broad-scale hydrological patterns of drying (Lake, 2003) and/or flooding (Lake *et al.*, 2006) may provide the physical template on which dispersal can be constrained or promoted. Peckarsky *et al.* (2000) provide an instructive example whereby the availability of oviposition sites is temporally aligned to the timing of spring flows, highlighting the benefits of considering the temporal arrangement of resources across multiple life-history stages. If the quality or spatial distribution of resource patches is temporally auto-correlated, then future conditions should reflect current conditions and conditional-dependent dispersal may evolve (Bowler and Benton, 2005). This is highly relevant to stream research because the predictability of resource availability in streams is intrinsically linked to disturbance regimes or seasonality, with ephemerality of flow an obvious source of variation. Thus, a species may have different dispersal characteristics in different systems resulting in different population structures. Few ecological studies endure long enough though for such patterns to be uncovered.

Hopefully we can begin to identify potential population bottlenecks and assess the applicability of general ideas such as the Recruitment Limitation Hypothesis (Chesson, 1998), for instance, where all new recruits are produced elsewhere and local population dynamics are driven greatly by the episodic arrival of immigrants. These ideas are important in other systems (e.g. Underwood and Keough, 2000), but are yet to be evaluated in a stream context. The various dispersal profiles of species coupled with stream architecture offer conceptual approaches for thinking about spatial structures of populations (e.g. Fagan, 2002). Concepts such as the ‘Stream Hierarchy Model’ and the ‘Death Valley Model’ were originally conceived for fish but provide a sound basis for examining other taxa (Meffe and Vrijenhoek, 1988). These models incorporate various amounts of hydrologic connectivity along dendritic networks and predict genetic flow within and between basins. Finn *et al.* (2007) recently proposed a ‘Headwater Model’ for invertebrate headwater specialists with some overland dispersal ability, in this case for giant hemipterans. Their results show that a high degree of habitat specialization does not allow gene flow to occur throughout the drainage network and limited short-distance terrestrial dispersal results in highly isolated populations.

In terms of biological interactions among species or biological differences among rivers, an obvious source lies in the nature and extent of riparian vegetation.

Riparian clearance and habitat fragmentation may alter dispersal success (Peterson *et al.*, 2004). Conversely, the replanting of riparian buffers may have negative consequences on dispersal by elevating the influence of terrestrial predators such as birds (Whitaker *et al.*, 2000). Within channels, the presence of drift-feeding predators such as trout can have effects on drifters (e.g. mayflies: Forrester, 1994), and it is interesting to speculate what effects the introduction of such predators into streams may be having on the population structure of insects.

A better understanding of the spatial structure of populations will ultimately provide a more robust framework within which to implement conservation, restoration and management activities (Lake *et al.*, 2007). The benefits of small, isolated restoration works, which typify most types of stream restoration, will always be limited if local population densities are set by processes or life-history stages occurring elsewhere. Until we know what factors regulate populations, particularly what powers positive population growth at low densities, it is very difficult to know what restoration needs to be done and where it might be most effective. Examples already exist (Bond and Lake, 2003) where the outcomes of stream restoration have been compromised by these things.

Conclusions

Our theoretical understanding of how populations might be structured across patchy landscapes has advanced considerably over the last decade and stream insects provide model species and systems. Streams offer characteristics (such as unidirectional flow; natural units such as catchments) that offer means for testing hypotheses that are difficult to tackle in other environments. Plus, we suspect that many stream insects will turn out to have far more complex (and much more interesting!) population structures across catchments than large patchy populations.

An obvious conclusion from this chapter is that sorting out the spatial structure of populations represents significant research programmes that will not fit neatly into the typical 3–4-year duration of research grants or PhD theses. We need multiple grants and dedication over significant periods to put together a story, but many of the recent trends in ecological science (a quest for ‘new ideas’ rather than basic data collection, demands by journals for short research papers, etc.) tend to militate against such steady work. Indeed, ecology is awash with far more ideas (some of them reinvented every few years bearing different names) than there are data to test them. We applaud our colleagues who have spent years working doggedly on particular systems and species to the point where they can ask sophisticated questions about them (see Peckarsky *et al.*, 2000; Kohler, Chapter 4, this volume). As Chesson (2000) has pointed out, even the simplest models that can explain important phenomena such as species coexistence are complex – they cannot be tested with few data and one or two experiments.

The interesting questions remain: what aspects of biology or environment allow predictability across species and systems? A topic hopefully for the next review!

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11

Polarization Vision in Aquatic Insects and Ecological Traps for Polarotactic Insects

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Abstract

We review the polarization vision of aquatic insects, which detect water from a distance by the horizontally polarized light reflected from the water surface. Reflection–polarization characteristics of different water bodies, as functions of sky conditions and solar elevation, are examined in relation to how they influence the detection of water bodies by polarotactic aquatic insects. Examples are given showing how aquatic insects can be deceived by, attracted to and trapped by highly and horizontally polarizing artificial reflectors, such as oil surfaces, horizontal black plastic sheets, asphalt roads, red or black car-bodies and black gravestones. We explain why mirages and polarizing black burnt stubble-fields do not attract polarotactic aquatic insects. The existence of a polarization sun-dial, which dictates the optimal time of day for dispersal by flying aquatic insects, is demonstrated. We finish by examining some unexpected aspects of polarization vision in insects: a polarotactic mayfly that never leaves the water surface and thus does not need polarotaxis, and polarotactic vision of several tabanid flies.

Polarization Vision in Aquatic Insects

Human observers can detect the presence of a distant water body by means of learned visual cues associated with water, such as mirroring of landmarks on the water surface, rippling of the surface or aquatic plants on the shore. These water-specific visual cues arise from the spatiotemporal distribution of the intensity and colour of light originating from water and the surrounding objects. As all these cues must be learned, a completely inexperienced human being (who has never encountered an open water surface) would be unable to recognize water.

The inexperienced person's lack of knowledge about water is similar to the situation when an aquatic insect leaves the water for the first time, driven by resource shortages or unsuitable environmental conditions. Larval and many adult aquatic insects live in water where they can gather information only about their aquatic environment. When adults leave the water for the first time, they face the task of detecting water while dispersing in order to return to water to avoid dehydration, oviposit, or simply return to the aquatic environment. As they have no opportunity to learn the visual cues associated with water, they need a genetically fixed and reliable method to detect water visually and from a distance. This sensory capability is polarization vision.

In the early 1980s, Rudolf Schwind (1983a,b, 1984a,b, 1985a,b) discovered that the backswimmer, *Notonecta glauca*, detects water by means of the horizontally polarized light reflected from the water surface, rather than by the intensity or colour of water-reflected light, or by the glittering or mirroring of the water surface. In the ventral eye region of *Notonecta*, Schwind *et al.* (1984) found ultraviolet-sensitive photoreceptors with horizontal and vertical microvilli that are highly sensitive to horizontally and vertically polarized light. This eye region is called the 'ventral polarization-sensitive area'. These photoreceptors can determine whether the direction of polarization of light from the optical environment is horizontal or not. In *Notonecta*, exactly or nearly horizontally polarized light stimulus elicits a typical plunge reaction, whereby the insect stops flying and attempts to re-enter the water (Schwind, 1984b). This attraction to horizontally polarized light is called positive polarotaxis.

Following from these initial studies, positive polarotaxis has been discovered in over 250 species of aquatic insects and from many different groups, including bugs, beetles, dragonflies, mayflies, tabanid flies and caddisflies (Schwind, 1985a,b, 1989, 1991, 1995; Kriska *et al.*, 1998, 2006a, 2007; Wildermuth, 1998; Horváth *et al.*, 1998; Bernáth *et al.*, 2001; Wildermuth and Horváth, 2005; Csabai *et al.*, 2006). The eyes of many aquatic insects are sensitive to the polarization of light in the visible or ultraviolet spectral ranges (Schwind, 1989, 1991, 1995). These insects find water using horizontally polarized light reflected from the water surface (Schwind and Horváth, 1993; Horváth, 1995). The spectral sensitivity of the polarization-sensitive photoreceptors of insects living in water is generally matched to the spectral composition of underwater light, which is quite diverse in different types of aquatic habitats (Lythgoe, 1979). Aquatic insects detect polarization in that region of the spectrum that is characteristic of their preferred habitat (Schwind, 1995). Depth, turbidity, transparency, colour, surface roughness of the water and substratum composition, as well as illumination, strongly influence the reflection–polarization characteristics of water bodies. These polarization patterns provide important information on the quality of freshwater habitats for polarotactic insects and can aid the orientation of these insects from a distance.

The Optomotor Response to Polarization Patterns in Aquatic Insects

The optomotor response is a turning reaction displayed in response to a cylindrical pattern of vertical black and white stripes being rotated around an animal.

This behaviour demonstrates the ability of an animal to detect movement of the optical environment on the basis of brightness cues; it helps to stabilize the animal's orientation in its environment and to maintain a straight course during locomotion (Varjú, 1959). If the underlying visual subsystem is sensitive to linear polarization, an optomotor response is likely to be elicited also by a rotating pattern of alternating direction of polarization.

Both the above- and underwater optical environments of backswimmers (Notonectidae) and waterstriders (Gerridae) (composed of the underwater world, the water surface, the riparian vegetation and the sky) are rich in polarized light. To test whether this polarization cue can be exploited for motion detection, in behavioural laboratory experiments Horváth and Varjú (2003, pp. 276–292) investigated the optomotor response of the waterstrider *Gerris lacustris* and the backswimmer *Notonecta glauca* to over- and underwater brightness and polarization patterns. They found that the latero-frontal eye regions in *Gerris* and *Notonecta* respond to certain contrasts in the direction of polarization, especially vertical versus horizontal polarization (Fig. 11.1). The function of this polarization-sensitive optomotor response may be a contrast enhancement for motion perception during compensation for passive drift and rotation of the body. They also showed that, in *Gerris* and *Notonecta*, the polarization-sensitive optomotoric reaction is mediated by the green receptors. In the aquatic habitat of these insects, brightness and polarization contrasts occur mainly in the visible and especially in the green part of the spectrum (e.g. riparian vegetation, water plants and phytoplankton in water).

Reflection–Polarization Characteristics of Different Water Bodies

In this and subsequent sections we make a distinction between 'dark water bodies' and 'bright water bodies'. Dark water bodies reflect little light, because they are deep, the water contains dark suspended particles or the bed sediments are dark. Bright water bodies reflect a lot of light, because the water is clear and shallow, the water contains bright suspended particles or the bed sediments are bright.

Schwind and Horváth (1993) and Horváth (1995) investigated, theoretically, the reflection–polarization characteristics of flat water surfaces in relation to the solar elevation. Using different kinds of imaging polarimetry, Horváth and Varjú (1997), Gál *et al.* (2001a) and Bernáth *et al.* (2002) measured the reflection–polarization patterns of various freshwater habitats in the red (650 nm), green (550 nm) and blue (450 nm) spectral ranges, under different meteorological conditions. According to Fig. 11.2d,e, the light reflected from the so-called Brewster zone (an annular region, the centre line of which is a circle at a nadir angle of 57.5°) of dark water surfaces is highly and always horizontally polarized. Thus, the light reflected from the Brewster zone is very attractive to polarotactic aquatic insects, even though the reflectivity R of the Brewster zone is only moderate as R increases nearly exponentially toward the horizon (Fig. 11.2f). What these insects identify as water are only those areas that reflect light with degrees of linear polarization p higher than the threshold p^* of their polarization sensitivity

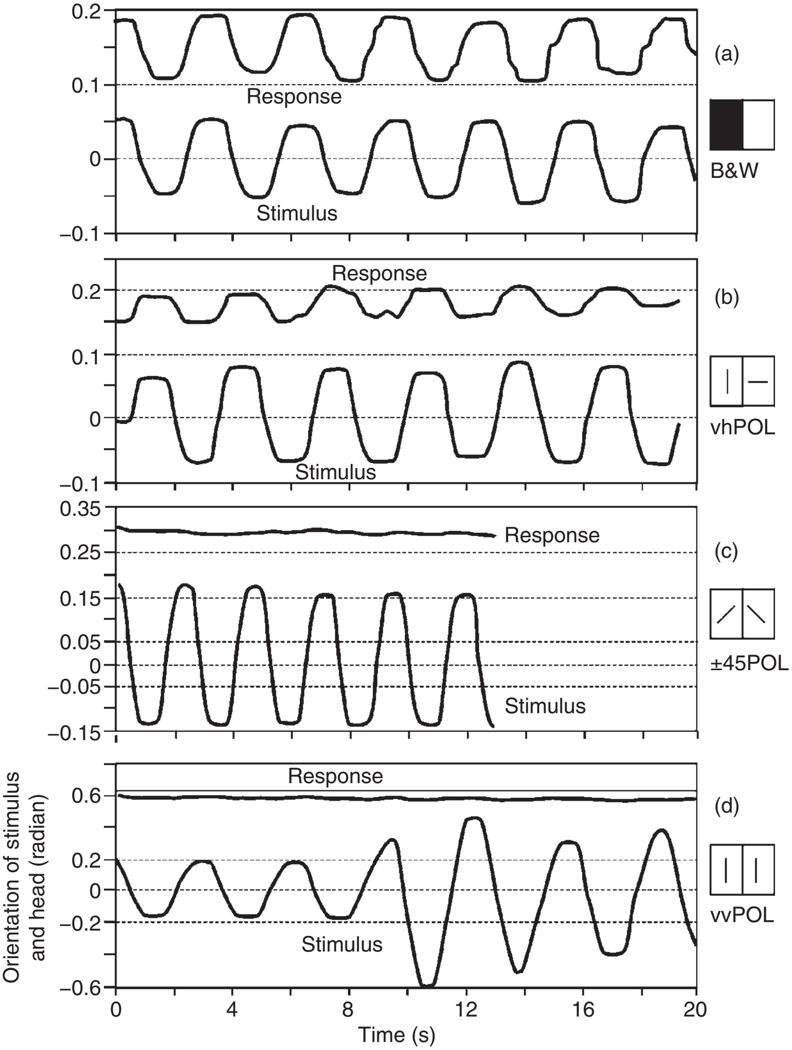

Fig. 11.1. Examples of the optomotor response of *Gerris lacustris* for different lateral stimuli in white light: (a) black-and-white intensity pattern (b–d) linear polarization patterns. The stimulus types are indicated by their symbols on the right side; bars represent the direction of polarization. The abscissa is the time and the ordinate is the oscillating orientation of the stimulus and the head of *Gerris* (response). The response is nearly zero to the ±45POL (c) and vvPOL (d) stimuli, while it is strong to the B&W (a) and vhPOL (b) ones.

($p > p^*$), and with angles of polarization α differing from the horizontal ($\alpha = 90^\circ$ from the vertical) by less than a threshold $\Delta\alpha > |90^\circ - \alpha|$. For example, the black region in Fig. 11.2G shows the area detected as water by a polarotactic insect whose thresholds are $p^* = 5\%$, $\Delta\alpha = 5^\circ$.

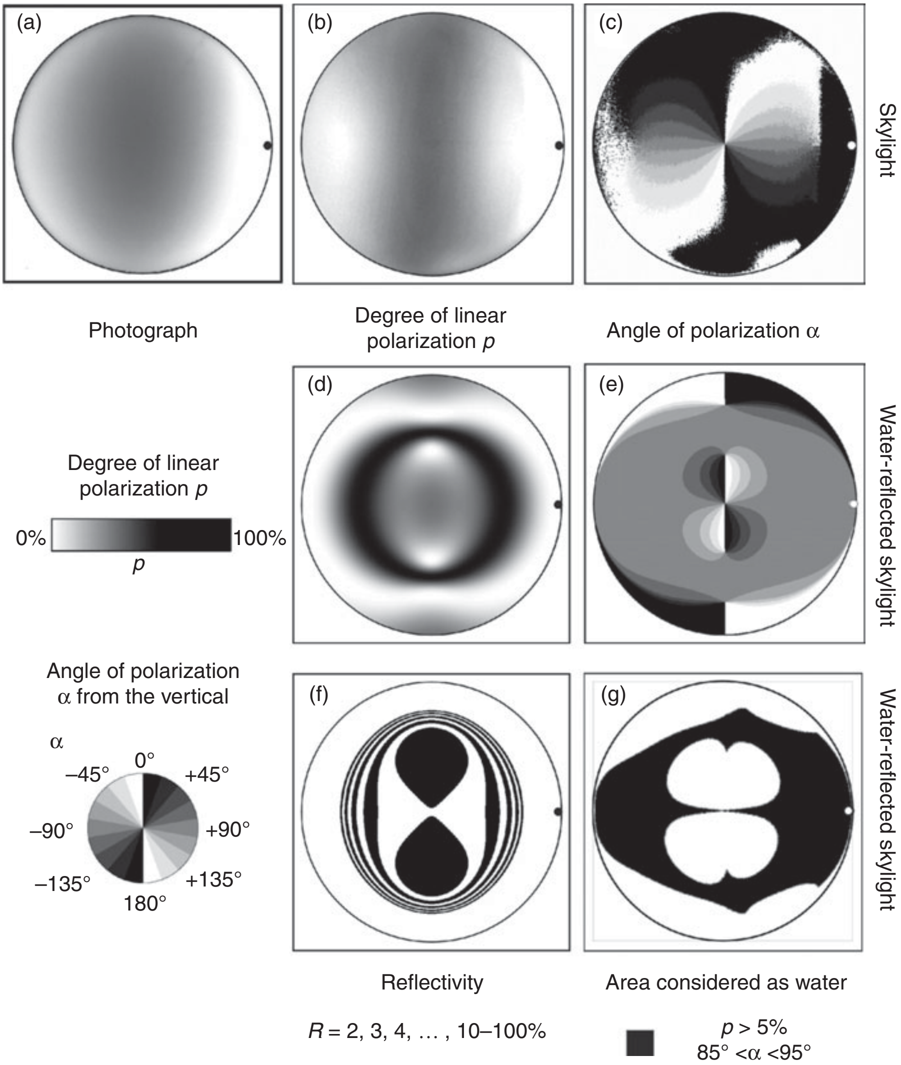

Fig. 11.2. Polarization patterns of the clear sky (a–c) and the flat water surface (d–f), and the area (black) detected as water by a polarotactic aquatic insect (g) at sunset. In the circular patterns the centre is the zenith (a–c) or the nadir (d–g) and the perimeter is the horizon. The central 8-shaped black patches in pattern f represent $R \leq 2\%$, the concentric oval and annular, alternately black and white narrow zones around these patches represent $R = 3, 4, 5, \ldots 10\%$ towards the periphery, the outermost annular white zone represents $R > 10\%$. The sun (a–c) and its mirror image (d–g) is represented by a dot on the horizon.

The light coming from the surface of a water body is a combination of that reflected from the water surface (which is partially horizontally polarized) and that refracted from within the water body (which is partially vertically polarized). The net polarization of light by water is governed, therefore, by the polarization

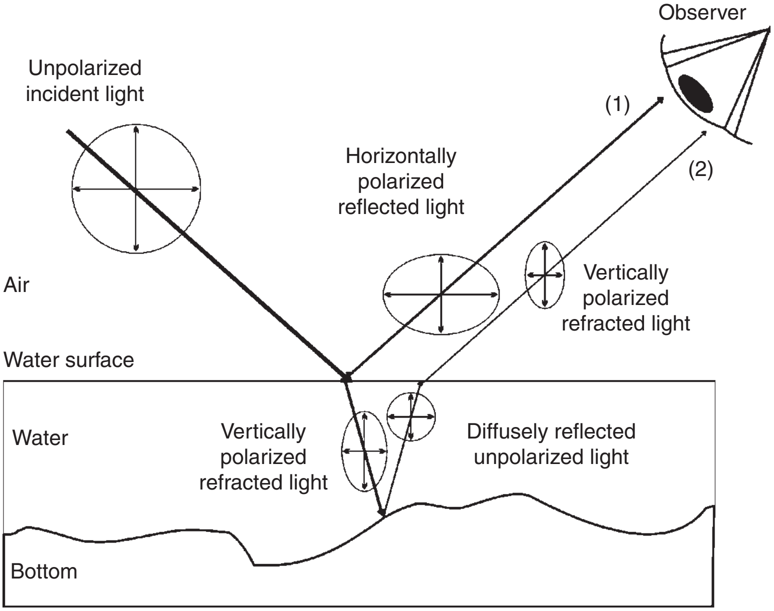

Fig. 11.3. Polarization of light returned from a body of water for unpolarized incident light. The returned light has two components: (1) the partially horizontally polarized light reflected from the water surface, and (2) the partially vertically polarized refracted light coming from the water. The ellipses and circles with vertical and horizontal double-headed arrows symbolize the state of linear polarization of light.

characteristics of these two components (Fig. 11.3). If, in a given part of the spectrum, the intensity of the first component is larger/smaller than that of the second one, then the water-returned light is partially horizontally/vertically polarized. If the intensities of both components are equal, the water returns unpolarized light. Consequently, the reflection–polarization characteristics of water bodies strongly depend on the spectrum of light backscattered by the particles suspended in water and of the light reflected by the bottom of water.

Shadows also influence the reflection–polarization characteristics of water bodies: in the case of dark waters, horizontally polarized surface-reflected light always dominates, and thus the direction of polarization is always horizontal for shaded and sunlit regions. The *p* of light reflected from the shaded regions of dark waters is lower than that from the sunlit regions because, in shaded areas, the amount of horizontally polarized, surface-reflected light is reduced. In the sunlit or shaded regions of bright waters, the direction of polarization can be horizontal or vertical, and *p* can be higher or lower, respectively. The *p* of light from bright water bodies is always much less than that from dark waters. Under windy conditions, the water surface undulates and this distorts the reflection–polarization patterns of flat water surfaces, reducing the extent of polarization.

Bernáth *et al.* (2002) showed that, from a distance and at an angle of view of 20° from the horizontal, dark water bodies are indistinguishable from bright ones based on the intensity and the polarization angle of the reflected light. Dark waters do, however, reflect light with a higher degree of linear polarization p than bright waters, in any part of the spectrum and in any direction of view with respect to the sun. Polarization-sensitive aquatic insects, therefore, may be able to use the p of reflected light as a visual cue to distinguish dark and bright water bodies from far away.

The reflection–polarization characteristics of the water surface are influenced also by the polarization of the sky. As moonlit and sunlit skies have the same polarization pattern, if the positions of the moon and sun coincide (Gál *et al.*, 2001b), the reflection–polarization patterns of a water surface are the same under sunlit and moonlit conditions for the same position of the sun and moon.

Polarization Sun-dial of Flying Aquatic Insects

Flying polarotactic aquatic insects are attracted to any surface where $p > p^*$ and $|\alpha - 90°| < \Delta\alpha$. The percentage Q of a reflecting surface identified polarotactically as water is the angular proportion Q of all viewing directions (relative to the angular extension of 2π steradians of the whole lower hemisphere of the field of view of the hypothesized insect) for which both criteria are satisfied. The higher the Q-value for a reflecting surface in a given visual environment, the larger its polarotactic detectability, i.e. the higher the probability that insects seeking water can find it by polarotaxis.

Using 180° field-of-view imaging polarimetry, Bernáth *et al.* (2004) measured the reflection–polarization characteristics of horizontal bright and dark reflectors (imitating bright and dark waters), in the red, green and blue spectral ranges in relation to the solar elevation angle θ from sunrise to sunset, under clear and partly cloudy skies. They found experimental evidence that the proportion $Q(\theta)$ of reflecting surfaces detectable polarotactically as water is always maximal at the lowest (dawn and dusk) and highest (noon) θ for dark waters, while $Q(\theta)$ is maximal at dawn and dusk (low solar elevations) for bright waters under both clear or partly cloudy skies (Fig. 11.4).

Csabai *et al.* (2006) found evidence for the influence of this effect on polarotactic attraction of aquatic insects in the field by 24-h trapping. The trap consisted of a strongly and horizontally polarizing shiny black plastic sheet laid on the ground, which is as attractive to polarotactic aquatic insects as a natural dark water surface (see below). They found that aquatic insects belonging to 99 taxa (78 Coleoptera and 21 Heteroptera) flew predominantly in mid-morning, around noon or at nightfall (Fig. 11.5). There are at least four different types of diurnal flight activity rhythm in these insects, characterized by peak(s): (i) in mid-morning; (ii) in the evening; (iii) both in mid-morning and the evening; and (iv) around noon and in the evening (Fig. 11.5). These activity maxima are quite general and cannot be explained exclusively by daily fluctuations of air temperature, relative humidity, wind speed and risks of predation, which are all somewhat stochastic (weather-dependent) and cannot be perceived in the water.

From the temporal coincidence between peaks in the diel flight activity of aquatic insects (Fig. 11.5) and the polarotactic detectability $Q(\theta)$ of water surfaces

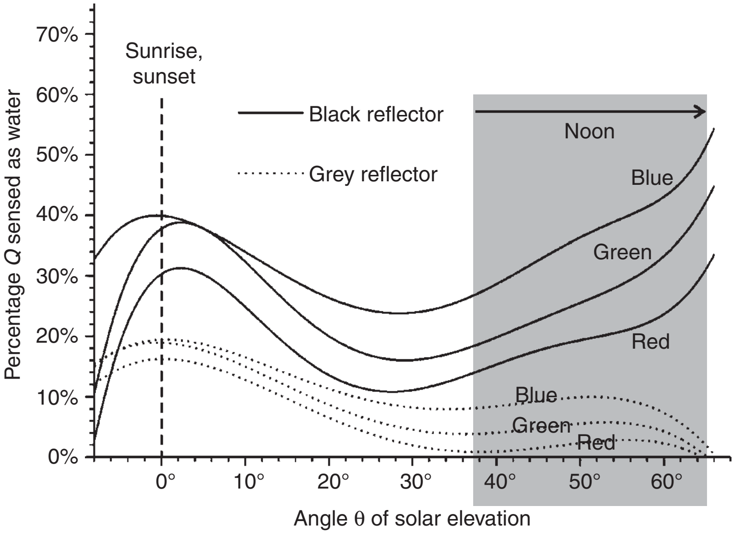

Fig. 11.4. Polarotactic detectability Q, that is, the percentage Q (%) of a black (continuous) and a grey (dashed) horizontal reflector that would be sensed as water by water-seeking polarotactic aquatic insects as a function of the solar elevation angle θ in the blue (450 nm), green (550 nm) and red (650 nm) parts of the spectrum under a clear sky. The angular shift of solar culmination (noon) from the beginning to the end of the 4-month monitoring of aquatic insects is marked by a grey band, where a horizontal arrow shows the shift direction.

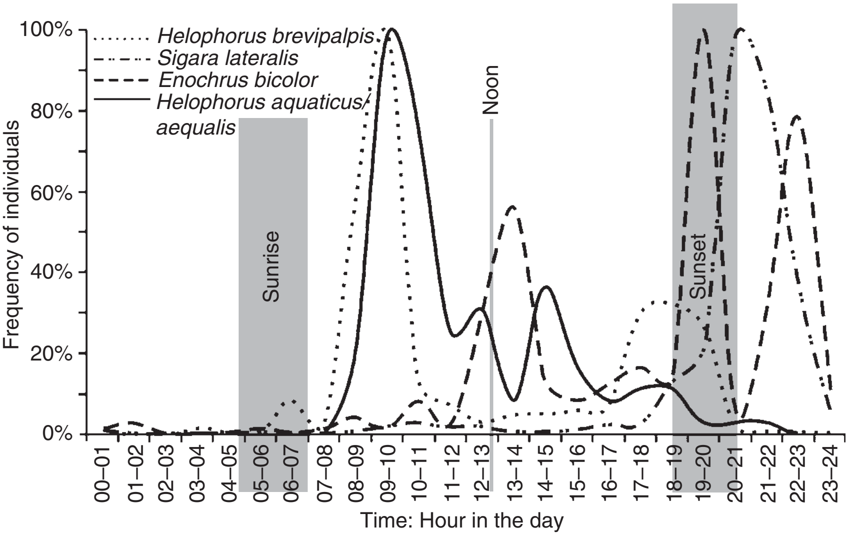

Fig. 11.5. Four different typical daily rhythms of dispersal by flying aquatic insects (*Helophorus brevipalpis*, *Sigara lateralis*, *Enochrus bicolor*, *Helophorus aquaticus/aequalis*). Time: local summer time = UTC + 2. The temporal shifts of sunrise and sunset from the beginning to the end of the 4-month monitoring of aquatic insects are marked by grey bands.

(Fig. 11.4), Csabai *et al.* (2006) concluded that the optimal times of day for aquatic insects to disperse are the periods of low and high solar elevations θ. The θ-dependent reflection–polarization patterns, combined with the influence of other factors, such as air temperature (usually too low for flight at sunrise), clearly explain why polarotactic aquatic insects disperse to new habitats in mid-morning, around noon or at dusk. These three optimal periods for dispersal, governed by the reflection–polarization pattern of the water surface, can be easily and reliably identified from the solar elevation θ, even underwater where air temperature, humidity and wind speed cannot be perceived. This phenomenon is called the 'polarization sun-dial' for dispersing aquatic insects.

Ecological Traps for Polarotactic Aquatic Insects

Here we examine evidence for ecological traps, *sensu* Schlaepfer *et al.* (2002), for polarotactic aquatic insects.

Oil surfaces

Kennedy (1917) gave an account of many individuals of the dragonfly *Anax junius* being killed as a result of mistaking an open surface of crude oil for water, and Kennedy (1938) cited cases where dragonflies were attracted to pools of petroleum. Similar phenomena were observed in oil ponds in the desert of Kuwait (Horváth and Zeil, 1996) and a waste oil lake in Hungary (Bernáth *et al.*, 2001). Many dragonflies, mayflies, water beetles (Dytiscidae, Coleoptera) and water bugs (*Belostoma* sp., Nepidae, Heteroptera) were found at the edge of these oil ponds, with females in particular often being trapped as they tried to lay eggs. Dragonflies were also frequently observed fighting and defending territory (Horváth *et al.* 1998), behaviours that are typical only above water surfaces (Corbet, 1999).

Horváth and Zeil (1996) suggested that polarotactic aquatic insects were attracted by the high and horizontal polarization of light reflected from the oil surface. Horváth *et al.* (1998) tested and supported this hypothesis in multiple-choice field experiments with dragonflies in Hungary. They compared the numbers of dragonflies being caught in water, crude oil and salad-oil traps with different reflection–polarization characteristics. They showed that positive polarotaxis is the most important mechanism guiding dragonflies during habitat choice and oviposition site selection, and this is why dragonflies can be deceived by, and attracted to, crude and waste oil, tar or asphalt. Using horizontally aligned test surfaces with different reflection–polarization characteristics in multiple-choice field experiments with dragonflies, Wildermuth (1998) obtained the same result.

There are several reasons, why oil and tar surfaces are more attractive than water surfaces to polarotactic animals: (i) oil is a better polarizing reflector than water, because oil has a higher refractive index (1.39–1.57) than water (1.33); (ii) due to the higher viscosity of oil, the reflection polarization of light is less distorted by wind-induced ripples; (iii) as dark oil is not transparent, the light reflected from flat oil surfaces is always horizontally and much more highly polarized than that reflected from transparent waters, due to the lack of vertically polarized refracted light.

Fig. 11.6 shows the patterns of the degree of linear polarization *p* and angle of polarization *α* of light reflected from the surface of crude oil, clear, transparent water and milky, translucent water. The dishes were positioned so that the lower half of their surface reflected specularly incident diffuse ambient light, while the upper half was in shadow. The light reflected from the lower half of the oil surface is almost totally polarized with horizontal direction of polarization. The top, shaded half of the oil surface reflects little and almost unpolarized ambient light

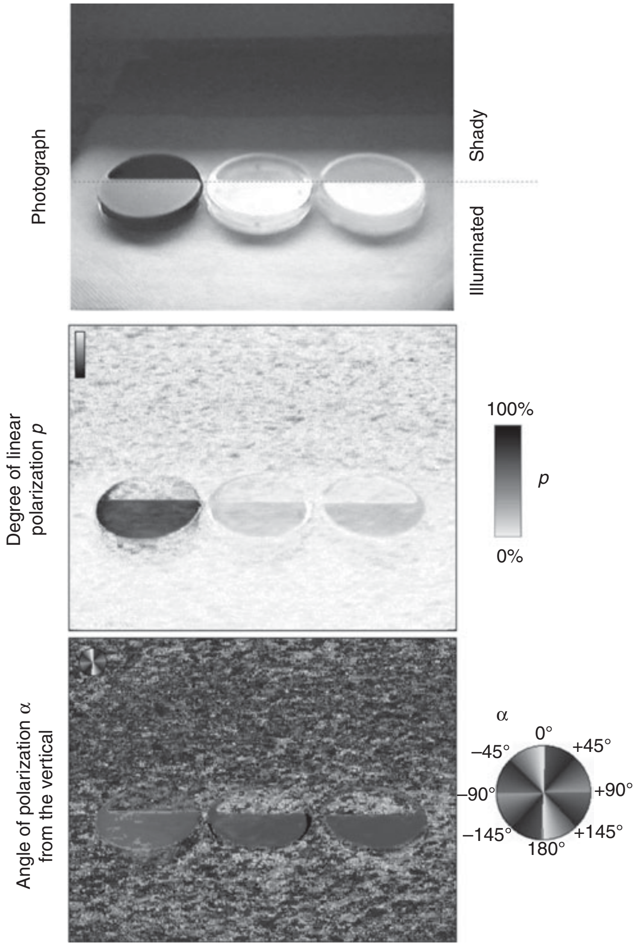

Fig. 11.6. Reflection–polarization characteristics of Petri dishes filled with black crude oil (left), clear water (middle) and milky water (right) measured by imaging polarimetry at 450 nm. The top half of the dishes is in shadow, the bottom half is illuminated by unpolarized diffuse light from an overcast sky. Viewing direction is −35° relative to the horizontal.

with horizontal direction of polarization. The top, shaded half of the water surfaces return mainly refracted light, which is scattered and reflected from the subsurface layer of water, while the bottom half returns a mixture of refracted and surface-reflected light. The specular surface reflection dominates in the bottom half of the water-filled dishes and has polarization characteristics similar to those of the oil surface (high *p* with horizontal direction of polarization). In the top shaded half of the water surfaces, however, the returned light is vertically polarized because of refraction at the water surface. Refraction polarization also reduces the net *p* in the bottom half of the water surface.

The water-filled dishes in Fig. 11.6 demonstrate well that light emanating from water is vertically polarized whenever the refracted light dominates, and horizontally polarized when surface-reflected light dominates. A similar effect cannot occur in an oil pond, because all the penetrating light is absorbed by the dark oil. The direction of polarization of light reflected from a flat oil surface is therefore always horizontal. The larger the *p* and the smaller the deviation from horizontal in the direction of polarization of reflected light, the more attractive the surface is to polarotactic aquatic insects. Consequently, dark oil can be even more attractive to polarotactic aquatic insects than bright water. Thus, for polarotactic aquatic insects, oil lakes appear to be exaggerated water surfaces acting as a supernormal, horizontally polarized stimulus.

Some ancient natural asphalt seeps in the Earth's history have acted as massive animal traps and their fossil remains are important in palaeontology. Examples include the Rancho La Brea tar pits in Los Angeles (Akersten *et al.*, 1983) and the asphalt seeps at Starunia in Western Ukraine (Angus, 1973). In Rancho La Brea, 95% of the entrapped animal species are insects, mainly aquatic ones. Most of the insect fossil remains found in Starunia are water beetles of the genus *Helophorus*.

A general view in palaeontology is that animals might have stumbled accidentally across tar seeps, which may have been camouflaged by dust or leaves (Angus, 1973; Akersten *et al.*, 1983). Alternatively, these asphalt seeps may have been covered by rain-water from time to time, thus attracted animals that then sank into the underlying tar, became entrapped and fossilized. Another possible scenario (Horváth and Zeil, 1996) is that polarotactic aquatic insects were deceived by and attracted to the tar pits, even in the absence of water, by the horizontal polarization of light reflected from the tar surface and mimicking a supernormally attractive body of water.

Plastic sheets

Horváth *et al.* (1998), Wildermuth (1998), Kriska *et al.* (1998, 2006a), Bernáth *et al.* (2001) and Csabai *et al.* (2006) performed multiple-choice experiments with polarotactic aquatic insects in the field using white and black plastic (polyethylene) sheets laid on the ground in different wetlands (Fig. 11.7). Such plastic sheets are commonly used in agriculture. The black plastic sheet reflects horizontally polarized light with high degrees of linear polarization *p*, while the white plastic sheet reflects vertically or obliquely polarized light with very low *p*

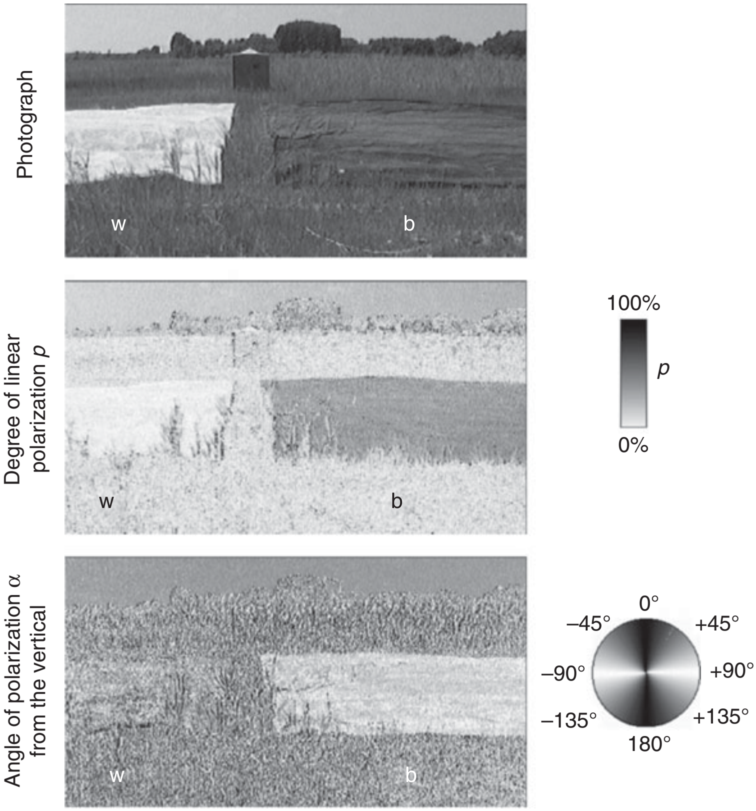

Fig. 11.7. Reflection–polarization patterns of a shiny white (left, w) and black (right, b) plastic sheet laid on the ground and measured by imaging polarimetry at 450 nm, under a clear sky at sunset. The viewing direction of the camera was −30° from the horizontal and perpendicular to the solar meridian.

(Fig. 11.7). Thus, the light reflected from a horizontal shiny black plastic sheet acts as a supernormally polarized stimulus for polarotactic water-seeking insects, as in the case of a black oil surface.

Bernáth *et al.* (2001) reported on the behaviour of great diving beetles *Dytiscus marginalis* on horizontal shiny dry black plastic sheets at sunset. The water beetles landed on the plastic sheet, touched and probed the surface, then flew up from the plastic and looked for another place. After landing again, the beetles tried to swim, crawl or creep on the smooth plastic surface. After about 30 min, the beetles were exhausted and unable to fly away, despite repeated attempts. Within an hour the beetles perished. This behaviour demonstrates how dangerous horizontally polarizing black plastic sheets can be for polarotactic aquatic insects.

Horizontal black plastic sheets attract aquatic insects, but white plastic sheets are totally unattractive (Horváth *et al.*, 1998; Wildermuth, 1998; Kriska *et al.*, 1998, 2006a; Bernáth *et al.*, 2001; Csabai *et al.*, 2006). The reasons for this are the reflection–polarization characteristics of the plastic surfaces (Fig. 11.7) and the polarotactic behaviour of aquatic insects. All aquatic insects behaved in a similar way on the black plastic sheet: landing, flying up, touching, crawling, egg-laying, copulating, reproductive activity and, finally, all of them dried out and perished. Dragonflies were also attracted to the black plastic sheet, but they did not perish. These experiments and observations show that horizontal shiny black plastic sheets can act as an ecological trap, by attracting and deceiving polarotactic aquatic insects due to the highly and horizontally polarized reflected light, while white plastic sheets are unattractive because the reflected light is weakly or not horizontally polarized.

Asphalt roads

Puschnig (1926) and Fraser (1936) reported that the dragonflies *Ophiogomphus forcipatus, Ictinogomphus ferox*, *Macromia magnifica* and several species of *Chlorogomphus* patrolled along asphalt roads instead of rivers and showed a typical water-touching behaviour above the asphalt surface. Kriska *et al.* (1998) witnessed a similar behaviour in mayflies swarming above dry asphalt roads. They observed that, near sunset, individuals of the mayfly species *Ephemera danica*, *Ecdyonurus venosus*, *Epeorus silvicola*, *Baetis rhodani*, *Rhithrogena semicolorata* and *Haproleptoides confusa* swarmed, mated above and landed on dry asphalt roads, shiny black plastic sheets and windscreens and roofs of cars close to their emergence sites (mountain streams). After copulation, the female mayflies laid their eggs on the dry asphalt surface instead of the water surface. The mayflies showed the same behaviour above the asphalt roads and black plastic sheets as at water surfaces. These observations, especially the egg-laying, suggest that the mayflies were apparently deceived by and attracted to the asphalt and plastic surfaces. Previous descriptions of mayfly swarming, mating and egg-laying behaviour have largely ignored or misinterpreted this phenomenon, suggesting that asphalt roads were acting as swarm markers, or that oviposition was due to the shiny surface of wet roads resembling streams (Ladócsy, 1930; Savolainen, 1978).

The first interpretation, however, cannot be applied to the observed egg-laying on asphalt roads because, normally, mayflies oviposit on to the water surface and not on to marker objects. The second interpretation cannot explain why egg-laying by Ephemeroptera frequently occurs also on totally dry asphalt surfaces.

Multiple-choice field experiments revealed that the six mayfly species mentioned above are polarotactic (Kriska *et al.*, 1998). Using imaging polarimetry, Kriska *et al.* (1998) showed that asphalt surfaces lit by skylight near sunset (when the investigated mayflies swarm), mimic a highly and horizontally polarizing water surface (Fig. 11.8). The polarization direction of sunlight reflected from sunlit asphalt roads is always perpendicular to the plane of reflection determined by the observer, the sun and the point observed. Thus, the direction of polarization of asphalt-reflected sunlight is usually tilted relative to the horizon, but it is always horizontal if the observer looks toward the solar or antisolar meridian because the plane of reflection is vertical. If the asphalt road is diffusely

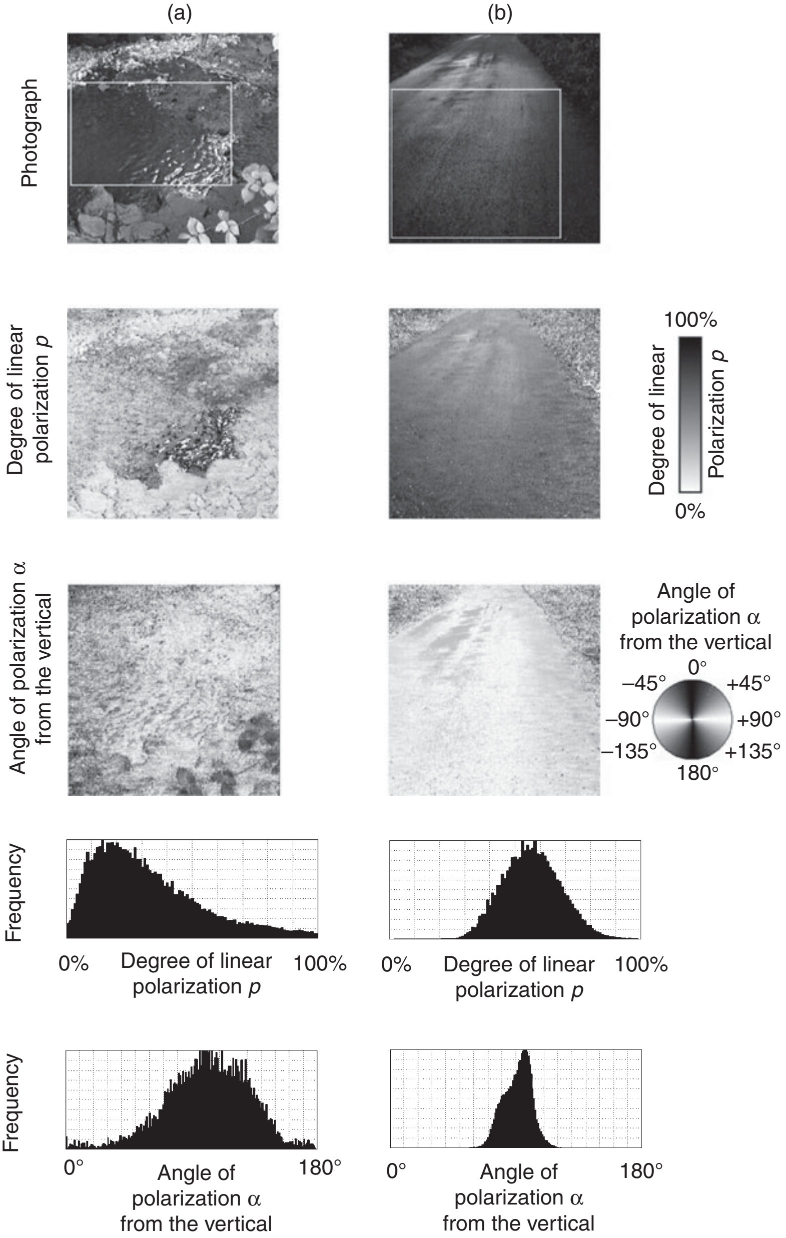

Fig. 11.8. Reflection–polarization characteristics of a reach of a mountain creek (a) and a section of an asphalt road (b) measured in the blue (450 nm) part of the spectrum. The creek was shadowed by trees and, through the foliage, the sky light illuminated the water surface from above right. The dry asphalt road was illuminated by the direct light from the setting sun under a clear sky, and the camera viewed towards the solar meridian. For both scenes, the optical axis of the polarimeter was –30° with respect to the horizontal. The frequencies (in arbitrary units) of p and α were calculated for the rectangular windows in the photographs.

illuminated by light from the sky (i.e. no direct sun), the reflected light is always horizontally polarized due to the extended sky, which illuminates the road from all possible directions. Kriska *et al.* (1998) also concluded that the darker and smoother the asphalt, the greater is its attractiveness to water-seeking polarotactic mayflies. Thus, the highly, and at sunset always, horizontally polarizing asphalt roads with a relatively homogeneous distribution of p and α (Fig. 11.8b), can be much more attractive to polarotactic mayflies than the water surface of their emergence site (Fig. 11.8a). Roads also may be attractive because the sky above them is usually visible, providing the males with an ideally homogeneous and bright background for the visual recognition of flying females. At sunset, asphalt may also have a slightly higher temperature than the surrounding areas.

Car paintwork and gravestones

Aquatic insects frequently land on red cars (Jäch, 1997; Nilsson, 1997; van Vondel, 1998; Kriska *et al.*, 1998; Bernáth *et al.*, 2001), which has been explained by the shiny appearance or the red colour of the car body (Jäch, 1997; Nilsson, 1997), or considered enigmatic (van Vondel, 1998). Dragonflies swarm above cars and oviposit on car bodies, sometimes causing damage to their coatings (Wyniger, 1955; Svihla, 1961; Watson, 1992; Wildermuth, 1998; Stevani *et al.*, 2000, Bernáth *et al.*, 2001, Günther, 2003; Torralba Burrial and Ocharan, 2003; Wildermuth and Horváth, 2005). Kriska *et al.* (2006a) found that horizontal red and black plastic sheets were equally highly attractive to aquatic insects (30 Coleoptera and seven Heteroptera taxa), while yellow and white ones did not attract insects. In the blue and green spectral ranges, the light reflected from red and black car roofs, bonnets and boots is highly and nearly horizontally polarized (Fig. 11.9a,c), which is very attractive to polarotactic aquatic insects. On the other hand, the horizontal surfaces of yellow and white cars reflect weakly and not always horizontally polarized light (Fig. 11.9b,d), which is unattractive to aquatic insects. Owing to depolarization by diffuse reflection, very dirty cars reflect light with much lower degrees of polarization than recently washed or waxed shiny cars. Thus, the most environmentally friendly car is white and dirty.

Recently, Horváth *et al.* (2007) observed that the dragonfly species *Sympetrum flaveolum*, *S. striolatum*, *S. sanguineum*, *S. meridionale* and *S. danae* were attracted by polished black gravestones in a Hungarian cemetery without any water body. These dragonflies showed the same behaviour to that which they display in the presence of water: (i) they perched persistently in the immediate vicinity of the chosen gravestones and defended their perch against other dragonflies; (ii) flying individuals repeatedly touched the horizontal surface of the shiny black tombstones with the ventral side of their body; and (iii) pairs in tandem position frequently circled above black gravestones. Tombstones preferred by these dragonflies had an area of at least 0.5 m^2 with an almost horizontal, polished, black surface, the sky was open above them, and there was at least one perch in the immediate vicinity.

The horizontal parts of black gravestones reflect highly and horizontally polarized light and, consequently, are attractive to polarotactic dragonflies

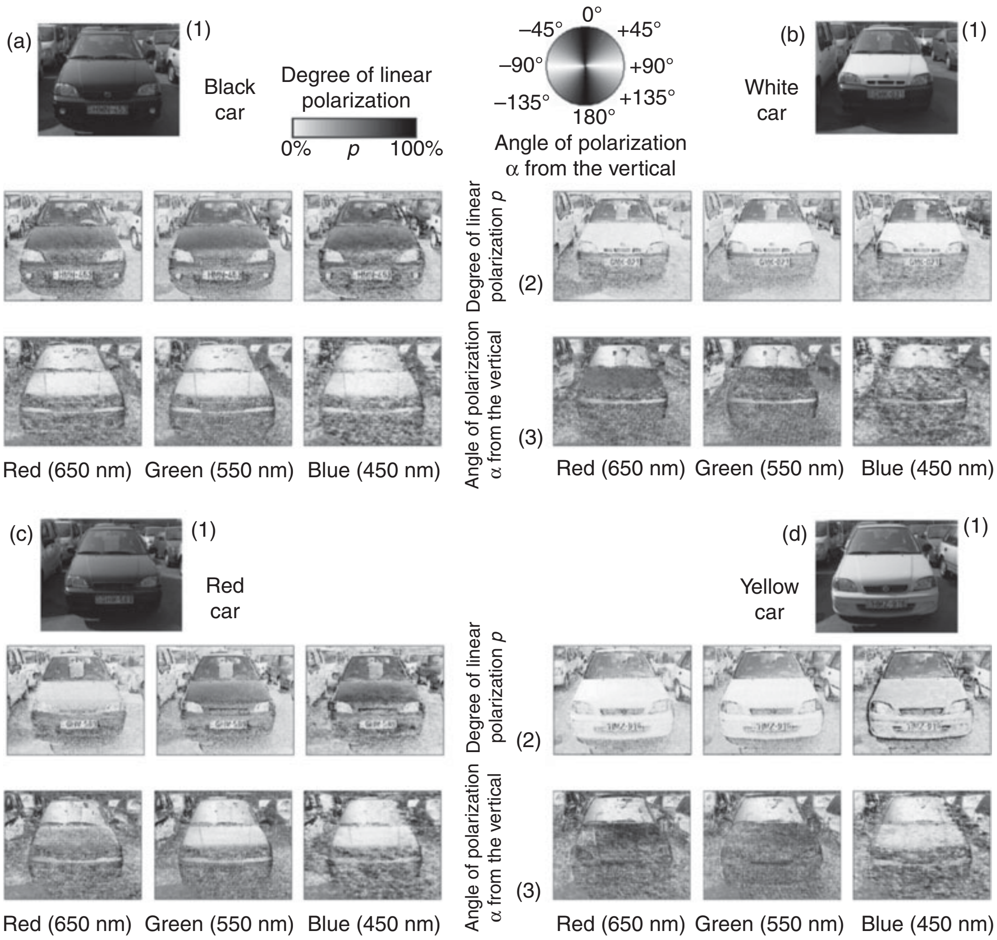

Fig. 11.9. Reflection–polarization patterns of a black (a), white (b), red (c) and yellow (d) car measured in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum under a clear sky at a solar zenith angle of 55°. The cars were illuminated from the left hand side by the sun, the long axis of the cars and the viewing direction of the polarimeter were perpendicular to the solar meridian, the angle of elevation of the optical axis of the polarimeter was –20°.

(Horváth *et al*., 2007). Gravestones with matt, bright or non-horizontal surfaces reflect light with low degrees of linear polarization or with non-horizontal direction of polarization, and thus are unattractive to polarotactic dragonflies. In double-choice field experiments, Horváth *et al*. (2007) showed that the dragonflies attracted to shiny black tombstones possess positive polarotaxis and therefore, under natural conditions, detect water by means of the horizontally polarized reflected light. The positive polarotaxis and the reflection–polarization characteristics of black gravestones explain why the observed *Sympetrum* dragonflies were attracted to black tombstones.

Reflecting Surfaces that Do Not Attract Polarotactic Aquatic Insects

The previous section discusses several different artificial shiny surfaces that attract polarotactic aquatic insects, because they reflect highly and horizontally polarized light. Some reflecting surfaces, however, do not attract aquatic insects, even though they are horizontal and sometimes highly polarizing. In this section two such surfaces are considered.

Why are aquatic insects not attracted by mirages?

On sunny days, mirages may appear on sunlit roads and hot plains: there appears to be a pool of shiny water in the distance, which dissolves on approach. The sky, landmarks and objects are mirrored in this 'pool', which deceives human observers. Can mirages also deceive polarotactic aquatic insects? To answer this question, Horváth *et al*. (1997) measured and compared the polarization characteristics of a mirage and a water surface in Tunisia. The light reflected from the sandy bottom of the desert is only weakly polarized. The skylight is partially polarized with various direction of polarization. As the light from the sky and the sky's mirage has the same degree p and angle α of linear polarization, there is no polarization difference between the sky and its mirage. On the other hand, there can be large differences in the intensity, as well as in p and α, of light from the sky and the water surface: the light reflected from the water surface is usually horizontally polarized and, near to the Brewster angle, its p is high, while both p and α of skylight change spatiotemporally.

Hence, there are significant differences between the polarization characteristics of water-imitating mirages and real water surfaces: flat water surfaces reflect usually horizontally polarized light, while undulating water surfaces reflect light with directions of polarization perpendicular to the plane of reflection. The p of reflected light depends upon the direction of view and the undulation of the water surface. If the water is far away from the observer, p is relatively low due to the grazing direction of view. If the horizon is defined by the border between the water surface and the sky, there is, in general, a high polarization difference between water and sky in both p and α. This is because skylight reflected from water surfaces gets repolarized (Fig. 11.10a). On the other hand, in the desert landscape there are no differences in intensity, p and α between the sky and its mirage. Mirages are not usual reflections, but are formed by gradual refraction and a total reflection of light (Fig. 11.10b): The nearer to the ground, the warmer the air and the smaller its index of refraction. Thus, the direction of grazing rays of light gradually changes to such an extent that the rays do not reach the ground, but after total reflection, they are deflected upward (Fig. 11.10b). This gradual deflection provides an observer with the same impression as mirroring does. Such gradual refractions and total reflection of light do not change the state of polarization.

Mirages may imitate water surfaces only for animals whose visual system is polarization-blind, but sensitive to intensity and colour differences (Horváth

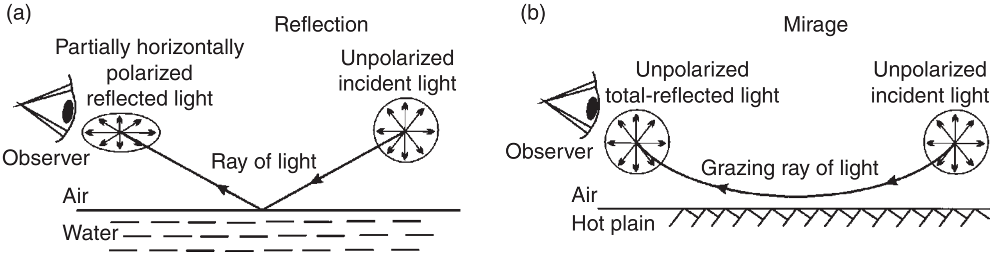

Fig. 11.10. (a) Unpolarized light becomes partially horizontally linearly polarized when reflected from the water surface. (b) Formation of a mirage above a hot plain, where the air temperature decreases and the refractive index of air increases exponentially with height above ground. The resulting gradual refraction and total reflection do not alter the polarization of light. Double-headed arrows represent the directions of polarization.

et al., 1997). Polarization-sensitive aquatic insects, however, can detect the polarization of mirage-reflected light. As this polarization differs considerably from that of water-reflected light (Fig. 11.10), they are not attracted to mirages.

Why do highly polarizing black burnt stubble-fields not attract aquatic insects?

As polarotactic aquatic insects can be attracted to dark oil surfaces, black or dark grey asphalt roads, black plastic sheets, black or dark-coloured car-bodies and black tombstones, one might assume that all ‘black anthropogenic products’, involving artificial surfaces that reflect light with high and horizontal polarization, can deceive and lure polarotactic aquatic insects. A typical and frequent black anthropogenic products is a burnt stubble-field (Fig. 11.11a,b). The black ash layer formed by the burning reflects highly polarized light due to the Umow effect (Umow, 1905; Können, 1985): the darker a surface, the higher the degree of linear polarization *p* of reflected light.

Black ash might be expected to attract polarotactic aquatic insects in large numbers, but Kriska *et al.* (2006b) showed that this is not the case. They monitored numerous highly polarizing black burnt stubble-fields, but never found aquatic insects or their carcasses in the ash, although flying polarotactic aquatic insects were abundant in the area, which was shown by attracting them to horizontal black plastic sheets close to burnt stubble-fields. From this, Kriska *et al.* (2006b) concluded that black burnt stubble-fields are unattractive to polarotactic aquatic insects, despite the high *p* of reflected light. To explain this, they measured the reflection–polarization characteristics of burnt stubble-fields at three different directions of view relative to the solar meridian (Fig. 11.11c). They established that: (i) *p* of light reflected from the black ash is high; (ii) *p* increases with the darkness of the ash; (iii) the direction of polarization of reflected light is nearly horizontal only towards the solar meridian (SM) and antisolar meridian (ASM), and it is tilted in other directions of view; (iv) the standard deviation of both the degree and the direction of polarization of reflected light is large.

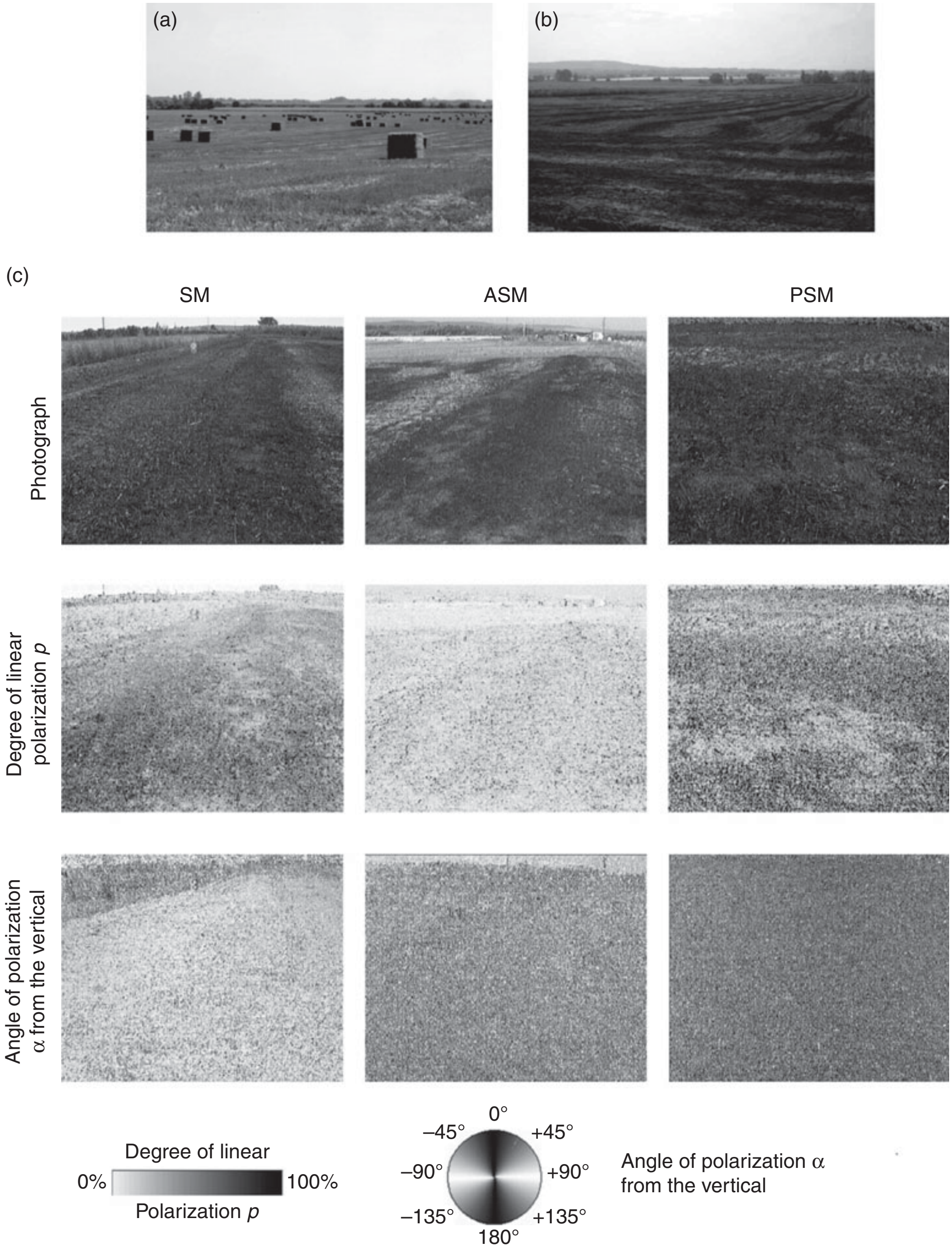

Fig. 11.11. A Hungarian stubble-field prior to (a) and after burning (b). (c) Photographs and polarization patterns of the burnt stubble-field measured under a clear sky in sunshine in the green (550 nm) part of the spectrum, when the direction of view of the polarimeter was towards the solar meridian (SM), antisolar meridian (ASM) and perpendicular to the solar meridian (PSM). The elevation angle of the optical axis of the polarimeter was –30° from the horizontal.

The latter two characteristics explain why burnt stubble-fields are unattractive to aquatic insects: burnt stubble-fields can be attractive only from directions of view towards the SM and ASM, where the light reflected from ash is horizontally polarized, on average. From other directions of view, burnt stubble-fields cannot be attractive, because the direction of polarization of reflected light is not horizontal.

The ash layer is a rough surface due to the random orientation of the charred stalks of plant material. One characteristic of rough surfaces is that the polarization direction of reflected light is always perpendicular to the plane of reflection (Können, 1985; Horváth and Varjú, 2003). In the case of sunlit, burnt stubble-fields, the plane of reflection passes through the observer, the sun and the point of the ash observed. This plane of reflection is vertical towards both the SM and ASM, and it is tilted for other directions of view. This explains why the average direction of polarization of light reflected from burnt stubble-fields is nearly horizontal towards the SM and ASM, and it is tilted in all other directions of view (Fig. 11.11c). These results may be important in the study of the wider environmental effects of postharvest burning.

Unexpected Aspects of Polarization Vision in Aquatic Insects

Polarotaxis in a mayfly that never leaves the water surface

Mayflies develop as larvae in water. After emergence they swarm and mate while on the wing, then lay eggs into the water. According to Brodskiy (1973), mayflies can be sorted into three groups based on their swarming site: group 1, species swarming immediately over water and never moving away horizontally from the water surface; group 2, species swarming over the littoral, but maintaining visual contact with the water; group 3, species swarming far from the water (<500–1000 m) and without visual contact with its surface. Kriska *et al.* (1998) showed that the mayfly species *Ephemera danica*, *Ecdyonurus venosus*, *Epeorus silvicola*, *Baetis rhodani*, *Rhithrogena semicolorata* and *Haproleptoides confusa* detect water by means of the horizontally polarized light reflected from the water surface. These six mayfly species belong to groups 2 and 3 *sensu* Brodskiy (1973). Species in group 1 do not require polarotaxis as they do not leave the water, but are mayflies in this group polarotactic?

The Tisza mayfly, *Palingenia longicauda* is a typical representative of group 1. It swarms exclusively over the surface of its name-giving river, the Tisza (Andrikovics and Turcsányi, 2001) (Fig. 11.12a), although there has been a report of an anomalous swarming of Tisza mayflies above a wet asphalt surface (Ladócsy, 1930). During swarming, Tisza mayflies fly immediately above the river in such a way that their cerci frequently touch the water or sweep its surface (Fig. 11.12b), using their tactile organs and hygroreceptors of their cerci and wings to detect water (Fink and Andrikovics, 1997) as well as by the intensity of light reflected from the water surface. They never swarm under windy conditions, when they could drift to the riparian vegetation. Hence, it is not obvious that Tisza mayflies need or possess positive polarotaxis.

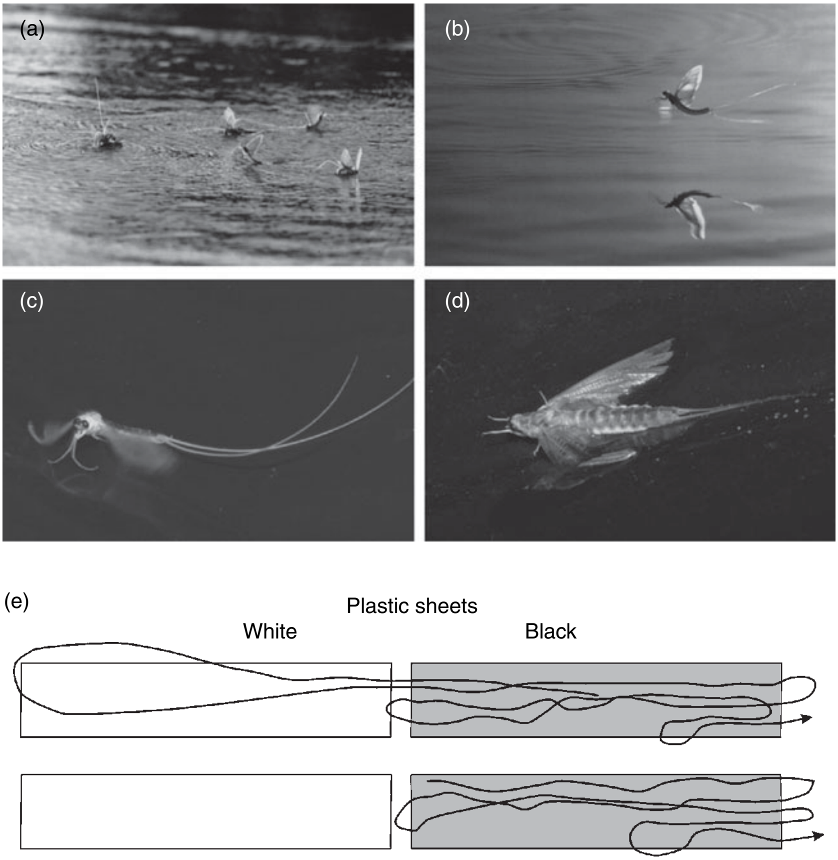

Fig. 11.12. (a,b) *Palingenia longicauda* mayflies swarm immediately above the river surface (photographs by Sándor Zsila). (c) A male *P. longicauda* flying immediately above a horizontal shiny black plastic sheet. (d) A female *P. longicauda* laying eggs on to a black plastic sheet. (e) Two typical trajectories of male *P. longicauda* mayflies released and flying immediately above shiny black and white plastic sheets laid on to the shore of the river Tisza, from which the water surface was not visible.

To reveal whether *P. longicauda* is, or is not polarotactic, Kriska *et al*. (2007) performed multiple-choice field experiments during the very short (only a few days) swarming period of Tisza mayflies. They showed that *P. longicauda* has positive polarotaxis, but this can be observed only under unnatural conditions (Fig. 11.12c,d), e.g. when animals are displaced from the water and released above artificial test surfaces (shiny black and transparent white plastic sheets, aluminium foil, matt black and white cloths). Only the shiny black and the transparent white plastic sheets influenced the flight of Tisza mayflies, and the black plastic sheet was preferred against the white one (Fig. 11.12e). The flying mayflies followed the black and white plastic sheets and turned back several times at the edges.

The demonstration of polarotactic water detection in a species that does not need it to locate water bodies would suggest that polarization-based water detection is an ancient, conservative ability among Ephemeroptera.

Polarotaxis in tabanid flies

The tabanid flies (Diptera: Tabanidae) are spread worldwide. Adult tabanids feed on nectar and pollen, and the females usually feed also on the blood of domestic animals and humans (Hall *et al*., 1998), which aids the development of their eggs, and are vectors of animal and human diseases and parasites (Foil, 1989). Understanding how tabanids locate their terrestrial mating and egg-laying sites would be very useful for control measures. Several different traps have been designed to catch tabanids (Malaise, 1937; Moore *et al*., 1996). According to Allan *et al*. (1987), the haematophagous female tabanids can find their host animals by odour, heat and visual cues. The optical cues relevant in the search for rendezvous and oviposition sites of tabanids are poorly understood. It is generally accepted that size, shape, motion, brightness and colour are factors that influence the attraction of tabanids (Thorsteinson *et al*., 1965).

In double-choice field experiments, Horváth *et al*. (2008) discovered positive polarotaxis in both males and females of numerous tabanid species (e.g. *Haematopota pluvialis*, *Heptatoma pellucens*, *Hybomitra ciureai*, *H. solstitialis*, *H. ucrainica*, *Tabanus bovinus*, *T. bromius*, *T. sudeticus*, *T. tergestinus*). The adults of all these tabanids are terrestrial, but lay eggs on the lower side of leaves of marsh plants overhanging the water where, after hatching, the larvae drop into the water where they develop. Horváth *et al*. (2008) proposed that, in these tabanids, the first step in the search for potential terrestrial mating and egg-laying sites happens indirectly by means of the detection of horizontally polarized light reflected from the surface of waters, on the shore of which appropriate plants for oviposition may occur.

The existence of polarotaxis in tabanids is surprising for two reasons. (i) Although the larvae develop in water, the adults do not lay their eggs directly into water. Attraction by horizontally polarized light has been found only in aquatic insects that oviposit directly into water (Schwind, 1991; Wildermuth, 1998; Horváth *et al*., 1998; Kriska *et al*. 1998, 2006a, 2007; Horváth and Varjú, 2003; Csabai *et al*., 2006). Positive polarotaxis has been described previously only in connection with the direct visual detection of water or moist substrata. (ii) Tabanids belong to the order Diptera, and no other dipteran species have been found to exhibit similar polarotaxis.

The discovery of polarotaxis in tabanids makes it possible to develop new, optically luring traps that are more efficient than the existing traps based on attraction by the brightness or colour of reflected light. The polarotaxis in male and female tabanids offers a new method for trapping both sexes. On the basis of this, the design of some new types of tabanid trap by the authors of this work is in progress.

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12

Evolution and Physiology of Flight in Aquatic Insects

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Abstract

Recent findings regarding the evolutionary origin of insects, their gas exchange physiology, wing development and flight ability are rapidly changing what we know and hypothesize about the history and biology of this major animal group. Hexapods now appear to be a sister taxon of branchiopod crustaceans, arising within the Pancrustacea. Developmental studies support the wings-from-gills hypothesis by identification of specific expression of orthologous genes during gill/wing formation in crustaceans and insects, and repression of abdominal appendages in modern insects by variants of genes that, in crustaceans, do not repress abdominal appendages. As gills evolved into wings, gas exchange physiology must have changed simultaneously and there is now evidence for this in both the origin of tracheae from cells in the wing primoridia, under control of wing-development genes, and in the discovery that some modern Plecoptera still express high levels of functional haemocyanin in their blood (i.e. insects that use both tracheal and blood-based gas exchange, similar to the overlap of dinosaur and avian traits in *Archaeopteryx*). Plecoptera and Ephemeroptera also display a wide range of mechanisms for aerodynamic locomotion across the surface of water, while their body weight is fully or partly supported by the water. These behaviours demonstrate a series of mechanically intermediate stages by which flapping gills could have evolved into flight-capable wings in an aquatic environment.

Introduction

Evolutionary history and a rich set of physiological mechanisms underlie the traits of contemporary aquatic insects and their population biology. Here I examine both evolution and physiology of flight in adult aquatic insects in order to contribute a broader understanding of this key phenotype that dominates adult behaviour and ecology. Flight has liberated adult aquatic insects from the high density and viscosity of water, along with the low oxygen content and often current experienced by immature life stages. Predictions from mechanical theory and data for speeds of animals moving through water versus air show a tenfold

(eds J. Lancaster and R.A. Briers)

increase in velocity of flying compared with swimming (Bejan and Marden, 2006); this difference is even greater if swimming involves moving upstream against a current, and is exacerbated by the approximately 30-fold difference in oxygen concentration (vol/vol, Schmidt-Nielsen, 1997) that allows aerial creatures to have much higher metabolic rates and endurance than gill-breathing aquatic animals. These physical and environmental factors, along with biotic influences such as predation, are major components of the natural selection regime that has driven the evolution of flight and thereby the adult form in aquatic insects.

Here I examine the origin of, and variation in, the flight ability of aquatic insects over the grandest possible scale – from the most meagre and evolutionarily incipient ability for winged locomotion, to physiological features of the most accomplished insect fliers. The aim is not to be all-inclusive, but rather reflects what I have learned by gravitating to extreme ends of a functional continuum. This contrast across mechanisms, levels of flight specialization and ecology provides insights regarding the origin and ongoing evolution of the adult stage in aquatic insects.

Evolutionary Origin of Insects

How did flying animals evolve wings and flight from non-flying ancestors? This question has a rich history that is much deeper in conjecture than it is in data, in large part because most attention has been paid to birds, a group whose contemporary species are so dissimilar from the evolutionary transitions of interest (Theropod to protobird; non-flying to flying) that most of the discussions address fossils rather than living species. Vertebrate studies have focused almost exclusively on adult birds and have overlooked clues revealed by the ontogeny of bird flight (Dial, 2003; Dial *et al.*, 2006). That problem is less severe in insects because insect orders have deep evolutionary roots and the retention of certain key traits in modern species permits exploration of genes, developmental pathways, ontogeny, anatomy, behaviour and mechanics relevant to flight evolution.

From where did insects arise? Studies over the last decade using molecular data, or combinations of molecular and anatomical data, have arrived at what many now consider to be a consensus (Glenner *et al.*, 2006); hexapods arose from within a group (Fig. 12.1) called Pancrustacea, as a sister taxon of Branchiopod crustaceans (e.g. Regier *et al.*, 2005; Mallatt and Giribet, 2006). This taxonomic affinity of hexapods and crustaceans is an important departure from the previously dominant view that traits such as the tracheal system and features of the head united hexapods with myriapods (for an overview of recent anatomical studies that refute myriapod–hexapod affinity, see Harzsch, 2006). Of primary importance for present purposes is that this new taxonomic arrangement sees hexapods as arising from water-breathing aquatic crustacean ancestors (using gills and blood-based gas exchange) rather than from terrestrial, tracheate air breathers. Furthermore, the emerging view that hexapods are most closely related to branchiopods suggests that insects originated in freshwater or hypersaline water rather than a marine environment. As I show below, this

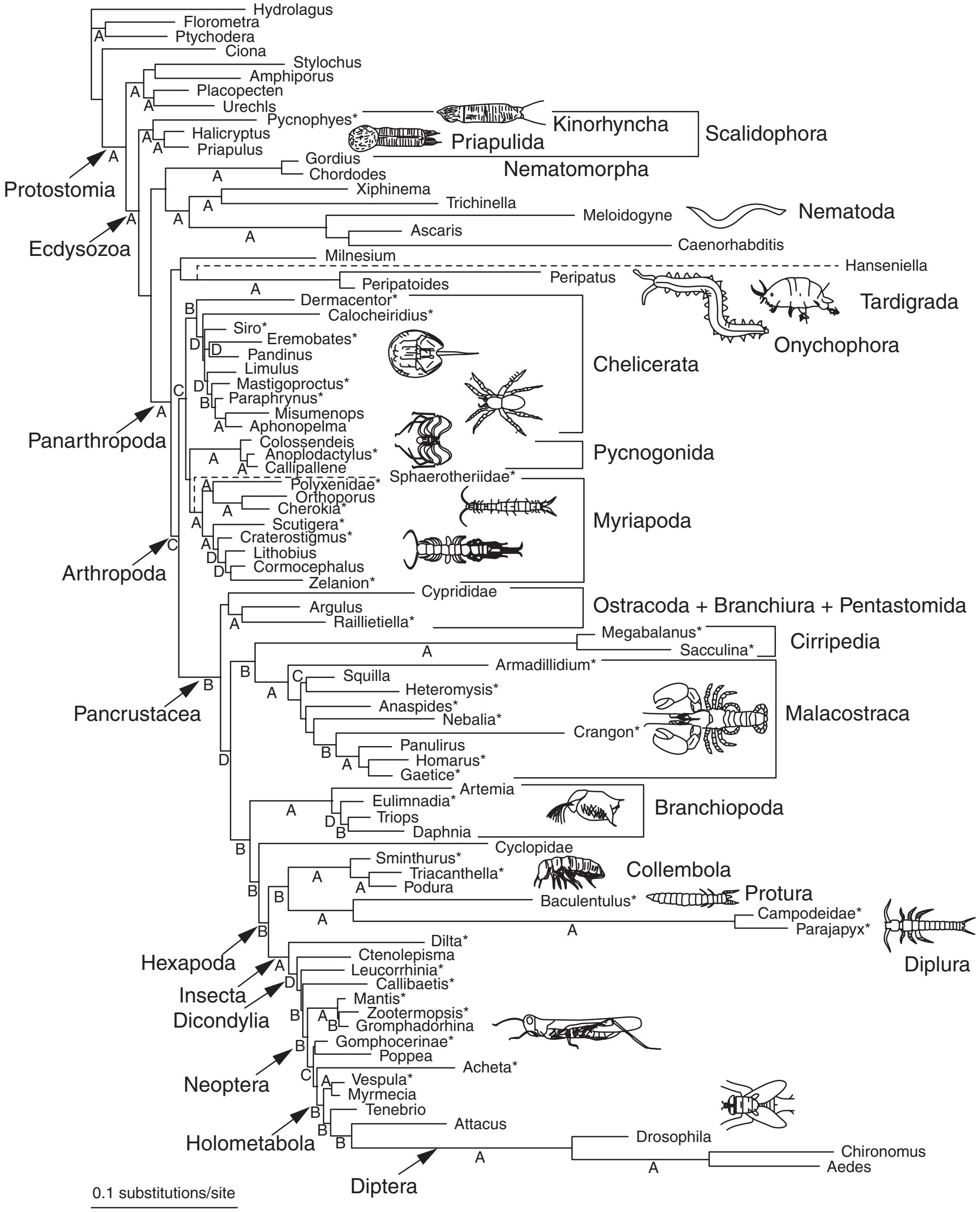


Fig. 12.1. A molecular phylogeny of Ecdysozoa (animals that molt their exoskeleton), constructed from combined 28S + 18S rRNA genes (reproduced with permission from Mallat and Giribet, 2006). Noteworthy for present purposes is the support for Pancrustacea and the sister clade status of Hexapoda and Branchiopoda. Regier *et al.* (2005) deduced a similar tree from a different set of protein coding genes, including a strongly supported Branchiopoda + Hexapodnode.

phylogeny and environmental setting can be combined with studies of wing development and known features of flight and respiration in relatively basal pterygotes to provide an integrated and coherent modern hypothesis for the origins of insect wings and flight. This hypothesis is not necessarily correct, as history is exceedingly difficult to prove or disprove; rather it is one viewpoint among many, uniquely rich in empirical support, that will stand among present (e.g. Dudley, 2000) and future competing theories.

Origin of Insect Wings

There is an almost century-old debate over the merits of two competing hypotheses for the anatomical origin of insect wings. One hypothesis is that wings arose *de novo* as lateral expansions of the dorsal thoracic cuticle, whereas the competing hypothesis maintains that wings are modifications of ancestral legs or gills. Using fossil and anatomical evidence, Kukalová-Peck (1978, 1983, 1987, 1991) has argued that insect wings arose from a dorsal outgrowth (epipod) of an ancestral jointed appendage. Either the entire appendage (which may originally have been a leg) or the epipod alone functioned as a gill. Support for this hypothesis has come from the finding that wings carry sensilla and chemoreceptors that are present on arthropod appendages, but not on the thoracic body wall (Dickinson *et al.*, 1997). Additional support has come from developmental studies showing that two genes, *apterous* and *nubbin*, are expressed at an early stage in the development of a dorsal epipod in both Malacostraca and Branchiopoda gills (Fig. 12.2), and in *Drosophila* wings (Averof and Cohen, 1997), thereby inferring homologies in their developmental programmes and therefore their origin. Importantly, *nubbin* is not expressed in the developing dorsal thoracic body wall of any insect that has been examined.

Other developmental support for the hypothesis that wings arose from a moveable jointed appendage comes from the observation that *Drosophila* carrying mutant (inactive) forms of the *ultrabithorax* (*Ubx*) and *abdominal-a* homeotic

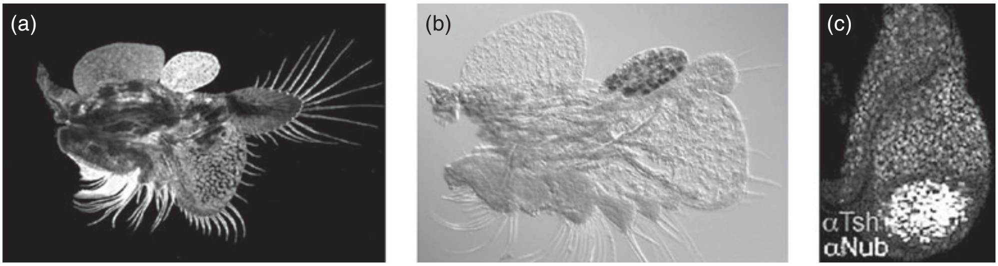


Fig. 12.2. A: Whole mount photograph of a mature *Artemia* thoracic limb. B: Expression of Nubbin protein (Af-PDM) in a dorsal epipod of the developing *Artemia* thoracic limb. C: Expression of Nubbin (light area) in an early third instar wing disc of *Drosophila.* A, B are high resolution versions (generously supplied by M. Averof) of figures from Averof and Cohen, 1997; C is reproduced with permission from Zirin and Mann, 2007.

genes develop wing primordia on the first seven abdominal segments (Carroll *et al.* 1995), in the same location that both fossil mayflies and modern mayfly nymphs have moveable gills (as do certain Odonata [Euphaeidae] and Plecoptera [Eustheniidae, Diamphipnoidae] nymphs). These gills have long been argued to be serial homologues of wings, whose thoracic equivalents were the evolutionary and mechanical precursors to wings (Kukalová-Peck, 1978, 1983, 1987, 1991). Thus, it appears that modern homeotic genes repress the initiation of wing/gill development on all but the meso- and metathorax of extant pterygotes (Carroll *et al.*, 1995). Ectopic expression of *Drosophila Ubx* (a gene that is normally expressed only in the insect abdomen) in the thorax strongly inhibits limb development, whereas thoracic expression of a brine shrimp *Ubx* orthologue does not (Galant and Carroll, 2002; Ronshaugen *et al.*, 2002). Mutant constructs of *Artemia Ubx* show a range of wing disc repressive effects, depending on the identity and extent of deletion of particular nucleotides. These experiments identify gene motifs that have apparently evolved to repress abdominal limbs in insects (Ronshaugen *et al.*, 2002), in part through phosphorylation that can be modified and therefore is flexible depending on local cellular conditions.

An important limitation of inferences about wing origins from this evo-devo work is that, aside from *nubbin*, the suite of genetic mechanisms controlling *Drosophila* wing development is not shared by all insect taxa, particularly more basal species in which legs and wings develop during different life stages (Jockusch and Ober, 2004). Jockusch and Ober (2004) rightly stress the need to examine a broader and less evolutionarily derived sample of insects before the developmental data can be judged as strongly supportive or non-supportive of a particular hypothesis for wing origins.

Replacing Gills with Wings

A number of early fossil insects possess both thoracic protowings and gill-like structures on their abdomen; these fossils led Kukalová-Peck (1991) to conclude that coexistence of wings and abdominal gills is the primitive pterygote condition. Fossil insects possessing both protowings and what appear to be gills, from the upper Carboniferous and lower Permian, are abundant and taxonomically diverse (Fig. 12.3a–d; Kukalová-Peck, 1978, 1991), including examples from the stem groups that led to modern Ephemeroptera, Hemiptera and Plecoptera, along with the extinct superorder Megasecoptera. Although it cannot be determined with certainty that these structures did in fact serve as gills, or even if these insects were associated with water, the similarity of the structures in Fig. 12.3a–c with gills of modern mayflies and stoneflies, including adults of certain extant species (Fig. 12.3e,f) makes this a reasonable interpretation.

An unexamined aspect of the wings-from-gills hypothesis is that it requires not only a change in mechanical function, but also a simultaneous change in gas exchange physiology. Starting with a branchiopod-like ancestor, a transition from gills to wings must have been accompanied by a respiratory system that replaced gills. This appears to have been accomplished by gradual loss of blood-based gas delivery to the tissues, and a gradual invagination of tracheae that

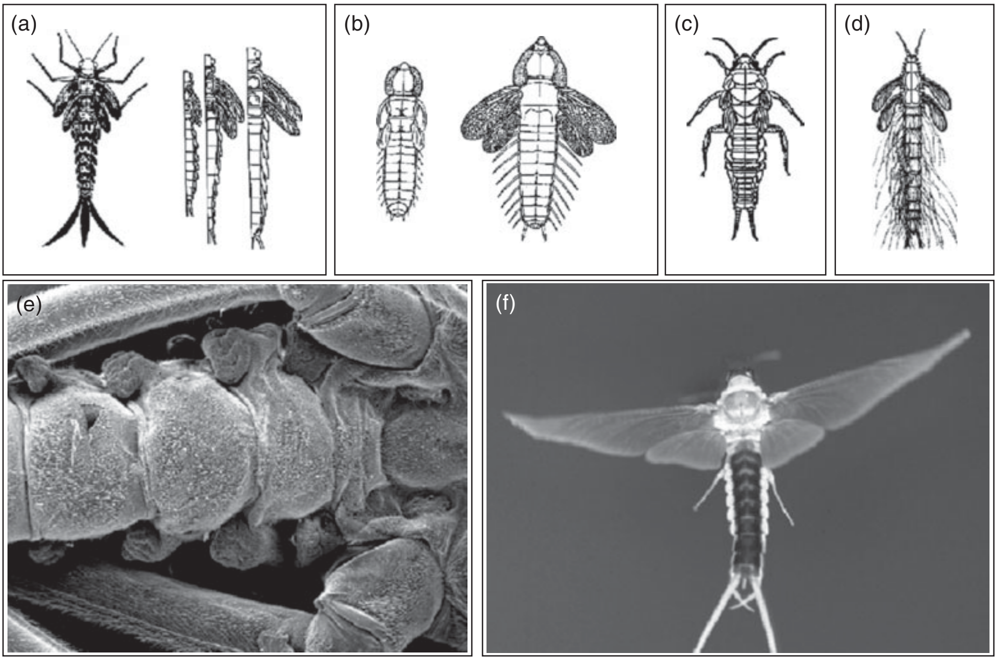


Fig. 12.3. (a–c) Fossil representatives (Kukalová-Peck 1978; reprinted with permission of Wiley-Liss, Inc.) of the stem groups of (a) Ephemeroptera, (b) Hemiptera, (c) Plecoptera, and (d) the extinct order Megasecoptera. Note the gills and/or wings on the thorax and abdomen, in what appear to be multiple life stages. (e,f) Similar gills on the abdomen of extant adult *Diamphipnopsis* stoneflies (e; from Marden and Thomas, 2003) and *Palingenia* mayflies (*f*, photo courtesy of J.L. Szentpéteri).

delivered air directly to the tissues. Remnants of this transition have recently been discovered in modern insects. A haemocyanin gene, previously unknown in insects, was found in an orthopteran (Sanchez *et al*., 1998), followed by the discovery that some Plecoptera still have an abundant haemocyanin that constitutes ≈25% of total haemolymph protein and reversibly binds oxygen (Hagner-Holler *et al*., 2004). Amino acid sequences of plecopteran haemocyanins cluster with crustacean haemocyanins in a molecular phylogeny (Hagner-Holler *et al*., 2004) and are ancestral to all of the known hexamerin proteins (including those from Hemiptera, Orthoptera, Blatraria and Isoptera) that insects use as a major mechanism for nutrient storage and transport (Hagner-Holler *et al*., 2007), with a molecular clock estimated age of about 470 My. A few insect species that inhabit low oxygen habitats have haemoglobin in their blood and it has recently been discovered that many types of insects express functional haemoglobins intracellularly in the tracheae and fat body (Hankeln *et al*., 2002, 2006; Burmester *et al*., 2006) where their function remains to be determined. These new findings indicate that the ground plan for hexapods and basal pterygotes includes blood-based gas exchange using haemocyanin, most likely in combination with direct gas exchange via tracheae and an intracellular role for haemoglobin.

Another recent discovery that is important for understanding the evolution of insect gas exchange is that tracheae arise from cells associated with the arthropod leg/gill. Franch-Marro *et al.* (2006) found that tracheal and leg primordia arise from a common pool of cells in *Drosophila*, with differences in their fate controlled by *wingless*, a gene that is an upstream regulator of wing development genes such as *nubbin* and *apterous* discussed above. This occurs even on abdominal segments, where appendage primordia ultimately repressed by modern homeotic genes (see above) are still expressed in association with cells that form tracheae. As with wing development genes, homologues of tracheal inducer genes are specifically expressed in the gills of crustaceans (Franch-Marro *et al.*, 2006). This suggests that internal elaboration of tracheae is likely to have co-occurred with external elaboration of gills/wings, so that loss of gill function for gas exchange was concurrently and incrementally replaced by tracheal gas exchange. Somewhere along this trajectory, blood-based gas exchange using haemocyanin as the respiratory pigment became increasingly less important in insects, as evidenced by the absence of haemocyanin in Ephemeroptera, Odonata and all of the Holometabola (Burmester and Hankeln, 2007).

A factor that may have been important in this trajectory is the weight of blood, which is greatly reduced in insects that use direct gas exchange via tracheae. Puncturing the cuticle of a 10–12 mg *Taeniopteryx* stonefly yields up to 5 μl of haemolymph (Fig. 12.4), whereas it is difficult to obtain more than 2 μl of haemolymph from a 500 mg *Libellula* dragonfly (e.g. Schilder and Marden, 2006) or a 120 mg *Melitaea* butterfly. I have found that flightless orthopterans (crickets) also have large blood volumes and, like stoneflies, they possess a haemocyanin gene (Sanchez *et al.*, 1998). These data, although scant, suggest that ancestral hexapods had more blood than is typically present in modern

Fig. 12.4. Blood (haemolymph) constitutes a relatively large portion of the body cavity volume of stoneflies (Plecoptera), which have tracheae but have also retained the ancestral gas exchange mechanism of reversible oxygen binding by hemocyanin in the blood. This photo shows hemolymph exuding from a superficial puncture near the base of the forewing of a *Taeniopteryx* stonefly. The droplet does not contain gut fluid, which has a much darker colour.

insects that lack haemocyanin. Reduction of blood volume and weight was presumably a target of natural selection for stronger flight ability, as has occurred in all forms of animal and human-engineered flying devices.

These discoveries of an ancient haemocyanin in insect blood are a startling finding that, combined with the now well-supported sister-taxa status of hexapods and branchiopod crustaceans, challenge the traditional view of the sequence of events in the evolution of insect gas exchange. It is often stated with complete certainty that early insects were terrestrial and breathed via tracheae (e.g. Eriksen *et al*., 1996; Gullan and Cranston, 2005). This is based in large part on the now obsolete notion that insects arose from terrestrial, tracheate, myriapod-like ancestors. The sister-taxa status of hexapods and branchiopod crustaceans, along with the recently discovered occurrence of haemocyanin in both apterygote and lower pterygote insects, changes this picture radically (Fig. 12.5). According to this new hypothesis, blood-based gas exchange using haemocyanin as the respiratory pigment was part of the ground plan of basal hexapods, probably along with at least rudimentary tracheae. Tracheae presumably allowed access to atmospheric oxygen at the water surface and terrestrial shorelines and emergent vegetation. Alternatively, tracheae may have developed first internally with no external openings (i.e. a closed or apneustic tracheal system). This novel idea is based on the osmotic challenge presented by freshwater and/or hypersaline habitats invaded by the common ancestor of branchiopods and hexapods, where fluxes of ions across the thin gill epithelium would have been reduced by the presence of an internal gas space between the epithelium and the haemocyanin-containing blood (Fig. 12.6). Such a water-to-air-to-blood pathway for gas exchange would have reduced ion loss and the energetic expense of ion uptake by active transport. Aquatic insects have a fairly impermeable integument but, because of their high surface to volume ratio and short distances for diffusion, an aquatic larva such as an *Aedes* mosquito loses about 50% of its total body NaCl per day across its cuticle (Withers, 1992), a loss that must be counteracted by active transport. Nymphs of the most basal pterygote insects (Ephemeroptera) inhabit fresh water and have a closed tracheal system that may be a retained ancestral trait in a continuously aquatic lineage rather than a derived trait from terrestrial ancestors with open tracheae, as has traditionally been assumed.

Flapping Gills to Flapping Wings: a Hypothesis for Flight Origins on the Surface of Water

Fossil and developmental evidence that wings arose from flappable gills of aquatic crustacean-like ancestors indicates that gills and an aquatic habitat may be retained ancestral traits that were part of the ground plan of the first hexapods (Fig. 12.5). According to this scenario, modern non-insect hexapods and apterygote insects lost gills as they invaded land, thereby diverging from a lineage that remained aquatic and gave rise to basal pterygotes. Alternatively, the traditional hypothesis of a terrestrial-to-aquatic transition between apterygote and basal pterygote insects requires that basal pterygotes re-expressed the nerves, muscles and anatomical features of flappable gills (with convergence upon branchiopod

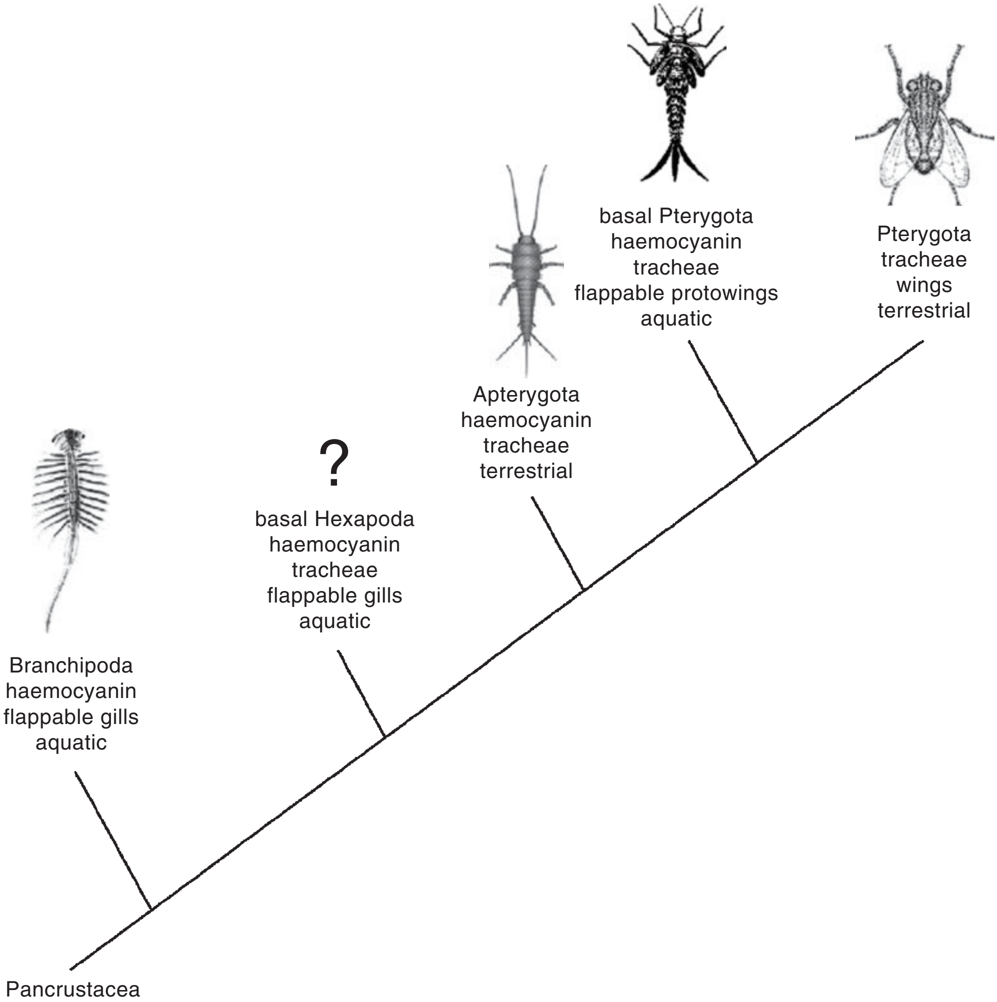
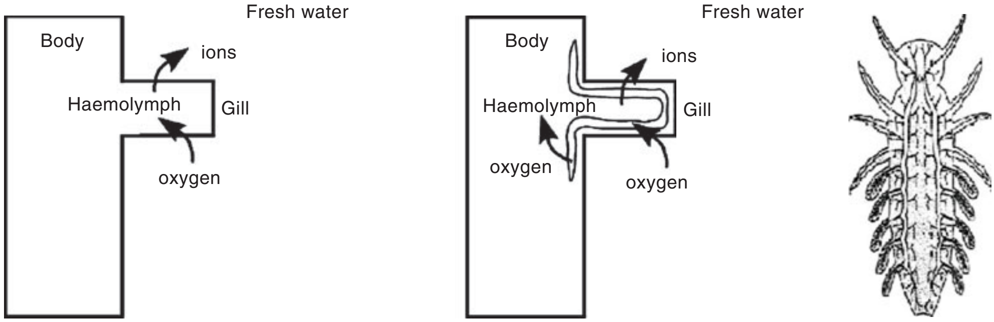


Fig. 12.5. A hypothesis for the phylogenetic distribution of gas exchange traits and habitat (aquatic vs. terrestrial) in branchiopod crustaceans and insects. 'Hemocyanin' refers to both the presence of this respiratory pigment and a blood-based gas exchange system. Taxa containing both hemocyanin and tracheae use a mixture of blood-based and direct delivery of gas to their tissues. Hemocyanin has been retained in modern Zygentoma (Apterygota), Plecoptera (basal Pterygota), and Orthoptera (Pterygota) (Hagner-Holler *et al.*, 2004).

gill developmental mechanisms, such as expression of *nubbin*) after returning to water from terrestrial apterygote-like ancestors. There is no objective basis for determining if multiple independent losses of gills during the divergence of apterygotes is more or less likely than a single reacquisition of a complex trait such as flappable gills so, lacking the necessary fossil record, this must remain a point of conjecture and opinion. Personally, I think that multiple independent losses of gills by new land-invading lineages of apterygotes is a highly likely



Ancestral state

Primoridial internal trachea to reduce ion eflux

Modern closed tracheal system with gills

Fig. 12.6. A hypothesis for the origin of tracheae in a freshwater aquatic environment where the original function was to reduce ion loss from the hemolymph to the surrounding fresh water. Elaboration of the tracheal system would create the arrangement seen in modern mayfly nymphs, in which internal gas exchange occurs via the closed tracheal network.

evolutionary outcome (more likely than retention of gills on land), whereas reacquisition of flappable gills after their loss in a terrestrial environment is a dubious scenario, even considering the repeated loss and reappearance of wings in stick insects (Whiting *et al.*, 2003), as the latter presumably occurred over a much shorter timescale and within a more conserved phylogenetic and developmental architecture than an apterygote-to-pterygote transition.

The final assumption of the traditional theory for terrestrial origins of basal pterygotes is that wings and winged locomotion necessarily evolved in a terrestrial setting. Surprisingly, not only is terrestriality not necessary for the origin of winged locomotion, it is actually much easier to show how flight can evolve from non-flight in an aquatic environment than in a terrestrial one. Flight is difficult, requiring not only complex neural and anatomical features to create useful beating patterns of sufficiently rigid and structurally sophisticated wings (Wootton, 2001), but also at least 12–15% of body mass must be flight musculature (Marden, 1987). Except for wings, animals do not have muscle groups this large that power articulated forelimbs (as opposed to the body axis, which contains more than this amount of muscle in fish and shrimp), which indicates that primordial wings and muscles must have undergone directional selection (i.e. incremental improvement in function) before acquisition of the ability to generate enough lift to support body mass. Hypotheses for terrestrial flight origins rely on a jumping or falling scenario in which incrementally larger wings extend the glide path, reduce descent velocity or control direction (Wootton and Ellington, 1991; Yanoviak *et al.*, 2005). None of these, however, address the problem of directional selection required to turn gliding wings and rudimentary flight muscles into flapping wings capable of counteracting gravity. Furthermore, analyses of the origin of bird flight show that crude flapping reduces gliding performance, thereby hindering the ability of gliding wings to evolve into flapping wings (Caple *et al.*, 1983).

Adaptive Stages Leading to Flight, Exemplified by Living Forms

In contrast to the problematic nature of a terrestrial gliding-to-flapping transition, there is empirical evidence demonstrating a stepwise pathway that could have transformed the structure and function of appendages that served originally as gills to appendages that served ultimately as wings. Certain modern Plecoptera and Ephemeroptera (stoneflies and mayflies; these two orders arose near the base of the early split between Neoptera and Palaeoptera and have retained many primitive morphological features, including flapping gills in the larval stages) use behaviours that demonstrate how gills could have evolved into wings in an aquatic habitat. These insects use aerodynamic locomotion to move in two dimensions across the surface of water, in some cases by using fairly rudimentary wings and wing motions (Marden and Kramer, 1994, 1995; Kramer and Marden, 1997; Ruffieux *et al.*, 1998; Marden *et al.*, 2000; Marden and Thomas, 2003). Video segments of these behaviours are available at www.bio.psu.edu/People/Faculty/Marden/PNASFig2.html and www.famu.org/mayfly/sartori/movies.php. In stoneflies, these behaviours are basal and phylogenetically diverse (Thomas *et al.*, 2000). One stonefly that uses its forewings as oars to row on the water surface, *Diamphipnopsis samali,* even possesses the primitive pterygote condition of co-occurring wings and what appear to be functional gills on the adult abdomen (Fig. 12.3e; Marden and Thomas, 2003), a mixture of ancestral and modern traits analogous to what occurs in *Archaeopteryx*. Unlike *Archaeopteryx*, these are living animals that we can study.

The hypothesis that insect flight originated on the surface of water (Marden and Kramer, 1994) has become known as the surface-skimming hypothesis. It poses that flying insects evolved from aquatic ancestors that used rudimentary flapping wings to achieve two-dimensional locomotion across water surfaces. Because the body weight of skimmers is supported by water, aerodynamic force output can be small, wings can be weak (i.e. do not require structural rigidity to support body weight; Wootton, 2001) and even minor improvements in thrust generation can be advantageous and selected. Thus, a fundamental strength of the surface-skimming hypothesis is that it provides a mechanical solution for the puzzle of how a small, weak flight motor and wing primordia could be useful and gradually elaborated prior to the evolution of true flight.

Taeniopteryx stoneflies accomplish surface-skimming when their wings are experimentally reduced to small stubs and the air temperature is lowered to near freezing (i.e. very low muscle power output, likely equivalent to what small gill-flapping muscles could produce at warm temperature; Marden and Kramer, 1994). Another species, *Allocapnia vivipara*, shows no ability to flap its wings, but raises its wings in response to wind, thereby sailing across the water surface (Marden and Kramer, 1995). A survey of surface-skimming behaviour (Marden *et al.*, 2000; Marden and Thomas, 2003) has shown that there is an incremental increase in velocity as contact with the water surface is reduced (Fig. 12.7). Stoneflies that keep their entire abdomen in contact with the water while they undulate their body in a swimming-like motion (Austroperlidae; labelled 'swim-skim' in Fig. 12.7) or while they use their forewings to row (*Diamphnopsis*) achieve the lowest velocity (yet substantially faster than swimming by stonefly nymphs).

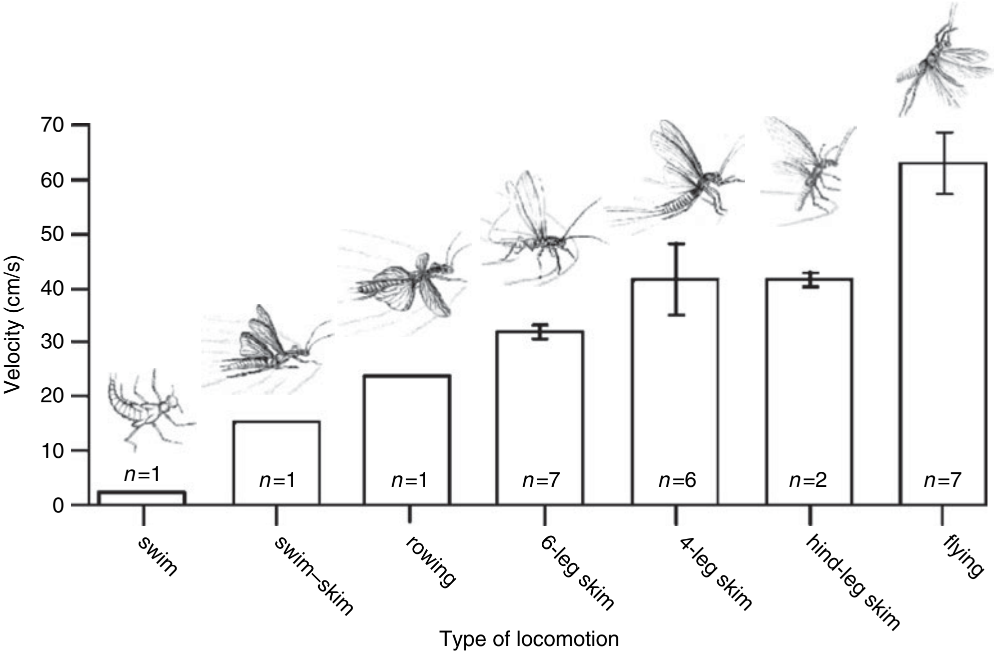


Fig. 12.7. Mean velocity of stoneflies using different forms of aquatic, semi-aquatic, and aerial locomotion. Sample sizes refer to the number of species; error bars represent the standard error of the grand mean (i.e. variability among means derived from multiple species).

Taeniopterygid stoneflies that raise their entire body above the water while keeping all six legs in continuous contact with the surface (labelled '6-leg skim' in Fig. 12.7) attain the next highest velocity. Species that raise their forelegs or their fore and middle legs (labelled '4-leg skim' and 'hind-leg skim' in Fig. 12.7) attain the highest skimming velocities, but are slower than stoneflies that break completely free of the water surface in true flight. These results show that the water surface is a habitat where rudimentary wings, muscle power and aerodynamic locomotion in two dimensions can progress in a stepwise fashion through mechanically intermediate stages that lead to true weight-supported flight in three dimensions. There had been no equivalent body of data or even theory for a detailed incremental pathway to flapping flight in a terrestrial environment, until recent analyses of incline running by juvenile birds (another way that flapping flight may have evolved without a jumping/falling/gliding/parachuting origin) revealed a possibly analogous scenario (Dial, 2003; Bundle and Dial, 2003; Dial *et al*., 2006).

Surface-skimming also occurs in mayflies (Ephemeroptera), the most basal pterygote insects. Subimagoes from a number of mayfly families in the northeastern USA use four-leg skimming at cool air temperatures (<13°C, Marden *et al*., 2000). Four-leg skimming by mayflies has also been observed at warm temperatures in subtropical Madagascar. Three species in the genus *Cheirogenesia* move about on the water surface using four-leg skimming (Ruffieux *et al*., 1998; M. Sartori, personal communication). Male imagoes skim to search for females

Fig. 12.8. A huge swarm of male *Palingenia longicauda* mayflies skimming across the surface of the Tisza river in Hungary, searching for emerging females. This is the same mayfly species that has gill remnants on the abdomen (Fig. 12.3f). Photo generously provided by J.L. Szentpéteri.

and the females do not progress beyond the subimago stage. Notably, this species exists in a river system that lacks surface feeding fish, which suggests that, in the absence of modern forms of predation, the locomotor and mating behaviour of modern aquatic insects, even at warm temperatures, can readily collapse from three-dimensional to two-dimensional and still remain mechanically and ecologically viable.

A mayfly mating system that involves a mixture of flying and skimming has also been found in *Palingenia* mayflies in Hungary (Fig. 12.8). Extraordinary video collected by Sartori (www.famu.org/mayfly/sartori/movies.php) and still photography (Szentpéteri, 2003) shows huge swarms of males skimming to locate emerging female subimagos with whom they mate on the water surface. This mating system appears to involve a high degree of scramble competition among males, for whom skimming speed is likely to have a strong effect on mating success. Both genders of this species also possess strong flight ability, so they use skimming by choice rather than necessity, probably as a way for males to gain the earliest mating access to emerging females. This is an important observation because it shows how intrasexual scramble competition could have driven improvements in aerodynamic locomotion prior to the evolution of true flight.

Dragonfly Flight: the High End of the Flight Ability Spectrum

Odonates are another group of basal pterygotes that we could examine for clues about the origin of insect wings and flight, but their adult body forms are so highly specialized for powerful flight that they retain little if any evidence instructive for reconstructing flight origins. Dragonflies present few opportunities to examine the transition from leg-based locomotion to wing-based locomotion because they use their legs only for perching (sometimes on water surfaces, including wing-based sailing, Samways, 1994) and predation; other than a weak ability to move along stems, they are completely unable to walk. Another major difference between dragonflies and even the best-flying stoneflies and mayflies is that odonates have much more extensive flight musculature in the thorax (Fig. 12.9). In Libellulidae, it is not uncommon for the flight muscles to comprise 50–60% of total fresh body mass in mature males. Experiments in which dragonflies have been loaded with lead weights have shown that they can lift

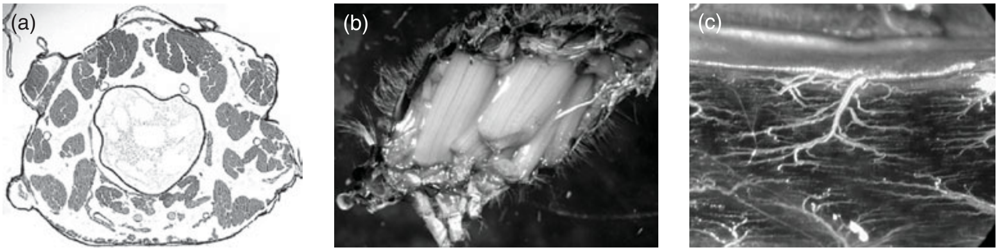


Fig. 12.9. (A) Cross section of the mesothorax of a *Taeniopteryx burksi* stonefly (Plecoptera). Note the sparse flight musculature and large fluid space between muscles. Some moderately sized tracheae are apparent. (B) Sagittal section of the pterothorax of a dragonfly, with flight muscles filling nearly the entire volume and very little hemolymph. (C) Highly developed tracheal system in a dragonfly.

three to four times their unladen body weight (Marden, 1987). They use this reserve flight power in nature to compete for territories, pursue females, and defend ovipositing females from abduction by other males (Marden, 1989).

These features highlight the continuum of flight ability in modern aquatic insects, which spans from meagre flight ability of stoneflies, to intermediate flight ability of mayflies (superior to stoneflies perhaps because non-feeding and short-lived mayfly adults have jettisoned mouth and digestive structures, thereby reducing their payload), and extreme flight ability of dragonflies. Stoneflies appear to be built for minimal aerial requirements, with just enough aerodynamic force output to travel in two dimensions or marginally in three dimensions. At the other end of the spectrum, dragonflies are so specialized for flight performance that they accomplish elaborate aerial manoeuvres such as copulation and abduction of females during oviposition on territories of rival males, and have even evolved mechanisms to regulate (and often downregulate, Marden *et al.*, 2001; Marden and Cobb, 2004) the performance of their flight muscles so as to maintain energy homeostasis. Fossil odonatoid wings from the Palaeozoic are similar to those of modern dragonflies and appear to have been used for aerial predation, but they lack some performance-related structural enhancements present in modern dragonfly wings (Wootton and Kukalová-Peck, 2000). Those authors suggest that dragonfly flight ability increased over time in response to flight improvements of their prey. If correct, the continuum in flight ability among basal aquatic insects that we see today is perhaps less an outcome of chance differences among lineages, but rather a long-standing gradation in which a predatory group has managed to maintain its relative advantage as the community of prey insects has diversified and in many cases improved its ability to evade capture.

Limited Flight Ability as a Challenge for Populations

Ecological ramifications of the ability to move through the environment are numerous and have profound effects on population and metapopulation biology.

For example, theory has shown that a metapopulation can persist in a habitat patch network (i.e. regional scale viability) only when a threshold condition is met that relates landscape features (number, size, and connectivity of habitat patches) to a combination of life history traits, among which dispersal ability is particularly important (Hanski and Ovaskainen, 2000). Ponds occupied by odonates fit the assumptions of metapopulation models, but to date there has been fairly little research examining regional persistence by odonates and how persistence is affected by dispersal (but see McCauley, 2007). Stream insects such as mayflies and stoneflies occupy linear, advective habitats in which there is presumably greater connectivity of habitat patches, at least in the downstream direction. Theoretical analyses of the population biology of downstream drift and either random or directed dispersal are fairly well developed for stream insects (Anholt, 1995; Pachepsky *et al.*, 2005), but how these processes interact with dispersal to affect regional persistence is unknown (but see Speirs and Gurney, 2001).

One interesting comparison that can be made between dragonflies and stoneflies is spatial genetic structure across populations, which should be affected by differences in dispersal ability. Genetic studies of stonefly populations tend to show unusually strong spatial structure (Hughes *et al.*, 1999), with significant differentiation by distance between streams, but usually less so along streams, where connectivity by downstream drift is high. For example, stoneflies in headwaters of streams on the Atlantic slope of the Appalachian mountains show significant genetic differentiation from stoneflies in headwaters of very nearby streams (approximately 250 m) that are part of the Gulf of Mexico drainage basin (Schultheis *et al.*, 2002). Populations of the non-flying (but probably sailing) stonefly *Allocapnia recta* show significant differentiation of alleles in the highly conserved 16s rRNA gene between rivers separated by about 15 km, whereas populations of the fairly strong flying stonefly *Leuctra tenuis* show no differentiation across these sites (Yasick *et al.*, 2007). These results are supported by direct measures of stonefly adult dispersal showing that 90% of the population of even relatively strong-flying genera such as *Leuctra* move less than 50 m (Petersen *et al.*, 1999). In another study, labelling a massive number of larval *Leuctra* stoneflies with a stable isotope resulted in recapture of a small number of marked adults at adjacent streams between 800 m and 1.1 km away from the source population, including a headwater of a different river system (Briers *et al.*, 2004), thus detecting the rare events that affect genetic structure of connected populations.

Comparable studies of odonate spatial genetic structure have revealed low or non-significant genetic differentiation over short distances (Geenen *et al.*, 2000; Wong *et al.*, 2003; de Block *et al.*, 2005; Watts *et al.*, 2007) or significant differentiation between populations of small damselflies (Zygoptera) separated by larger distances (10–100 km; Andrés *et al.*, 2000, 2002). An exception is the finding of significant genetic differentiation and isolation by distance in a small, sedentary, endangered *Coenagrion* damselfly (Watts *et al.*, 2004). There appear to be no such data available for dragonflies (Anisoptera), perhaps because their high dispersal ability virtually assures a finding of no genetic differentiation over even fairly large spatial scales, thereby greatly reducing the motivation to perform such studies. Indeed, a recent study on large and robust *Anax* dragonflies showed that even when carrying 300 mg radio transmitters (one-third of unladen body mass), migrating individuals moved an average of 58 km over a period of less than a week (Wikelski *et al*., 2006).

Conclusions

Aquatic insects present many fascinating and promising avenues for new findings regarding their evolution, development, physiology, behaviour and population biology. Recent discoveries have yielded novel insights regarding the origin of wings and tracheae, the genetic regulation of appendage development, retention of ancestral gas exchange physiology, behaviours relevant to the origin of flight, regulation of muscle power output, how such regulation affects mating success, and how flight ability affects spatial genetic structure among populations. All of these are interrelated and affect the way that aquatic insects interact with their environment. Biology is entering a period of both detailed inquiry and broad integration across levels of organization, and this is beginning to change the way we study and understand even non-model organisms such as aquatic insects, where narrow specialization has been the tradition. Much of what I have written here contradicts long-accepted interpretations of the evolutionary history of insects and how they arrived at their present form. Given the pace of discovery, it seems fully possible that another author 10 years from now will be able to overturn much of what I have concluded and paint yet another new and different picture. That would be an exciting development indicative of a thriving field of inquiry.

Acknowledgements

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13 Evolutionary Drivers and the Ecological Traits of Adult Aquatic Insects

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Abstract

Insects living in freshwaters possess a suite of adaptations in the aquatic larval and terrestrial adult phase. In this review, we suggest that there are three key aspects of the freshwater habitat templet that forge different sets of ecological traits in adults. (i) For most aquatic insects, the evolutionary stability of freshwaters reduces the need for adult dispersal and its associated morphological and physiological adaptations. For herbivorous species, the paucity of freshwater angiosperms favours dietary generalists, further mitigating against the evolution of highly developed dispersal adaptations to locate larval food plants. (ii) For species with obligate predatory juveniles, principally the Odonata and the larger predatory Coleoptera and Hemiptera, the discrete nature of freshwater habitats may generate intraspecific competition for prey resources, leading to density-dependent mortality. This may drive the evolution of advanced adult feeding, dispersal and oviposition strategies to maximize survival and growth of aquatic nymphs. (iii) Discrete water bodies attract a spatially predictable supply of terrestrial animals to drink, favouring the evolution of blood-feeding behaviour in adults of the aquatic Diptera. The high-quality adult diet may allow these dipterans to colonize small, ephemeral habitats and habitats with poor larval resources.

Introduction

In his essay 'Thoughts on aquatic insects', Evelyn Hutchinson argued that insects living in water possess a characteristic suite of species traits that distinguish them from terrestrial insects, including cryptic coloration, respiratory adaptations and a trend to omnivory (Hutchinson, 1981). Differences between the two groups are not confined to aquatic stages, however. Many terrestrial adult aquatic insects, particularly those of the orders Ephemeroptera, Plecoptera, Trichoptera and Diptera (hereafter referred to as the EPTD), typically are inconspicuous, small, short-lived, cryptically coloured, non-feeding (or at least

Aquatic Insects: Challenges to Populations (eds J. Lancaster and R.A. Briers)

non-protein feeding) and with poor powers of flight. Such traits have made them easy to ignore and hard to study. Perhaps unsurprisingly, then, most studies on aquatic insects have focused on the immature, aquatic stages. Only for the Odonata and larger predatory aquatic Coleoptera and Hemiptera (hereafter referred to as the OCH) is the ecology of adults commonly studied in any detail. Adults of this group show striking contrasts to the EPTD in that they are typically large, brightly coloured, with good flight and dispersal abilities, and relatively long adult lives. The Odonata are distinguished from almost all other insects in the remarkable flight speed and manoeuvrability of the adults. The OCH are frequently top predators in aquatic systems, in both their larval and adult stages. In this they are distinguished from most terrestrial insects that are predated by a wide range of vertebrate and invertebrate predators (including non-flying mammals, bats, birds, reptiles, amphibians and spiders), and from the EPTD that have a relatively narrow range of predators in their larval and adult stages. Blood-feeding Diptera (hereafter referred to as the BFD) provide a further contrast in that, although actively feeding as adults, like the OCH group, their larval stages are more like those of the EPTD, in that they are usually non-predatory and often consume poor quality detrital food resources. With a few exceptions, the BFD all have immature stages associated with freshwaters or riparian habitats. Although these three groups (EPTD, OCH, BFD) do not contain all aquatic insects, they comprise the majority of species found commonly in freshwaters.

Two ecological trait axes broadly distinguish between the adults of EPTD, OCH and BFD – flight and dispersal ability, and adult feeding behaviour (Fig. 13.1). The EPTD generally have low to moderate dispersal ability and are characterized by non-feeding or carbohydrate-feeding adults, including the Chironomidae (Diptera) and the larger Limnephilidae and Phryganeidae (Trichoptera), although some stoneflies feed on terrestrial plant- and animal-based protein. The OCH consume animal protein as adults and typically have superior flight and dispersal abilities, although some predatory Hemiptera are flightless. The BFD have moderate to high dispersal ability and females that feed on vertebrate host blood as adults. The two axes of adult flight and dispersal ability, and adult feeding may be interpreted as adaptations to two evolutionary drivers of insect life history: habitat stability and larval food resource availability (Fig. 13.1). Low habitat stability (e.g. ephemeral, fragmented or highly disturbed habitats) may select for strong dispersal and flight by terrestrial adults. For phytophagous insects, most flowering plants present a fragmented and ephemeral resource over evolutionary time. Larval resource limitation (e.g. due to low abundance or quality of food) may also select for compensatory feeding by adults, to ensure sufficient resource intake for flight and dispersal and, for females, oogenesis. The opposite scenario may also operate where high-quality food resources available for mobile adults (e.g. fruit, mobile prey, pollen and nectar) allow aquatic larvae to exploit low-quality diets.

In this review, we speculate that the evolution of adult feeding and dispersal ability in the three groups of adult insects can be attributed to three key aspects of the freshwater habitat templet: (i) the relatively high stability, and low plant diversity and abundance of freshwater habitats may drive the

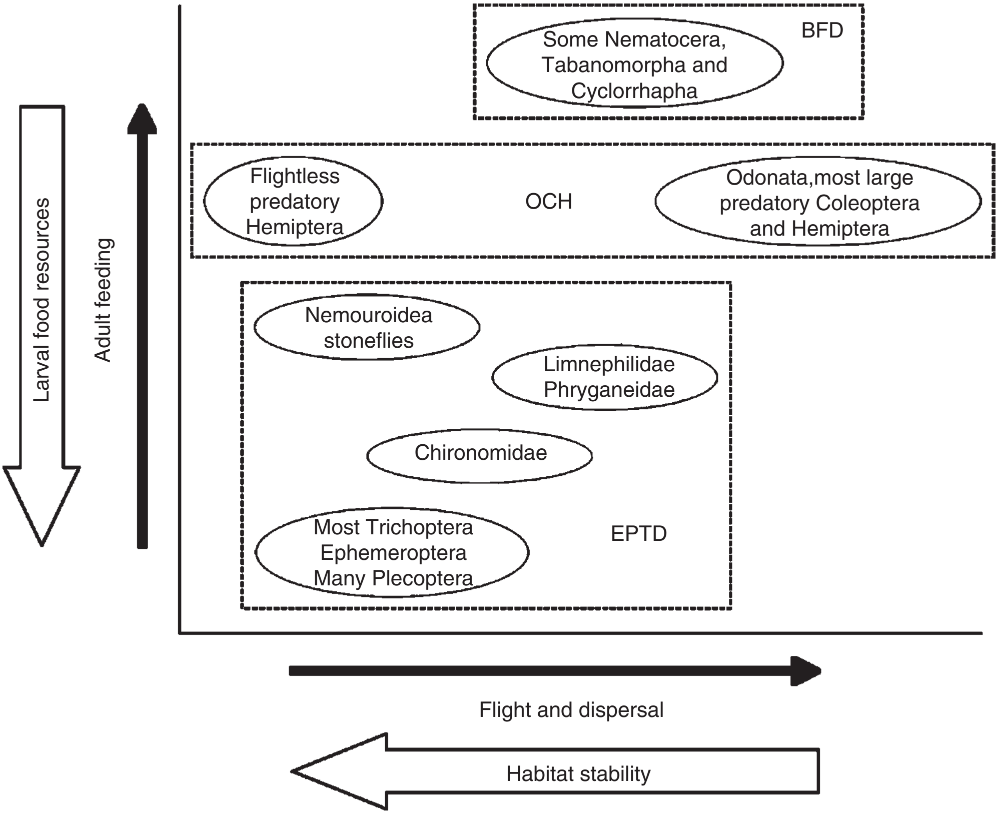

Fig. 13.1. Schematic diagram of the dispersal and feeding adaptations of adult aquatic insects. See text for explanation.

relatively weak dispersal and feeding behaviour of the adult EPTD; (ii) the well-developed feeding and dispersal ability of the adult OCH may be a function of resource limitation among predatory aquatic larvae, leading to density-dependent competition, mortality and cannibalism; (iii) the spatially and temporally predictable supply of terrestrial vertebrate blood hosts in riparian habitats may have been the evolutionary driver of adult feeding behaviour in the BFD.

Adaptations to the Evolutionary Stability, and Low Plant Diversity and Abundance of Freshwater Habitats

The disturbed nature of lotic waters has fostered a belief that overland dispersal by winged adults of lotic insects is a major determinant of populations and assemblages (Bilton *et al.*, 2001). The common assumption of widespread and frequent dispersal by adults of freshwater invertebrates is not supported by available data, however, and numerous studies have now shown that many taxa, particularly lotic species, exhibit only weak dispersal behaviour (Sweeney, 1993; Bohonak and Jenkins, 2003). Ephemeroptera are almost all short-lived as adults and rarely disperse far from water. Following emergence, adult Plecoptera, Trichoptera and Diptera also tend to fly and disperse within the immediate riparian zone along the stream corridor (Jackson and Resh, 1989; Sode and Wiberg-Larsen, 1993; Collier and Smith, 1998; Petersen *et al.,* 1999; Delettre and Morvan, 2000; MacNeale *et al.,* 2005; Winterbourn, 2005).

Habitat stability plays a dominant role in the dispersal ecology of insects (Southwood, 1962, 1977; Roff, 1990; Zera and Denno, 1997; Denno *et al.*, 2002). Although subject to frequent small-scale disturbance, freshwaters are, in general, more stable features of a landscape over geological timescales than terrestrial habitats (Southwood, 1962). For terrestrial insects, plant-based habitats will be subject to high temporal variation as a result of periodic climate shifts and shorter-term changes driven by physical and biological disturbance. Temporal variation of aquatic insect habitats, which are generally not based on particular plant species, will have a less profound impact on insect populations. The dispersal ability of freshwater insects (particularly from lotic habitats, which can be persistent landscape features), should thus be lower than that of most terrestrial insects. Within aquatic insects, lentic species are better dispersers than lotic species (Southwood, 1962; Roff, 1990; Ribera and Vogler, 2000). In a large-scale study of insects caught in light traps in the UK, Crichton (1971) and Crichton *et al.* (1978) reported that, while most caddis families were found only in traps situated near to water, species of Limnephilidae and Phryganaeidae were often found far from water. Both families are typically found in small standing waters (Wissinger *et al.*, 2003).

Adult insect dispersal ability is also positively related to the spatial distribution of larval food resources (Southwood, 1962). For phytophagous insects, species whose larval host plants are rare and patchily distributed tend to have greater flight and dispersal ability than species whose larval host plants are common and evenly distributed (e.g. Scott, 1975). The abundance and diversity of flowering plants is lower in freshwater compared with terrestrial habitats, as a result of low light levels, hydraulic forces and low concentrations of carbon dioxide (Sand-Jensen and Jacobsen, 2002). This may explain why there are so few monophagous specialists among freshwater insects, the most important insect consumers of submerged plants being unspecialized shredder–detritivore–herbivore trichopterans (Berg, 1949; McGaha, 1952). Given the broad detritus/plant diet of many non-predatory insect larvae, there would be little selective advantage for flying adults to locate macrophyte-based oviposition sites, as the added costs of adult dispersal and longevity would likely outweigh any gain in larval nutrition.

The evolutionary stability of freshwaters and the contiguous spatial distribution of food resources for species with non-predatory larvae, together may explain why most adult aquatic insects generally have low flight and dispersal ability relative to terrestrial insects. Adults of the EPTD group exhibit a suite of morphological, physiological and behavioural adaptations across most of their constituent species that may be related to reduced dispersal needs. Within the group there are differences in flight and dispersal (and associated adaptations) that may reflect the evolutionary stability of habitats, principally the difference between the lentic and lotic habitats.

Trade-off between dispersal and fecundity

Advantages of dispersal include avoiding inbreeding, locating to a site with more resources, fewer intra- and interspecific competitors and predators, and escaping unsuitable habitat conditions. Disadvantages include the frequent failure by individuals to locate a suitable new site, predation *en route*, failure to locate a mate and outbreeding depression (Bilton *et al*., 2001). Critically, dispersal and flight necessitate a suite of metabolically costly adaptations in an adult insect, including adaptations to counter predation, desiccation and inclement weather. The resting metabolic rate is also higher in insects with well-developed flight, due in part to the high respiratory burden of large flight muscles (Reinhold, 1999). These costs then reduce the resources that can be allocated to fecundity (Roff, 1977, 1990; Bilton *et al*., 2001). The evolutionary stability and predictability of aquatic habitats, compared with that of terrestrial habitats, may thus be expected to forge ecological traits that favour fecundity over dispersal. In insects with non-protein feeding adults, larval resources determine both adult size and fecundity, as the maximum number of eggs is present at adult emergence. In species with feeding adults, however, egg mass and number are largely determined by resources available to adults. Honěk (1993) found that increasing female body size conferred a greater advantage in terms of fecundity of the first group than of the second group. Thus, the trade-off between fecundity and dispersal ability should be biased towards fecundity in insects with non-feeding adults and towards dispersal in insects with feeding adults. Such a trade-off in the EPTD has been shown by genetic studies. Bunn and Hughes (1997) found that the genetic population structure of some lotic insects was dependent on stochastic recruitment and dispersal events, where recruitment at the reach scale was likely the result of oviposition by only a few highly fecund females, consistent with generally low dispersal between reaches. Masters *et al.* (2007) demonstrated that inter-catchment dispersal of individual adult Ephemeroptera, Trichoptera and Plecoptera can occur on a reasonably frequent basis. Critically, however, it is likely to be limited in terms of number of individuals and probably accidental and non-directional, being driven more by wind than innate adult behaviour.

Recent research has also shown that the trade-off between dispersal and fecundity differs between lentic and lotic species in the Trichoptera. Stevens *et al.* (2000) showed that a lentic limnephilid caddis, *Glyphotaelius pellucidus*, when starved of larval food, retained thoracic body mass and therefore the ability to disperse, but had reduced fecundity. A lotic species, *Odontocerum albicorne*, however, when depleted of larval food reserves, retained abdominal mass and thus fecundity, but reduced thoracic body mass (i.e. dispersal ability).

Body morphology

The energetic demands of flight and dispersal require that strongly flying adult insects contain sufficient energy reserves for flight and longevity and have bodies that are structurally robust and able to withstand desiccation. Aquatic insect adults have strikingly different body mass–length relationships compared with terrestrial adult insects, terrestrial insects are generally heavier, wider and contain less water than aquatic insects (Sabo *et al.*, 2002). This again is consistent with reduced dispersal behaviour in aquatic insects compared with terrestrial insects. The relatively weak sclerotization and poor adaptation to desiccation shown by many aquatic insects also act, along with weak flight ability, to constrain them to remaining within wind- and heat-protected humid riparian zones (Jackson, 1988; Collier and Smith, 2000). High wind speed can influence the successful flight and reproduction of adult stoneflies (Briers *et al.,* 2004) and mayflies (Wright *et al.*, 1981; Savolainen, 1978). Crepuscular emergence and flight may be an adaptation to the cooler, calmer, more humid conditions prevailing at dusk (Jackson, 1988).

Feeding, emergence and longevity

Adults of the EPTD group exhibit a range of feeding behaviours, from the non-feeding Ephemeroptera to the protein-feeding nemourid stoneflies. For most species, however, adult feeding is poorly developed and largely restricted to the intake of sugar-rich fluids. Most EPTD species thus gain sufficient nutrition as larvae for successful reproduction and adults of many species of Trichoptera and Ephemeroptera contain fully formed eggs at emergence. Feeding as an adult prolongs life, provides energy (carbohydrate) for flight and dispersal, and provides protein for oogenesis (Wheeler, 1996). We should expect, therefore, to find adult feeding in the EPTD to be prominent in those species that: (i) exhibit asynchronous emergence (thus needing to prolong life while waiting for suitable mates to emerge); (ii) disperse long distances; or (iii) have protein-poor larval diets. Ephemeroptera do not feed as adults, rarely disperse far from emergence sites and many are well known for synchronous population emergence, generally interpreted as a predator-swamping strategy (Sweeney and Vannote, 1982). Among the Plecoptera, many species within the superfamily Nemouroidea gain considerable weight as adults by feeding on terrestrial pollen, fungi and lichens (Zwick, 1990; Tierno de Figueroa and Sánchez-Ortega, 2000; Derka *et al.*, 2004). These adults also typically have extended asynchronous adult emergence periods. Their nymphal diet, furthermore, is predominantly poor-quality detritus, so adult feeding may also compensate for poor larval nutrition. In families with predatory late-instar nymphs, such as the Perlidae, adult feeding is less evident, possibly due to the intake of high-quality animal food just before adult emergence (Malmqvist and Sjöström, 1980). In a study of Trichoptera in the UK, Crichton (1957) found that adult fluid feeding was recorded most frequently in the widely-dispersing Limnephilidae and Phryganeidae. These two families also have the most highly developed mouthparts and some species are reported to feed on flowers at night (Crichton, 1957).

Oviposition behaviour

Oviposition locations can be broadly classed as places where adults are safe from predation or where larvae are likely to find adequate resources for development.

Oviposition site quality affects hatching success, larval performance, recruitment and consequent parental fitness and, thus, adults should be under strong selective pressure to discriminate and choose oviposition sites on the basis of expected larval performance (Resetarits, 1996). Behaviour to optimize larval success may not be adaptive, however, if the metabolic costs of sensory perception of oviposition sites are high or if spatially selective oviposition incurs high adult mortality (Resetarits, 1996). In terrestrial insects, the temporal and spatial patchiness of larval food sources should select for high discrimination ability between potential oviposition sites. In aquatic insects of the EPTD, however, the relatively low patchiness of larval food resources, coupled with high larval dispersal in water (particularly running waters), may select for non-specific oviposition behaviour (e.g. egg broadcasting by stoneflies and mayflies; egg-rafting by chironomids) that minimizes adult or egg mortality rather than maximizes larval feeding and survival (Reich and Downes, 2003). Species-specific differences in oviposition behaviour in lotic mayflies may be related to differences in pre-oviposition mortality from aerial and aquatic predators (Encalada and Peckarsky, 2007). The aggregative oviposition common to some aquatic insects (e.g. Lancaster *et al*., 2003) may be an adaptation to reduce the post-fertilization flight, dispersal and predation risk of mated females (Harrison and Hildrew, 1998).

The metabolic costs of locating oviposition sites incurred in many terrestrial insects is likely lower in aquatic insects, which need only locate water at large spatial scales (exceptions being species that oviposit in very specialized or widely dispersed habitats, such as phytotelmata). Many aquatic insects select oviposition sites, at a coarse scale, through polarotaxis (Schwind, 1991), although visual and tactile cues may be used to decide where to lay eggs at finer scales (Reich and Downes, 2003). Oviposition site detection through polarotaxis is possibly less metabolically expensive than more discriminating vision or olfaction adopted by terrestrial insects, but the costs of such a strategy can be *en masse* oviposition in inappropriate sites, such as car roofs (Kriska *et al.,* 1998).

Mating swarms

Adult mating swarms are common in the EPTD, but rare in terrestrial insects. For example, swarming is known from at least nine families of Trichoptera, but only two of the closely related Lepidoptera (Sullivan, 1981). This may be due to two main reasons. First, adult insects emerging synchronously (a feature of many of the EPTD) from discreet freshwater habitats will be spatially and temporally aggregated. This allows males to form swarms, and females to locate them, without the need for metabolically expensive longevity or dispersal ability. If the males swarm adjacent to oviposition sites, then this will further reduce the flight and dispersal cost to females of post-fertilization dispersal. Most aquatic insect mating swarms are associated with a visual marker (Sullivan, 1981), which may similarly function to reduce the costs of mate finding. Second, the patchiness of larval resources and resulting competition for oviposition sites is probably lower for aquatic than for terrestrial insects, as larval resources are rarely based on individual plant species. Competition for oviposition sites in terrestrial insects occurs across a broad taxonomic range, suggesting that such competition may be of general importance (Jaenicke, 1990). Mating swarms in terrestrial insects would result in a pronounced spatial and temporal aggregation of fertilized females, so increasing competition for oviposition sites. The reduced costs of mate finding would then have to be balanced against the increased costs of higher density-dependent mortality in larvae and higher dispersal mortality of post-fertilization females. The fluid-mediated dispersal of some aquatic larvae away from oviposition sites might further weaken oviposition site specificity in some lotic insects. Little information exists about competition for oviposition sites in aquatic insects (Resetarits, 1996), possibly because of its rare or sporadic occurrence, or because it is rarely studied.

Interestingly, stoneflies do not swarm. Instead, males of almost all northern hemisphere stoneflies attract mates by drumming (Stewart, 1994; Zwick, 2000) although, curiously, southern hemisphere families do not (Zwick, 2000; Winterbourn, 2005). A possible explanation may be that an extended and asynchronous emergence period may mitigate against swarming. If adult emergence is temporally unpredictable, neither sex would gain a selective advantage from swarming, with its flight-associated costs, given a low density of potential mates at any one time. Acoustic signalling may be a more cost-effective way of attracting mates from a limited pool, particularly given the tendency of stoneflies to remain near the natal stream for most of their adult lives. Alternatively, the weak flight capability of stoneflies may prevent the adaptation of swarming as a mating strategy. As swarming is so common in other orders (and thus clearly under strong positive selection pressure), it seems likely that stronger flight ability could have evolved in the several hundred million years that stoneflies have existed.

Antipredator adaptations

The temporally aggregated emergence of aquatic insects from discreet water bodies offers terrestrial predators a spatially and temporally predictable, and abundant food source, compared with terrestrial food (Gray, 1989; Whitaker *et al.,* 2000). Adult aquatic insects can suffer high predation in riparian habitats from spiders (Kato *et al.*, 2003; Briers *et al.,* 2005), ground beetles (Paetzold and Tockner, 2005), lizards (Sabo and Power, 2002), birds (Murakami and Nakano, 2002) and especially bats (Racey, 1998; Fukui *et al.,* 2006). Resident riparian predators, although dependent on aquatic food for at least part of the year, will be subsidized by non-aquatic insect prey from the riparian or adjacent habitat at other times. Temporary residents, such as migratory insectivorous birds, will be subsidized by prey far from the riparian zone. Terrestrial predator pressure on aquatic insect adults can, in this way, be heavily subsidized by non-aquatic prey and, as a result, be proportionately much higher than aquatic predator pressure on immature stages, which are not subsidized to the same extent by prey from other habitats. In the Breitenbach stream in Germany, Werneke and Zwick (1992) estimated the mortality of *Baetis* mayflies between emergence and oviposition to be 92–99%, at least as high, or higher, than larval mortality. Similarly, Enders and Wagner (1996) estimated the mortality of females of the limnephilid caddis *Apatania fimbriana* during the adult phase between emergence and oviposition to be approximately 80%, compared with 11% for larvae. Despite this pressure, aquatic insects of the EPTD differ from terrestrial insects in their lack of antipredator adaptations (Witz, 1990). Many species of Lepidoptera have well developed antipredator adaptations including plant-derived chemical defences, cryptic coloration, mimicry, flash warning coloration, acoustic detection and escape. Their sister order, the Trichoptera, possess few of these adaptations, although some Phryganeidae are suggested to have aposematic coloration (Wiggins, 1998) and some caddis can release an unpleasant odour to deter predators (Fryer, 1991).

Tympanate hearing has evolved in at least six different terrestrial insect orders (Orthoptera, Lepidoptera, Neuroptera, Hemiptera, Homoptera and Dictyoptera), almost certainly as a defence mechanism against predation (Hoy *et al.*, 1989; Yager, 1999). Some moths also emit ultrasonic clicks in response to bat echolocation calls, which may serve as acoustic aposematic signals, or startle or confuse the bat (Rydell *et al.,* 1996). The EPTD, however, are not known to possess any such auditory adaptations, despite many species being crepuscular or nocturnal-flying and heavily predated upon by bats. Antipredator acoustic ability must, presumably, incur a metabolic cost to the insect (Witz, 1990) and secondary loss of the auditory system is closely correlated with the secondary loss of flight (wing reduction or absence) in species that use hearing to evade bats (Yager, 1999). By living in environments where the need for flight and dispersal is reduced, adult aquatic insects will reduce their exposure to aerial predators, thereby minimizing the need for metabolically expensive antipredation adaptations. Antipredation measures adopted by aquatic insects generally take the form of predator avoidance and include crepuscular emergence (avoiding day-flying birds and night-flying bats), dispersal of emerging insects away from the heavily predated riparian zone, mass emergence, swarming under tree canopies to minimize aerial predation and oviposition near to swarming sites. The minimization of flight and antipredator costs may thus tend to increase the energy available for reproduction and may be fundamental to the evolution of aquatic insects.

Adaptations to Resource Limitation Among Predatory Aquatic Larvae, Leading to Density Dependence and Cannibalism

Odonata and the larger predatory aquatic Coeloptera and Hemiptera present radically different ecologies compared with the EPTD, principally in body size, flight ability, coloration and adult predatory behaviour. The Ephemeroptera and Odonata are ancient pterygote orders and both evolved in freshwater habitats at approximately the same time (Wootton and Kukalová-Peck, 2000). Within pterygote insects, the two orders represent two extremes of flight and dispersal ability. The two adult ecologies may be driven by different evolutionary pressures operating within the same habitat. Critically, the OCH are obligate predators in both immature and adult stages, and are frequently top predators.

Juveniles of top predators potentially face limiting resources as they grow, as the density of prey biomass declines relative to their own. Intraspecific competition for food among top predators can lead to population control by cannibalism (Polis, 1981). This will be particularly true for spatially discrete systems, such as many freshwater habitats (Eubanks and Denno, 1999; Alimov, 2002; Bohonak and Jenkins, 2003). Intraspecific competition leading to cannibalism and density-dependent population regulation occurs in larvae of many predatory aquatic insects, particularly the Odonata (Corbet, 1957; Van Buskirk, 1989, 1992; Anholt, 1990; Wissinger and McGrady, 1993; Johansson, 1993; Hopper *et al.*, 1996; De Block and Stoks, 2004) and larger aquatic Hemiptera (Fox, 1975; Orr *et al.,* 1990; Klingenberg and Spence, 1996). Such resource-driven, density dependence among juveniles of large aquatic insect predators may lead to selective pressure on adults to oviposit in habitats where competition from other individuals is reduced. This may be achieved in several ways: (i) selective oviposition in small temporary habitats, which are unlikely to have been colonized by many potential competitors; (ii) territorial defence of ovipostion sites; and (iii) widespread dispersal of adults and oviposition in multiple sites to reduce the risk of intra-cohort cannibalism of larvae, and to increase the likelihood of ovipositing in a site with few competitors. Protein feeding by adults is advantageous under these circumstances, enabling species to compensate for limiting larval resources and to extend adult life and dispersal capability. Adults of the predatory OCH are generally large, long-lived, possess good flight and dispersal ability, are themselves active predators and may possess well-developed, metabolically expensive anti-predator traits.

Large size is advantageous for catching prey, but will also contribute to the ability of predatory aquatic insects to disperse widely. Superior dispersal ability would be advantageous for species with large larvae, which are likely to experience greater resource limitation, density-dependent mortality and cannibalism. Large odonates generally disperse further than small ones (Corbet, 1980; Angelibert and Giani, 2003). Mass, large-scale migrations are also seen in large Anisoptera (Russell *et al.,* 1998), possibly in response to sudden, high densities of adults emerging from the water and leading to competition among adults for oviposition and feeding sites. Large predatory dytiscid beetles also disperse more widely than smaller omnivorous and phytophagous aquatic beetles, and oviposit in small temporary pools (despite poorly developed food webs and perhaps low prey density), possibly to avoid intraspecific competition (Fairchilds *et al.*, 2000).

Flight, feeding and long adult life will bring adults of large predatory aquatic insects into more contact with aerial predators (and aquatic predators, in the case of Coleoptera and Hemiptera), thereby driving the evolution of antipredator adaptations. The large size and extreme manoeuvrability of dragonflies renders them almost invulnerable to predation from birds (Corbet, 1957). Although there has been little research on the function of colour in odonates as antipredation aposematic coloration, compared with the wealth of information about intra-specific sexual signalling, the striking colour patterns (particularly species with black and yellow coloration) may serve a secondary function as warning coloration. Predatory aquatic Hemiptera, such as the Veliidae and Notonectidae, also possess contrasting colour patterns, which may function as aposematism to visual predators such as birds. Many dytisicid, gyrinid and elmid beetles secrete distasteful chemicals to deter fish predators (Newhart and Mumma, 1979a,b;

White, 1989). Veliidae are distasteful to brown trout and frequently spat out when captured (Brönmark *et al.*, 1984). Arntz (1972) found that both *Notonecta obliqua* and *Nepa cinerea* reacted to airborne sound within the range of 700–10,000 Hz; *Nepa* displayed an intimidatory posture when detecting such sound, suggesting an antipredator adaptation. In contrast, large Gerridae avoid bats by simply moving away from exposed open surfaces of the water at dusk, towards marginal areas of the habitat where bats find it hard to forage (Svensson *et al.,* 2002). This is probably a metabolically inexpensive antipredator response, although the cost of not feeding during dusk must be considerable.

Although the OCH are large and conspicuous, they are not the only aquatic insect predators. Many families of the Plecoptera and Trichoptera, in particular, are predatory as larvae. Why do they not share the characteristic adult traits of the OCH? The mouthparts and feeding behaviour of the immature stages of the OCH are all adapted to predation, effectively making them obligate predators. In predatory EPTD, however, there may be less dietary specialization and recent studies have shown that omnivory is more widespread in this group than previously thought (Lancaster *et al.*, 2005). Even the larger perlid and perlodid stoneflies consume algae and plant detritus as larvae (Fenoglio and Bo, 2004; Lancaster *et al.*, 2005; Fenoglio *et al.*, 2007). Such omnivory in otherwise predatory insects has been hypothesized to compensate for low prey abundance (Eubanks and Denno, 1999; Lancaster *et al.*, 2005) and may reduce intraspecific competition among larvae. Importantly, predatory EPTD are probably less cannibalistic than the OCH and rarely top predators. The selective pressure on adults to disperse widely in order to avoid larval aggregation and to feed on animal protein to compensate for limiting larval resources, would thus be lower in the EPTD predator/omnivores and thus explain the lack of highly developed adult dispersal and feeding adaptations seen in the OCH.

Adaptations to the Spatially and Temporally Predictable Supply of Vertebrate Blood

Most female adult dipterans must take in protein to produce eggs (Wheeler, 1996). Among freshwater Diptera, a common adult feeding strategy is to consume vertebrate blood, which can provide a high-quality meal for adults seeking to maximize fecundity. Blood-feeding has evolved at least five times in the Diptera (Yuval, 2006). Within the Nematocera, four families of the Culicimorpha and one family of the Psychodomorpha have blood-feeding species. Two families of Tabanomorpha (sub-order Brachycera) and five families in the Cyclorrhapha also have blood-feeding adults (Yuval, 2006). With the exception of the Cyclorrhapha (stable flies, tsetse flies and parasitic flies of vertebrates), these blood-feeding Diptera have larvae that are either aquatic or live in damp soil (Tabanomorpha).

Why should blood feeding be so closely associated with freshwaters? The evolutionary pathway suggested for blood feeding in aquatic Diptera involves pre-adapted mouthparts becoming specialized for piercing plants or prey, and then secondarily becoming adapted to pierce vertebrate hosts (Yuval, 2006).

Although evolving the ability to consume blood rather than plant sap or fruit juice would be beneficial in terms of food quality, locating the blood food source presents a high cost. Large vertebrate consumers are less abundant and more spatially and temporally unpredictable than plants. Thus, blood feeding requires adaptations to detect and locate vertebrate hosts. However, nearly all vertebrates drink water and their spatial and temporal aggregation near water represents an energy-rich food source for an adult blood-feeding insect, with relatively low associated detection and location costs.

The adoption of blood feeding as an adult may have led to further larval and adult adaptations. The high quality of blood as an adult food might allow larvae to feed on low-quality food – enough to grow, emerge and pupate, but not to produce eggs. Thus, in female mosquitoes that emerge undernourished, at least one adult meal is necessary to bring the body fat and ovaries to competency (Wheeler, 1996). Blood feeding as adults therefore allows larval diets to include poor quality but abundant food (such as small organic particles), with low resource competition from other consumers. For example, larval Simuliidae are filter feeders on very small particles ($<5\ \mu$m) in flowing waters and their adults are blood feeders (black flies). In general, the smaller the organic particle, the lower the food quality in terms of C:N ratio (Allan, 1995). Larval food for Simuliidae is thus likely to be low in protein, which must be compensated for as adults through protein feeding. The very high densities of larval Simuliidae in some systems are testament to the adaptive advantage of adult blood feeding.

Blood feeding by Simuliidae also transfers energy between aquatic and terrestrial zones, albeit in the opposite direction to many spatial subsidies, but may indirectly increase the availability of particulate food within stream channels. Larval simuliids filter fine particles out of the water and in doing so retain and transform very fine organic matter into animal matter and larger ($>50\ \mu$m) faecal pellets, that would otherwise be lost downstream. Terrestrial vertebrate blood may thus contribute considerably to the organic matter budget and ecosystem functioning of freshwaters, by facilitating the consumption and incorporation of otherwise inedible organic particles by larval dipterans.

Energy-rich blood feeding by adults may allow females to invest more heavily in metabolically costly adaptations to locate and assay small and patchy oviposition sites. These adaptations would allow females to oviposit in habitats rich in larval food and to avoid competitor and predator pressure. Many studies have shown that female mosquitoes, unlike almost all other aquatic insect adults, use chemosensory information to detect aquatic predators in potential oviposition sites (Petranka and Fakhoury, 1991; Kats and Dill, 1998; Stav *et al.*, 1999; Angelon and Petranka, 2002; Blaustein *et al.*, 2004). They can also chemically detect competitors (Edgerly *et al.,* 1998), larval food in the form of filamentous algae (Bond *et al.*, 2005) and nutrient-enriched water (Hoekman *et al.*, 2007).

Conclusions

The ecological traits of the three groups of adult aquatic insects described here, although very different from each other, can all be argued to be adaptations to an aquatic habitat (Fig. 13.1). For freshwater insects, the aquatic habitat presents an evolutionary stable and predictable environment. The poor dispersal ability of many aquatic insects (adult EPTD) may be, at least in part, attributed to this stability. Certainly, for a non-predatory adult aquatic insect living in all but the most ephemeral systems, there may be little selective advantage in dispersing away from the site of adult emergence, given the evident suitability of the aquatic habitat for larvae and the risk of predation in the terrestrial environment. The low diversity and abundance of flowering plants in freshwaters does not favour the adoption of specialized phytophagy, which is common in terrestrial insects. Unlike terrestrial insects, therefore, herbivorous aquatic insects rarely need to disperse away from emergence sites to locate new sources of larval food, as their larvae will be able to feed on the range of plants, algae or detritus dependably present in the habitat occupied by previous generations. The suite of adaptations shown by the adults of the EPTD may be a function of the lack of directional dispersal between habitats and may reflect a reduction in the metabolic cost of dispersing and avoiding predators, in favour of allocating resources to fecundity.

The very different adult feeding and flight adaptations of the Odonata and larger predatory Coleoptera and Hemiptera (OCH), we argue, may be a response to density-dependent food limitation and mortality of immature aquatic stages within spatially constrained habitats. Protein feeding as adults allows these species to subsidize the resource-limited habitat of predatory larvae, which are often top predators. Such predatory feeding necessitates relatively long-lived adults with good flight and dispersal ability. Cannibalism among larvae will also promote adult dispersal to locate oviposition sites with low larval density. For aquatic blood-feeding Diptera, blood of vertebrates coming to drink at a water body represents a predictable and nutritious food source for adults. This adult food may allow species to adopt larval feeding habits where food supply is restricted in quantity or quality, but also where competition for food is likely to be weak. The superior quality of adult food also may allow adult Diptera to adopt a metabolically costly, highly discriminatory oviposition behaviour, in contrast to other aquatic insects.

The scenarios we have presented to account for differences among the adult stages of aquatic insects are by no means exhaustive and there may be equally plausible alternatives. Some aquatic insects also do not ‘fit’ neatly into the three groups. Notably, smaller aquatic Coleoptera and Hemiptera may be intermediate between EPTD and OCH. Many of these species feed on plant material and animal prey as both immature and adult stages, have weaker dispersal and flight ability, and less well-developed antipredator adaptations compared with the larger OCH.

Relating how the ecology of larval aquatic insect dictates, or is dictated by, adult ecology is under-studied, necessitating a doubling of methods and expertise. This area, however, promises to reveal much about the evolutionary drivers of adult ecology. Particularly fruitful would be research into links between larval and adult ecologies within groups such as the Odonata, where both larvae and adults are well studied and tractable to such dual investigations, or groups such as the Trichoptera, which exhibit a range of feeding modes as aquatic immature stages.

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14

Population Genetic Structure in Stream Insects: What Have We Learned?

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Abstract

This chapter synthesizes data from 41 studies on 32 species of stream insects in an attempt to answer three questions: First, what is the major dispersal mechanism in aquatic insects, i.e. stream drift or adult flight? If it is stream drift, then genetic variation would be expected to fit the Stream Hierarchy Model of Meffe and Vrijenhoek (1988). If it is adult flight, populations would be expected to be panmictic at small scales, i.e. among populations in neighbouring catchments. Most stream insects with an adult flight stage do not fit the Stream Hierarchy Model, suggesting that adult flight is the major mechanism of dispersal. Second, at what scale are populations of stream insects structured? Across all studies, there was a significant positive relationship between F_{ST} and geographic distance for studies using mitochondrial DNA. The isolation-by-distance relationship for allozyme studies was significant only when studies with high numbers of Hardy Weinberg Equilibrium (HWE) deviations were excluded. Third, what can recent analysis of DNA sequence data contribute to our understanding of historical processes affecting stream insects? Several recent phylogeographic studies using mitochondrial DNA sequence data provide evidence of population and range expansions and contractions, along with past fragmentation, all estimated to have occurred during the Pleistocene.

Introduction

Understanding the patterns and mechanisms of dispersal and connectivity among populations is critical for predicting the long-term viability of species and their ability to recover from natural and anthropogenic disturbances. For example, sites containing populations that are isolated from one another, whether due to limited dispersal ability or to the presence of distinct geographical barriers, are much less likely to be recolonized naturally following an extinction event. Alternatively, where populations are connected by widespread dispersal, natural recolonization is a likely outcome (Hughes, 2007).

(eds J. Lancaster and R.A. Briers)

Evaluating mechanisms and patterns of dispersal in aquatic insects is extremely difficult by direct means such as mark–recapture, because individuals moult periodically during their life cycle, dispersal is often a rare event making detection unlikely and also very large numbers of individuals need to be marked in order to recapture even a small proportion away from the source population (Bohonak, 1999; Feral, 2002; Bohonak and Jenkins, 2003). For these reasons, many studies have attempted to address dispersal questions using indirect methods, such as genetic markers.

The rationale for using genetic markers for estimating dispersal is that when populations are isolated and dispersal among them is limited, allele frequencies will diverge from one another as a result of genetic drift, natural selection or a combination of both (Slatkin, 1985). In contrast, when populations are connected by high levels of dispersal, gene flow will tend to homogenize gene frequencies, leading to negligible genetic differentiation. Thus, by measuring allele frequencies and genetic divergence among populations, it is possible to infer relative levels of dispersal (Slatkin, 1985). Since the late 1980s, population genetic techniques have been used to understand the mechanisms and patterns of dispersal in a range of animal and plant species. Early studies used allozymes (e.g. Allendorf and Phelps, 1981), while more recently mitochondrial sequence data (e.g. Pauls *et al*., 2006), microsatellites (e.g. Gibbs *et al*., 1998) and amplified fragment length polymorphisms (e.g. Miller *et al*., 2002) have largely replaced allozymes as the markers of choice.

Most stream insect species have a relatively long larval life spent in the stream, accompanied by a short stage as a winged adult. Duration of the adult stage can range from a few hours to a few weeks depending on the species (Peters and Campbell, 1991; Bilton *et al*., 2001). The relative importance of these two stages in the dispersal ability of a species can be assessed by applying the Stream Hierarchy Model (SHM) developed by Meffe and Vrijenhoek (1988). Meffe and Vrijenhoek (1988) pointed out that for organisms restricted to movement within a stream (in their case freshwater fish), populations are likely to be connected in a hierarchical fashion, reflecting the dendritic architecture of streams. Dispersal will be more likely between populations within the same stream than between streams or between subcatchments. They therefore proposed that genetic variation should also be organized according to the same hierarchy, such that populations in the same stream should be more similar genetically to each other than to populations in different streams within a subcatchment, and that populations from different subcatchments should be more different again. If larval dispersal, via drift and/or swimming and crawling, is the major dispersal mechanism, then the genetic structure of stream insect populations should be expected to fit the predictions of the SHM. On the other hand, if adult flight is the major dispersal mechanism, stream structure will be less important and populations are likely to be panmictic at small spatial scales, regardless of catchment boundaries. Evidence from studies that have addressed this question will be examined in an attempt to develop general conclusions about the relative importance of larval versus adult dispersal.

In addition to answering the question concerning the major dispersal mechanism in stream insects, the other major question is ‘at what scale are populations of stream insects structured?’. Where gene flow is limited to distances smaller than the natural range of a species, we would expect a positive relationship between genetic differentiation and geographic distance (Wright, 1951). Many studies have attempted to estimate the extent of dispersal among populations of stream insects. These studies have ranged enormously in geographic scale, from 6 km to greater than 2000 km. This chapter will examine the results of these studies and attempt a broad generalization as to the distance at which gene flow appears to be restricted among populations.

More recent empirical studies have used DNA sequence data to attempt to unravel historical from contemporary effects of gene flow on stream insect genetic structure. These studies will also be reviewed to determine the relative importance of historical processes on stream insect population structure. The aims of this review are:

1. To review evidence for a fit to the predictions of the stream hierarchy model in aquatic insects.
2. To attempt to show the geographic scale at which most stream insect populations are structured.
3. To examine evidence for the importance of historical effects on genetic structure of stream insects.

Adult Flight versus Larval Drift

Early studies of aquatic invertebrates in south-east Queensland, Australia, used allozymes to test predictions of the stream hierarchy model in a shrimp (*Paratya australiensis*) (Hughes and Mather, 1996), a mayfly (*Bungona narilla*) (Schmidt *et al.*, 1995), a caddisfly (*Tasiagma ciliata*) (Hughes *et al.*, 1998) and a winged waterstrider (*Rheumatometra* sp.) (Bunn and Hughes, 1997). While the data for the shrimp fitted predictions of the SHM perfectly, none of the insect species conformed. All three species showed a pattern that was the reverse of predictions of the SHM, with the largest genetic differentiation among reaches within a stream and the smallest differentiation between catchments.

Since the mid-1990s, many other studies have also tested the fit to the SHM, although some did not explicitly mention the model. They did, however, assess genetic variation at two scales, for example, among sites within a catchment (F_{SC}) and between catchments (F_{CT}). Of 23 studies listed in Table 14.1, the majority (15) did not support the SHM model, suggesting that adult flight, rather than larval dispersal, was the major dispersal mechanism in most species. Only eight showed any evidence for a fit to the SHM, i.e. recorded significant F_{CT} values (differentiation at the highest level of the hierarchy) that were greater than F_{SC} values (differentiation at a lower level). Of these eight studies, two were based on mitochondrial DNA and allozyme data on the same species, a net-winged midge (*Elporia barnardi*) (Wishart and Hughes, 2001, 2003). *Elporia barnardi* has extremely flimsy wings and is considered a poor flyer, so adult dispersal almost certainly is unimportant in this species. The stonefly (*Yoraperla brevis*) from the Rocky Mountains in Montana (Hughes *et al.*, 1999) also appeared to fit the SHM. Streams in which this species occurs flow through

Table 14.1. Studies of population genetic structure of stream insects where a hierarchical analysis was performed. Studies are grouped by orders. F_{CT} shows the value for the highest level of the hierarchy, F_{SC} shows value for the next highest level. 'Level tested' is the highest level used in the analysis.

Order	Location	Marker	F_{CT}	F_{SC}	Level tested	Support for SHM	Reference
Ephemeroptera							
Baetis bicaudatus	Rocky Mts, USA	allozymes	0.000	0.044*	stream	no	Hughes *et al.*, 2003b
Baetis bicaudatus	Rocky Mts, USA	mt COI	0.121*	0.082*	stream	yes	Hughes *et al.*, 2003b
Bungona narilla	Sub-trop. Australia	allozymes	0.006	0.073*	catchment	no	Hughes *et al.*, 2000
Bungona narilla	Sub-trop. Australia (wet)	mt COI	0.057*	0.021	stream	yes	Hughes *et al.*, 2003a
Bungona narilla	Sub-trop. Australia (dry)	mt COI	0.023	0.028*	stream	no	Hughes *et al.*, 2003a
Baetis alpinus	Swiss Alps	allozymes	0.08*	0.02*	catchment	yes	Monaghan *et al.*, 2001
Rhythrogena layolaea	Swiss Alps	allozymes	0.02*	0.05*	catchment	no	Monaghan *et al.*, 2002
Allogamus auricollis	Swiss Alps	allozymes	0.045*	0.01*	catchment	yes	Monaghan *et al.*, 2002
Trichoptera							
Cheumatopsyche sp.	Temperate Australia	mt COI	0.013	0.009	catchment	no	Baker *et al.*, 2003
Tasiagma ciliata	Subtropical Australia	allozymes	0.004	0.070*	catchment	no	Hughes *et al.*, 1998
Tasimia palpata	Subtropical Australia	mt COI	0.001	0.036*	catchment	no	Schultheis and Hughes, 2005
Tasimia palpata	Temperate Australia	mt COI	0.003	0.000	stream	no	Schultheis *et al.*, 2002
Plectrocnemia conspersa	England	allozymes	0.000	–0.016	catchment	no	Wilcock *et al.*, 2001
Helicopsyche mexicana	Arizona	AFLPs	0.069*	0.042*	catchment	yes	Miller *et al.*, 2002
Gumaga griseola	Arizona	AFLPs	0.008	0.025*	catchment	no	Miller *et al.*, 2002
Hemiptera							
Rheumatometra sp.	Sub-trop. Australia	allozymes	0.002	0.060*	catchment	no	Bunn and Hughes, 1997
Ambrysus thermarum	Arizona	AFLPs	–0.001	0.004	catchment	no	Miller *et al.*, 2002

(*Continued*)

Table 14.1. *continued*

Order	Location	Marker	F_{CT}	F_{SC}	Level tested	Support for SHM	Reference
Diptera							
Prosimulium neomacropyga	Rocky Mts, USA	mt COI	0.014	0.350*	catchment	no	Finn *et al*., 2006
Elporia barnardi	Table Mountain, S. Africa	allozymes	0.230*	0.043*	stream	yes	Wishart and Hughes, 2001
Elporia barnardi	Table Mountain, S. Africa	mt COI	0.860*	0.150	stream	yes	Wishart and Hughes, 2003
Coleoptera							
Psephenus montaus	Arizona	AFLPs	0.013	0.047*	catchment	no	Miller *et al*., 2002
Plecoptera							
Yoraperla brevis	Rocky Mts, USA	allozymes	0.156*	0.002	stream	yes	Hughes *et al*., 1999
Peltoperla tarteri	Appalachian Mts, USA	mt control region	0.070	0.140*	catchment	no	Schultheis *et al*., 2002

AFLPs, amplified fragment length polymorphisms.

*$P < 0.05$

deeply incised canyons into the Bitteroot River. It seems likely that, even though adults may be capable of flight, the extreme montane terrain may restrict flight between streams. Of the other five studies, the possibility of cryptic species in the sample cannot be ruled out in two (Monaghan *et al*., 2001, 2002), and the pattern was not consistent between markers (Hughes *et al*., 2003b) or sampling times (Hughes *et al*., 2003a) in two others. Thus, overwhelmingly, flight appears to be the major dispersal mechanism in stream insects, except in cases where adult flight capability is very poor or where terrain is extremely mountainous.

An unexpected pattern was observed in several studies where the pattern of genetic differentiation did not fit the predictions of the SHM. In these studies, the expected hierarchical pattern was reversed so that significant genetic differentiation was observed at the smallest spatial scale (among reaches within a stream), while variation was not significantly partitioned among catchments (e.g. Schmidt *et al*., 1995; Hughes *et al*., 1998). If adult flight is widespread causing homogenization of allele frequencies among sites, regardless of whether they are in the same catchment, non-significant genetic differentiation would be expected at all levels of the hierarchy, especially at the lowest level of between reaches in a stream. One explanation is that selection is affecting allele frequencies at some sites, but selection would be expected to affect particular loci, which was never the case (Hughes and Mather, 1996). An alternative explanation for this unusual pattern, which was first observed in species in subtropical rainforest streams in south-east Queensland, Australia, was put forward by Bunn and Hughes (1997). They proposed that this pattern could be explained if adult dispersal was widespread across the study area, if the larvae in a particular pool resulted from only relatively few matings (thus they were unrepresentative of the total gene pool) and if larval movement among pools via stream drift was limited or ineffective. Several predictions of this hypothesis were supported by further studies. Estimates of genetic differentiation among reaches for the same populations differed between different allozyme loci (Hughes *et al*., 1998), levels of genetic differentiation were similar between sites on a single sampling occasion, to levels between sampling occasions at a site (Hughes *et al*., 1998, 1999) and deviations from Hardy–Weinberg predictions occurred randomly across sites and loci.

Patterns observed in these stream insects were similar to those observed in some marine species, where a similar mechanism has been proposed to explain the patterns of patchy recruitment of discrete families of larvae settling at a particular section of shoreline (Johnson and Black, 1984) or coral reef (Doherty *et al*., 1996). Thus it was labelled the Patchy Recruitment Hypothesis.

As part of the explanation for the Patchy Recruitment Hypothesis, it was proposed that, in subtropical species, asynchronous emergence occurs over the whole year, with only a few adults emerging on any given night. This information came from light trap and emergence trap data (S. Bunn, personal communication). It was proposed that similar patterns would not be expected in North American and southern Australian species, because emergence tended to be more synchronous and larger numbers of adults would be swarming at one time.

These propositions have been tested in two recent studies. Using allozymes, Wilcock *et al*. (2003) found evidence of deviations from HWE expectations in a widespread European caddisfly *Plectronemia conspersa*. A follow-up study used microsatellites to determine whether larvae found in close proximity in a stream tended to be more closely related than expected by chance (Wilcock *et al.*, 2005). While their genetic methods could easily detect differences between egg masses and suggested that most were the result of single mating events, there was no evidence that larvae within a particular reach were the offspring of a limited number of matings, as would be expected under the Patchy Recruitment Hypothesis. Genetic analysis of a baetid mayfly (*Baetis bicaudatus*) in the Rocky Mountains (Hughes *et al.*, 2003b) found only limited genetic differentiation at both levels of the hierarchy that were examined (between reaches within streams and between streams) using allozymes. Support for the SHM was found, however, using mitochondrial DNA (Hughes *et al.*, 2003b). This result could be explained in two ways. First, mitochondrial DNA, because it is maternally inherited and is haploid, has a fourfold smaller effective population size relative to nuclear DNA (reflected by allozymes), so it is much more sensitive to restrictions of gene flow than is nuclear DNA (Birky *et al.*, 1989). Alternatively, mitochondrial DNA is maternally inherited and thus will only reflect the dispersal patterns of females, whereas nuclear DNA reflects dispersal of both sexes. Thus the observed pattern may be expected if females disperse only within their own streams, whereas males disperse more widely. This is an exciting result, which is supported in part by early ecological observations of individual female behaviour (Müller, 1982) and needs to be investigated in more species.

Patchy recruitment has also been invoked to explain extensive deviations from Hardy–Weinberg proportions within reaches in two other northern hemisphere studies (Monaghan *et al.*, 2001; Kelly *et al.*, 2001). However, these studies do not appear to fit the pattern observed in the subtropical species. This is because the deviations from HWE were not random across sites and loci, but were very large and tended to occur at particular loci (Table 14.2). These patterns are more suggestive of processes other than patchy recruitment leading to the results. Clearly, more studies of a range of insect species in both temperate and tropical habitats are required to determine the significance of these patterns for the ecology of the species.

At What Scale are Populations of Stream Insect Structured?

Given that adult flight appears to be a dominant mode of dispersal in stream insects, our aim in this part of the review is to assess the spatial scale over which populations are structured. In other words, at what geographic scale are we likely to detect significant genetic differentiation between populations? It is important to emphasize that genetic estimates of population structure are indirect and that the estimates themselves, as well as their statistical significance, are surrogates for direct measures of organism movement and demographic population structure. In theory, if adults can disperse across the whole natural range of a species, genetic differentiation should be absent no matter how large-scale the study. If most stream insects with an adult flight stage have a similar capacity for dispersal, then important constraints on dispersal, such as geographic distance between populations, should affect population structuring of most species in a similar way.

Table 14.2. Results of tests for differences in F_{IS} values among loci for 13 studies of stream insects. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Species	No. of sites	No. of loci	% out of HWE	Mean F_{IS}	F value (from ANOVA)	Reference
Ephemeroptera						
Siphlonisca aerodromia	6	5	27	0.04	3.40*	Gibbs *et al*., 1998
Bungona narilla	19	6	25	0.08	0.59	Hughes *et al*., 2000
Bungona narilla	14	6	36	0.10	2.95	Hughes *et al*., 2003a
Bungona narilla	19	6	24	0.06	1.36	Hughes *et al*., 2003a
Baetis bicaudatus	18	5	21	0.12	2.15	Hughes *et al*., 2003b
Baetis alpinus	23	6	50	0.33	15.25***	Monaghan *et al*., 2001
Rhythrogena layolaea	12	5	24	0.16	2.06	Monaghan *et al*., 2002
Allogamus auricollis	6	6	10	0.09	2.11	Monaghan *et al*., 2002
Trichoptera						
Tasiagma ciliata	10	4	15	0.06	1.38	Hughes *et al*., 1999
Tasiagma ciliata	8	4	16	0.03	1.25	Hughes *et al*., 1999
Tasiagma ciliata	8	4	27	0.12	0.74	Hughes *et al*., 1999
Mesophylax aspersus	5	9	37	0.09	7.95**	Kelly *et al*., 2001
Diptera						
Elporia barnardi	14	6	28	0.24	2.99*	Wishart and Hughes, 2001

The scale of population structuring has been addressed in a few studies by assessing isolation by distance and determining at what scale significant population structure is detected. For example, Wilcock *et al.* (2003) examined the relationship between geographic distance and genetic differentiation (allozymes) and showed that for *Pletronemia conspersa* (Trichoptera), there was a highly significant isolation by distance relationship and that significant genetic structure was never detected below 20 km, and often not even at 500 km. Finn *et al.* (2006) (mtDNA) showed a significant isolation by distance relationship in an alpine black fly, at an even smaller spatial scale of about 10 km. In this chapter, we have attempted to examine the general trend across all the species, rather than looking at each species individually. In order to do this, we assessed the total range of each study (based on maps provided in individual studies) and recorded the overall F_{ST} value for the species. With the exception of Wilcock *et al.* (2003), who specifically analysed a number of spatial scales, and Kelly *et al.* (2001, 2002), who analysed two Canary Islands separately, only one value was included for each species.

For 29 allozyme studies of stream insects, 26 had more than 5% of site/locus tests that were significant for Hardy–Weinberg deviations. Most of these studies proceeded to calculate F_{ST} values and interpret the values in terms of gene flow and dispersal among conspecific populations. Possible explanations for significant deviations from HWE at a site include mis-scoring of gels, selection acting on specific loci, inbreeding, patchy recruitment and the presence of cryptic species in the sample. Mis-scoring of gels and selection are unlikely to affect all loci equally. When we closely examined studies where more than 5% of comparisons were significant, 13 had sufficient data for a statistical analysis of differences among F_{IS} values, which give a measure of how the proportion of heterozygous genotypes deviates from expectations of HWE. We performed one-way ANOVA between loci, using sites as replicates. Of these 13 studies, four showed significant differences between F_{IS} values (Table 14.2). Therefore the possibility of gel mis-scoring and/or selection cannot be ruled out and the overall F_{ST} values are likely to be misleading. Inbreeding is likely to affect all loci equally, but we considered it unlikely for most insect populations studied here, as all had large populations, allowing the collection of multiple samples. The presence of cryptic species will not necessarily cause equal deviations from HWE at all loci, as it will depend on how much allele frequencies differ between species for each locus. However, the presence of cryptic species in a sample will cause deviations from HWE across a number of loci, deviations from HWE will be a result of heterozygote deficiencies so F_{IS} values will be positive and there will be significant gametic disequilibrium.

Cryptic species will confound estimates of population structure when the relative proportion of different species varies among populations, so that the apparent level of population differentiation is a product of the species composition at each site rather than of gene flow. Unintentional inclusion of multiple species in any analysis of gene flow and dispersal will almost certainly give extremely misleading results. For example, we recently undertook broad-scale sampling to examine at what scale the mayfly *Bungona narilla* was structured. Dispersal and recruitment in this species have been studied in some detail, but only previously at small spatial scales, within a single mountain range, across two catchments

(Schmidt *et al.*, 1995; Hughes *et al.*, 1998, 2003a). When wider sampling was undertaken to determine at what scale populations were structured, several populations showed highly significant deviations from HWE (McLean, 2007). Of 47 locus/site tests, 20 (42%) were significant and of these 20, 19 had positive F_{IS} values. There were also 24 of 69 significant deviations from gametic equilibrium. Phylogenetic analysis of a 533 bp fragment of the cytochorome oxidase I (COI) gene using MrBayes ver. 3.1.2 (Ronquist and Huelsenbeck, 2003) revealed four distinct clades, differing from each other by 19–21% (sequence divergence) (Fig. 14.1). Admixture clustering of the allozyme data using STRUCTURE (Prichard *et al.*, 2000) indicated that the most likely number of populations was four. The four populations corresponded exactly with the four mitochondrial clades, with 100% of individuals being assigned to their correct clade using an assignment method (Rannala and Mountain, 1997) (Fig. 14.1). Taken together, these results indicate the presence of four reproductively isolated species (likely to have diverged as long as 10 million years ago!). We assessed the effect of incorrectly including cryptic species in a sample to assess gene flow, by calculating F_{ST} values with and without the cryptic species. When all allozyme data for all four species were treated as a single species, the overall F_{ST} value across the 150 km study area was 0.328 ($P < 0.001$). When data for a single common clade (i.e. species) were isolated and analysed separately, the F_{ST} value was more than an order of magnitude lower, 0.027 ($P < 0.01$). The effect was even more extreme when F_{ST} values among sites within catchments were assessed. For example, an F_{ST} value of 0.656 was obtained for differentiation between sites within a single catchment, which resulted from totally different species at the three sites. Overall, results obtained from multiple taxa reflect different distributions of the taxa, rather than anything significant about gene flow. We believe that some of the early published allozyme work on aquatic insects may have unknowingly included multiple cryptic species.

When the relationship between overall F_{ST} and scale of study was tested for 25 studies that had used nuclear markers, there was no significant relationship ($r = 0.024$, $P = 0.91$, $n = 25$) (Fig. 14.2). When we removed six studies where cryptic species or mis-scoring of gels were suspected and one study of a net-winged midge, which probably should be treated as a non-flying aquatic insect (Wishart and Hughes, 2001), there was a just positive relationship (Fig. 14.2, closed symbols denote studies that were retained, $r = 0.477$, $P = 0.045$, $n = 18$). The main difference between the two sets of data was that most points representing high F_{ST} values at small spatial scales were removed, with only a single F_{ST} value of greater than 0.1 at scales of less than 100 km. This was a small stonefly in the Rocky Mountains, which lives in streams in deeply incised canyons that are likely to be significant barriers to dispersal. Using the regression equation (which admittedly only weakly fitted the data), the distance at which an F_{ST} value of 0.1 is expected is 350 km, while an F_{ST} value of 0.05 is expected at about 40 km. By inference, this result suggests that constraints on dispersal translate into appreciable genetic differentiation between populations at a geographic scale of 40–350 km for many stream insect species.

When a similar analysis was undertaken using mitochondrial DNA sequence data, again excluding the net-winged midge (Wishart and Hughes, 2003), there was a strong positive relationship ($r = 0.795$, $P = 0.002$, $n = 12$) (Fig. 14.3).

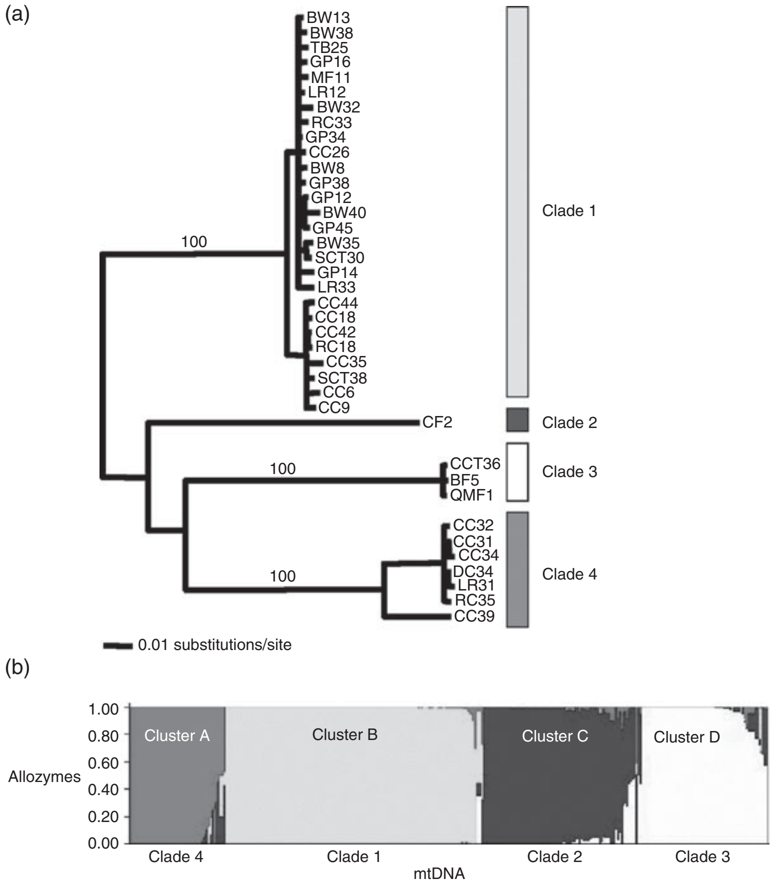

Fig. 14.1. Genetic analysis of cryptic *Bungona* spp. mayflies sampled from upland streams in south-east Queensland, Australia. (a) Bayesian phylogram depicting relationships among four mtDNA clades based on a 533 bp fragment of the COI gene. Data include 38 haplotypes recovered from 127 individuals from 14 populations. Bayesian phylogenetic analysis was performed using MrBayes, version 3.1.2 (Ronquist and Huelsenbeck, 2003). Searches were performed using general time reversible (GTR) model parameters including proportion of invariant sites and gamma-shaped rate variation. Searches were based on 2 million generations starting from random trees and sampling every 100 generations using default settings. Convergence of parameter estimates was assessed using run diagnostics in the MrBayes output. Clade posterior probability values are presented above branches and clades are different shades of grey to correspond with STRUCTURE analysis of allozyme data. (b) Results of Bayesian admixture clustering of multilocus allozyme genotypes implemented in STRUCTURE, version 2.1 (Pritchard *et al.*, 2000). Data includes four loci (*Pgi*, *Pgm*, *PepB*, *PepC*) genotyped for 412 individual *Bungona* spp. sampled from 14 populations. The summary plot shows the estimated assignment of each individual in each of four clusters. Each individual is represented by a single vertical line divided into four shaded segments proportional to the estimated membership of the individual in each of the four clusters. Shades of grey correspond to the four mtDNA clades shown in the mtDNA phylogram.

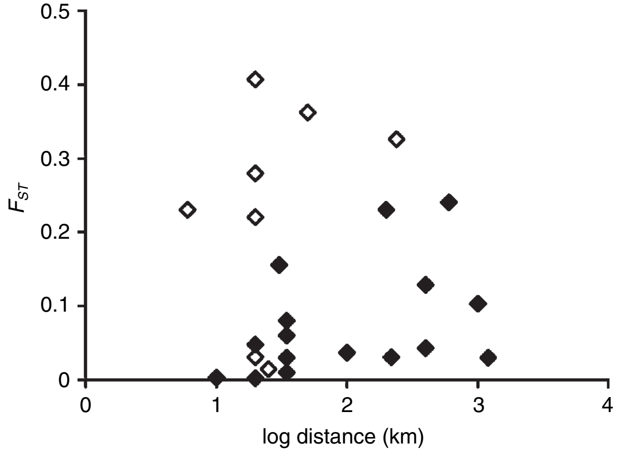

Fig. 14.2. The relationship between F_{ST} based on nuclear markers and geographic scale of study for 25 analyses of stream insects where F_{ST} values and geographic scale were presented. Studies represented by filled symbols: Bunn and Hughes (1997) (three species), Gibbs *et al.* (1998), Guinand (1994), Hogg *et al.* (2002) (two species), Hughes *et al.* (1999), Hughes *et al.* (2003), Kelly *et al.* (2001) (two islands), Kelly *et al.* (2002) (two islands), Miller *et al.* (2002) (four species), Monaghan *et al.* (2001), Smith *et al.* (2001) (two species), Watts *et al.* (2006), Wishart and Hughes (2001), Wilcock *et al.* (2001) (three different scales). Studies represented by open symbols: Guinand (1994), Kelly *et al.* (2001) (two islands), Kelly *et al.* (2002) (two islands), Monaghan *et al.* (2001), Wishart and Hughes (2001).

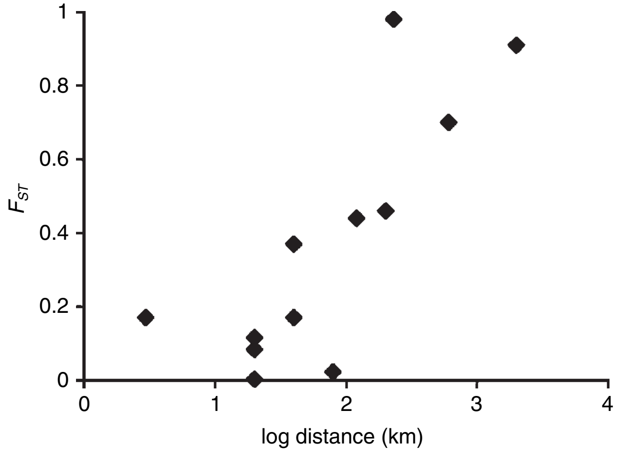

Fig. 14.3. The relationship between F_{ST} based on mitochondrial DNA and geographic scale of study for 13 studies of stream insects where F_{ST} values and geographic scale were presented. Studies represented: Baker *et al.* (2003), Finn *et al.* (2006), Finn and Adler (2006), Galacatos *et al.* (2002) (one species), Hughes *et al.* (2003a), Hughes *et al.* (2003b), Myers *et al.* (2001) (two species), Pauls *et al.* (2006), Schultheis *et al.* (2002), Schultheis and Hughes (2005) and Smith *et al.* (2006).

Also, the actual values are greater for mtDNA than for nuclear DNA, with almost all values greater than 0.1. F_{ST} values of 0.1 are predicted at very small distances (about 10 km).

Differences in the observed F_{ST} values between mitochondrial and nuclear data are partly explained by the fourfold lower effective population size of mitochondrial genes relative to nuclear genes (Birky *et al.*, 1989). Given the same number of males and females moving between sites, mitochondrial genes are expected to show close to a fourfold higher F_{ST} value than nuclear genes, especially when F_{ST} values are small (less than 0.05) (Crochet, 2000). An alternative explanation, however, is that females are less effective dispersers than males. Unfortunately, only a few studies have used both mitochondrial and nuclear markers on the same species and populations. For the net-winged midge *Elporia barnardi*, in which dispersal is very limited, the F_{ST} value for mtDNA was six times greater than for nuclear DNA (Wishart and Hughes, 2001, 2003) (Table 14.3). For the alpine baetid mayfly *Baetis bicaudatus* (Hughes *et al.*, 2003b) it was 17 times greater, for the subtropical baetid mayfly *Bungona narilla* it was between four and 27 times greater (McLean, 2007) and for the New Zealand mayfly *Acanthophlebia cruentata* (Smith and Collier, 2001; Smith *et al.*, 2006) it was 16 times greater. These values are mostly greater than the fourfold effect expected from different effective population sizes (Ne) of the markers. Clearly, more studies are needed comparing male versus female dispersal potential that combine data from mtDNA and nuclear markers.

The fact that the relationship between the spatial extent of the study and F_{ST} values is much stronger in mitochondrial than in nuclear genes could be explained by several factors, in addition to sex-biased dispersal. First, allozyme loci are more likely to be affected by selection, which may confuse the pattern. Second, some allozyme studies have included cryptic species in the data sets, even though we tried to exclude these from the analysis. Cryptic species are less likely in data sets involving mitochondrial sequence data, because highly divergent clades are easily identified. Taken together, these observations suggest that in future, such studies should include both mitochondrial DNA sequence data and a nuclear marker, preferably microsatellites, which are less likely to be affected by selection than allozymes (Schlötterer, 1998).

As well as distance alone creating a dispersal barrier for stream insects, several studies have identified particular geographic factors that cause dispersal barriers for some species. These include steep canyons (Hughes *et al.*, 1999), oceans (Wilcock *et al.*, 2001) and lowland areas (Pauls *et al.*, 2006; Murria and Hughes, in press).

What has Phylogeographic Analysis Added to our Understanding of Stream Populations?

Recently, several studies of stream insects (e.g. Schultheis *et al.*, 2002; Hughes *et al.*, 2003b; Finn *et al.*, 2006; Pauls *et al.*, 2006; Smith *et al.*, 2006) have used mitochondrial sequence data to address questions of contemporary gene flow and of historical processes that have led to observed geographic distributions

Table 14.3. Results of Fu's *F*s tests for eight studies presenting mitochondrial DNA sequence data.

Species	Habitat	Clade analysed	Fu's Fs	Expansion time	Reference
Trichoptera					
Chematopsyche†	Temperate Australia	3–1	–15.02*	149,000	Baker *et al.*, 2003
		3–2	1.64	–	
Tasimia palpata	Sub-tropical Australia	Northern	–26.76*	642,000	Murria and Hughes, in press
		Southern	–33.12*	805,000	
Drusus discolour‡	Alpine, Europe	Eastern Alps	–10.37	?	Pauls *et al.*, 2006‡
		Thuring Forest	–3.31	?	
		N. Carpathians	–1.80	?	
Ephemeroptera					
Bungona narilla	Sub-tropical Australia	3–1	–10.33*	490,000	McLean, 2007
		3–2	–3.83*	167,000	
Acanthophlebia cruentata†	New Zealand	3–1	–14.91*	50,000	Smith *et al.*, 2006
		3–2	–0.14	–	
Baetis bicaudatus	Alpine, USA		–14.03*	149,000	Hughes *et al.*, 2003b
Diptera					
Elporia barnardi†	Temperate South Africa	Table Mountain	0.24	–	Wishart and Hughes, 2003
		Erste River	–1.17	–	
Prosimulium neomacropyga†	Alpine, USA	1	–8.73*	283,000	Finn *et al.*, 2006
		2	–1.64	–	

**P* < 0.02. Note, where significant phylogeographic structure was detected, clades were analysed separately.
†Fu's *F*s calculated for this paper. Timing of expansions calculated using the mismatch method of Harpending (1994).
‡Pauls *et al.* analysed 12 clades, only the three shown were significant for Fu's *F*s.

and patterns of genetic structure. While early interpretations of these patterns were totally qualitative (Avise, 2000), more recently, Templeton (Templeton *et al.*, 1995; Templeton, 2004) has introduced a semi-quantitative technique to infer the most likely processes that have shaped observed distributions, Nested Clade Analysis.

Three studies of Australian upland stream insects [two caddisflies *Cheumatopsyche* sp. (Baker *et al.*, 2003) and *Tasimia palpata* (Murria and Hughes, in press), and a mayfly *Bungona narilla* (McLean, 2007)] have used patterns of variation in the mitochondrial cytochrome oxidase 1 gene to examine phylogeographic structure. In each of these, the structure of the gene network suggested that the populations had recently expanded in size and statistical tests for population growth using Fu's *F*s statistic (Fu, 1997) support this inference. Applying molecular clock estimates, the expansions were estimated to have occurred during the Pleistocene: 150,000 years ago for *Cheumatopsyche* sp. and about 150,000–850,000 years ago for *Tasimia* and *Bungona* (Table 14.3). There was also evidence of past fragmentation followed by subsequent range expansion detected in the nested clade analyses of all three species. These results have been interpreted to reflect alternating contractions and expansions of available upland habitat during the Pleistocene. During restrictions of available habitat, populations of each of the species are proposed to have become isolated from one another in upland refugia. Subsequent expansions of habitat are proposed to have caused not only expansions in population size, but also expansions of range and opportunities for more gene flow, thus causing mixing of previously isolated lineages (Baker *et al.*, 2003; McLean, 2007; Murria and Hughes, in press).

Examination of seven similar studies from outside Australia revealed only two that had identified evidence for recent population expansions. *Baetis bicaudatus* (Ephemeroptera) from the Rocky Mountains was suggested to have undergone a population expansion around 150,000 years ago, although this expansion probably did not occur at the study site, as it would have been glaciated during the most recent Pleistocene glaciation only 18,000 years ago (Hughes *et al.*, 2003b). Similarly, some populations of the widespread European caddisfly *Drusus discolor* showed evidence of expansions during the Pleistocene, also longer ago than 18,000 years ago (Pauls *et al.*, 2006).

The other five species were not tested explicitly for evidence of expansions. We have calculated Fu's *F*s statistics for three of these studies, based on the data available in the papers (Table 14.3). Fu's *F*s value was highly significant for another alpine black fly (*Prosimulium neomacropyga*) from the same area of the Rocky Mountains (Finn *et al.*, 2006) (Table 14.3). Using the method developed by Harpending (1994), we estimated the time of the expansion in *P. neomacropyga* to be about 280,000 years ago. Of the two remaining species, the New Zealand mayfly (*Acanthophlebia cruentata*) showed evidence of an expansion about 50,000 years ago in one of two clades, while the other showed a non-significant Fu's *F*s. The South African net-winged midge (*Elporia barnardi*) (Wishart and Hughes, 2003) was the only species to show no evidence of expansions during the Pleistocene, suggesting the population has been relatively stable during this time.

This summary seems to suggest that almost all stream insects with a flying adult stage show evidence of past population expansions in their genetic signatures. The Australian studies of temperate and subtropical species show evidence of Pleistocene fragmentation (isolation of populations in isolated upland refugia) followed by subsequent range expansion and secondary contact when conditions became warmer and wetter. Three of the northern hemisphere species (a mayfly and two black flies) show evidence of population expansions, but no history of fragmentation. This may be because the population had expanded from a single refugium. For the European caddisfly studied by Pauls *et al.* (2006), the genetic signature suggests multiple refugia, with maintenance of much of the isolation even following glaciation.

Interestingly, the pattern of population expansions during the Pleistocene is not a common feature of all stream taxa. For example, Australian freshwater crayfish that occupy similar upland habitats to those from which the insects were sampled, show extremely low levels of genetic diversity on each mountain range (Ponniah and Hughes, 2006) and no evidence of recent expansions. Similarly, the freshwater shrimp *Paratya australiensis* shows limited genetic variation within streams and no evidence of population expansions during the Pleistocene (Hurwood *et al.*, 2003). This difference may reflect the fact that these crustaceans have not been affected in the same way by increases in available habitat, being unable to disperse between patches of rainforest either during glacials or interglacials.

Differences observed between mobile stream-dwelling insects and less mobile insects and crustaceans, in terms of population structuring and demographic expansion, are also reflected in comparisons of terrestrial invertebrates with contrasting dispersal abilities. For example, terrestrial species with limited dispersal ability and life-history characteristics that predispose them to refugial isolation in response to climatic changes show high levels of population structure and no evidence for recent expansions, e.g. saproxylic invertebrates (Garrick *et al.,* 2004; Sunnucks *et al.*, 2006); montane grasshoppers (Knowles, 2001). Terrestrial insects with more efficient dispersal capabilities may show evidence of refugial isolation, but have high levels of contemporary gene flow and strong signatures of recent population expansion, e.g. butterflies (DeChaine and Martin, 2004) and beetles (Smith and Farrell, 2005). Similar patterns seen in aquatic insects may indicate that flight is an important mechanism maintaining cohesion of species across landscapes that have little or no hydrological connection.

Can These Results Assist in Managing Populations of Stream Insects?

This review shows that overwhelmingly, adult flight is the major dispersal mechanism for most stream insects. The only convincing exception is the net-winged midge, where adult flight is ineffective (Wishart and Hughes, 2001, 2003). We should point out that our analysis only examined species that had an adult flight stage in their life history. Work by Zera (1981) using allozymes and Galacatos *et al.* (2002) using mitochondrial COI showed a very different pattern in several species of water-striders that lacked a flight stage. The genetic structure of these species resembled more the pattern seen for many aquatic crustaceans and non-diadromous fish (Hughes, 2007).

The implication is that, where local extinctions of aquatic insect species occur within a catchment, natural recolonization is highly likely from across the catchment boundary. This conclusion differs markedly from those based on genetic structure of some other groups of aquatic organisms, such as crustaceans and molluscs (Hughes, 2007), where recolonization from across the drainage divide is considered highly unlikely.

Based on the overall analysis of mitochondrial DNA and nuclear data available, it seems that most species of stream insects are significantly structured at a scale of approximately 100 km, although clearly studies using mitochondrial DNA detect structure at smaller spatial scales, as little as 10 km. If it is possible to generalize this conclusion, this has implications for the management and conservation of many stream insects. First, it implies that if local extinctions occur, then recolonization by many aquatic species is likely to occur from within 100 km or less. If no other habitat patches occur within this radius, then the likelihood of natural recolonization is low. Similarly, for upland species that regularly disperse between mountains or mountain ranges, there need to be stepping stone habitat patches to facilitate gene flow. If intervening habitats are destroyed, so that remaining habitats are significantly more than 100 km apart, then movement patterns are likely to be severely affected and local extinctions are unlikely to be naturally recolonized.

It appears that many of the species studied to date are limited to forested areas in upland streams. Evidence from phylogeographic analyses suggests that many of these species have been severely affected by climate change in the past. For example, contraction of rainforest in south-east Queensland, during the Pleistocene caused fragmentation of populations and reduced gene flow between them (Murria and Hughes, in press). Future climate change is likely to have similar effects and will isolate populations to a few suitable areas. For example, south-east Queensland is currently suffering its worst drought in history and streams in the only piece of rainforest (Brisbane Forest Park) between two major rainforest habitats have dried up. This means that this potential stepping-stone habitat has already been lost for species occupying these upland areas.

Finally, if a pattern of male-biased dispersal suggested by some studies is confirmed and found to be widespread among stream insects, this will have implications for the potential for recolonization of depleted populations. This is because, if females are restricted to streams, and males move between them, gene flow will occur while all sites contain animals. When populations go extinct in particular streams, however, only the females can found a new population. Thus, depending on how limited female movement is, the possibility of recolonization may well be much less than would be predicted from estimates of gene flow provided from nuclear markers.

Conclusions

Only a handful of studies of stream insects have utilized both nuclear and mitochondrial information, sometimes in different papers. While mitochondrial sequence data can provide useful information about historical events, use of mitochondrial data in isolation suffers pitfalls because it represents only a single locus and it reflects only female dispersal behaviour. Where possible, studies should utilize both types of marker. While allozymes have proved useful for early analyses of population structure, they can be affected by selection, difficulty of gel interpretation and low levels of variation. Ideally, microsatellites or single nucleotide polymorphisms should be used in future.

The majority of studies of stream insects have concentrated on species that inhabit upland streams. Almost nothing is known about insects that inhabit lowland streams. In addition, more effort needs to be placed into addressing evidence for male-biased dispersal that has been suggested by some studies. This will mean using high-resolution nuclear markers such as microsatellites along with mitochondrial DNA markers at small spatial scales.

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15

Habitat Constraints and the Generation of Diversity in Freshwater Macroinvertebrates

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Abstract
Freshwater aquatic invertebrates occupy a range of habitats, which can broadly be classified into running or standing waters. The contrasting habitat permanence over geological timescales of these two habitat types imposes different constraints on their invertebrate populations. Species in more ephemeral lentic water bodies are forced to disperse when the habitat disappears, and are thus predicted to have higher dispersal abilities and inter-population gene flow, resulting in larger, more dynamic geographical ranges and slower evolutionary turnover. In the more stable lotic habitats, species are predicted to have lower dispersal abilities, with higher persistence of local populations and reduced inter-population gene flow. This should result in smaller range sizes and a higher evolutionary turnover. Latitudinal diversity gradients of lentic and lotic species may also be expected to differ, as lotic species will be more dependent on historical factors and distance to glacial refugia, whereas lentic species will be closer to an equilibrium with current ecological and geographical conditions. Some of these predicted patterns have been demonstrated for a range of aquatic invertebrates across different geographical areas, although the underlying evolutionary and physiological mechanisms are still poorly understood.

Introduction

Spatial gradients in species richness are among the best documented and most robust ecological patterns (reviews in Brown, 1995; Gaston and Blackburn, 2003). Most of these patterns, however, remain descriptive, and there are still few answers to basic questions such as why closely related species may have widely different geographical ranges (Lester *et al.*, 2007). Despite the multiple explanations put forward, such as differences in niche breadth, body size, population abundance, environmental variability, colonization and extinction dynamics, and dispersal ability (Stevens, 1989; Brown, 1995; Gaston, 2003; Lester *et al.*, 2007), there are few data to allow any general conceptual framework beyond the counts of species numbers and their statistical correlates. The Habitat Templet

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concept (Southwood, 1977, 1988; Korfiatis and Stamou, 1999) may provide the basis for such a framework. In Southwood's concept, the habitat is the templet that drives the evolution of organisms, such that the constraints posed by the habitat characteristics influence the ecological traits of the species living on it. In freshwaters, one of the most influential of these habitat constraints is the divide between standing (lentic) and running (lotic) waters (see Harrison and Dobson, Chapter 13, this volume, for the effect of other types of ecological and biological constraints). This should not be interpreted in terms of intensity of water flux only, but in a wide range of associated physical and biological characteristics. Despite the existence of unavoidable grey areas, most of the freshwater habitats in which macroinvertebrates are commonly found (and studied) can be generally assigned to one of these two types. In a series of papers, Ribera and Vogler (2000) and Ribera *et al.* (2001, 2003) explored the possible implications of the different constraints that these two habitat types could impose on the populations, species and lineages living in them.

In the following chapter, I will first summarize the hypothetical model of how habitat type may influence the macroecology and macroevolution of species and populations of freshwater invertebrates. The assumptions of this model will be supported using data from other organisms and ecosystems (i.e. not necessarily related to freshwater habitats, or particularly to the lotic/lentic divide). Second, I will detail the results of the research with the explicit aim of testing the implications of the lotic/lentic habitat preferences. The review will end with a comment on possible caveats, problems to be solved and suggestions for further research.

An Integrated Framework for some Macroecological and Macroevolutionary Patterns in Freshwater Macroinvertebrates

Small- to medium-sized standing water bodies, such as those typically inhabited by many groups of aquatic macroinvertebrates, are generally short-lived and discontinuous in time and space (Hutchinson, 1957). Once a particular water body disappears, there is no direct physical connection to any other similar habitat. In contrast, running water bodies generally persist over longer geological periods and remain connected to other water bodies within the drainage network, despite changes in the exact location of the channel. The temporal scale of these differences is much longer than the possible seasonal variations within the lifespan of individual habitats; streams in some areas (e.g. Mediterranean) may be seasonal and dry regularly, but their long-term persistence is unaffected. Most freshwater macroinvertebrate species can be categorized as inhabiting either lentic or lotic waters, with comparatively few species able to inhabit both (Illies, 1978; Foster *et al.*, 1992; Larson, 1997; Ribera and Vogler, 2000). Differences in habitat preference occur at all phylogenetic levels, often among sister species, or groups of closely related species (Ribera *et al.*, 2001). Many insect groups have colonized freshwaters several times independently and, hence, provide independent replicates of the influence of habitat on insect ecology.

The contrasting habitat permanence of lotic and lentic waters is predicted to lead to a cascade of ecological and evolutionary implications ranging from the individual to the lineage (Table 15.1). Critically, species living in geologically long-lived habitats will be expected to have reduced dispersal ability compared with those species living in geologically more ephemeral habitats. It must be stressed that the term 'dispersal' is taken to mean the ability of a species to establish a new population in a non-contiguous habitat patch (i.e. emigration plus inter-patch movement plus immigration, *sensu* Bowler and Benton, 2005), but not 'dispersal' as movement of individuals, *sensu* Bilton *et al.* (2001). In the sense used here, dispersal may, or may not, be correlated with the ability of individuals to migrate or to travel long distances.

The higher mobility and colonization ability of populations of lentic species will then lead to more dynamic and larger geographical ranges, faster colonization of new areas (e.g. after deglaciation or of islands), lower beta diversity and a greater occupancy of potential niches than lotic species. Lotic species are predicted to be more sensitive to global change, as they will have more difficulty tracking rapid changes in a discontinuous habitat matrix. The higher mobility of lentic species is also predicted to increase gene flow between populations, resulting in reduced inter-population genetic variability and thus leading to a greater evolutionary cohesion of species. Over comparable geographical scales, this is predicted to lead to a less pronounced phylogeographical structure and a decreased probability of peripatric or allopatric speciation for lentic species. Their larger geographical range will further reduce the probability of extinction.

When habitat preferences or the size of the geographic range are maintained across speciation events, or the physical setting of an area favours the dominance

Table 15.1. Summary of the predicted characteristics of the populations, species and lineages living in lotic or lentic habitats, according to the model outlined in the text.

Populations/species	Lotic	Lentic
Geographic range		
Overall size	–	+
Edge dynamics (range shifts)	–	+
Frequency of 'outliers'	+	–
Colonization of new areas (deglaciated, islands)	–	+
Latitudinal gradients	+	–
Geographical turnover (beta diversity)	+	–
Fit between realized and potential distribution	–	+
Sensitivity to global change	+	–
Genetic flow		
Evolutionary cohesion of the species	–	+
Filogeographical structure	+	–
Probability of peripatric or allopatric speciation	+	–
Probability of extinction	+	–
Intrapopulation genetic variability	–	+
Age (intraspecific coalescence)	–	+
Lineages		
Evolutionary turnover	+	–
Propensity to generate radiations	+	–

of running or standing habitats for long periods of time (enough for successive cladogenetic events in the same lineage), it is expected that the consequences of habitat constraints will extend to macroevolutionary characteristics of whole lineages (Gould, 2002). The lower probability of speciation and extinction in lentic species would result in a lower evolutionary turnover, which would be higher in lotic species. On average, lentic species are thus expected to be older, with larger intraspecific genetic variability. Note that the higher probability of extinction in lotic clades increases the likelihood that the 'true' sister of a species is extinct, i.e. that the extant closest relative (the observed sister) may actually be rather distant. Ages of the species would thus have to be measured using the coalescent time and not the distance to their extant sisters.

The higher persistence of local populations, together with smaller geographical ranges and reduced gene flow, favours the specialization of lotic species. If this was the case, it seems likely that this could bias the probability of habitat shifts as, once a lotic specialization is established, the possibility of a transition to a lentic habitat may be impaired.

The total number of species within a clade at any given time will depend on the balance between speciation and extinction. As the same general factors promoting speciation also favour extinction (Stanley, 1979; Hubbell, 2001; Gould, 2002; Jablonski, 2007), there are no clear predictions as to which habitat type would promote higher species diversity at any given time (i.e. synchronic diversity), as opposed to the expected higher accumulated diversity of lotic lineages through time (i.e. diachronic diversity). However, the predicted high turnover in lotic species means that the potential for both fast radiations and complete extinction of whole lineages may be higher than in lentic species.

Justification of the Assumptions

Most of the assumptions of the model outlined above have been documented for different groups of organisms in different systems, but only rarely with aquatic insects.

Relationship between dispersal ability and geographical range

Despite much attention, the relationship between dispersal ability and size of the geographic range remains contentious (e.g. Lester *et al.*, 2007). As noted above, we need to distinguish between 'movement' and 'establishment' of individuals/populations. Standard measures of 'dispersal ability' are often only surrogates of the distance that individuals can travel, not of the ability of reaching a distant suitable habitat patch and establishing a new population. In some cases it may be assumed that there is no restriction to movement, and differences in dispersal ability relate only to the ability to establish new populations (e.g. plants in the arctic, Alsos *et al.*, 2007; some planktonic organisms, De Meester *et al.*, 2002). It is unsurprising, therefore, that the evidence for a strong relationship between dispersal ability and range size is equivocal (e.g. marine organisms, Lester *et al.*, 2007; moths, Beck and Kitching, 2007), although there are many examples of a positive correlation (presence of wings in beetles, Juliano, 1983; wing size in damselflies, Rundle *et al.*, 2007; flying ability in warblers, Böhning-Gaese *et al.*, 2006). In plants, dispersal ability is often measured in relation to mode of pollination or seed size, and a positive relationship between these surrogate measures and size of the geographical range has been reported (e.g. in New Zealand, Lloyd *et al.*, 2003; trees, Morin and Chuine, 2006; but see Lowry and Lester, 2006 for an opposite trend).

For marine organisms, it is generally accepted that species with feeding pelagic larval forms have larger ranges than species with direct, non-pelagic development or non-feeding larvae (gastropods, Scheltema, 1989; sea urchins, Emlet, 1995; Jeffery and Emlet, 2003; teleost fishes, Goodwin *et al.*, 2005; Indo-Pacific fishes, Lester and Ruttenberg, 2005). However, the relationship between range size and the duration of the planktonic larval stage is either equivocal, or non-existent (Scheltema, 1989; Lester *et al.*, 2007; Victor and Wellington, 2000).

When looking at surrogates of dispersal ability, it is also important to account for ecological or biological characteristics of the different groups. For example, while oviparous species of teleost fishes have larger ranges than viviparous species (Goodwin *et al.*, 2005), the opposite is true for elasmobranchs, where eggs of oviparous species are fixed and develop in situ, so that the egg is not a dispersal stage, as in teleosts.

Relationship between dispersal ability and gene flow/phylogeographic structure

The relationship between range size and phylogeographic structure has received much less attention than that between range and dispersal ability, probably because of the difficulty in obtaining suitable data. Several recent studies, however, support the prediction that, at similar geographical scales, species of lower dispersal ability have a more pronounced phylogeographic structure. In two closely related species of water mite, the one (*Arrenurus angustilimbatus*) with larvae that ecto-parasitize and disperse on adult mosquitoes possesses a broader and more continuous geographic distribution, with higher allozyme heterozygosity and less population differentiation, than the species (*A. rufopyriformis*) with larvae that do not ecto-parasitize mosquitoes and have more limited dispersal abilities (Bohonak *et al.*, 2004). Comparing two more distantly related species (Ephemeroptera and Amphipoda) with contrasting dispersal abilities, Zickovich and Bohonak (2007) report similar differences in genetic structure.

In marine organisms, the mode of development is a determining factor of phylogeographic structure. Species with direct development (embryonic development taking place through yolk feeding in an egg capsule or egg mass deposited directly on the substrate with no pelagic stage) have higher levels of population structure than do species with planktonic development (e.g. gastropods, Collin, 2001; corals, Hellberg, 1996; sea cucumbers, Arndt and Smith, 1998; fishes, Hunt, 1993; Riginos and Victor, 2001). Within marine cowries, species that possess planktonic larvae have greater mean pairwise genetic distance within each taxon than species without planktonic larvae (and hence having restricted dispersal and narrow ranges) (Meyer and Paulay, 2005). In this study, intraspecific variation (as measured by depth of coalescence) was uncorrelated with interspecific divergence, indicating that 'older' species (those without close extant relatives) do not have more intraspecific variation than 'younger' species (those with close living relatives).

In a review of factors determining genetic structure in plants, Duminal *et al.* (2007) found few significant traits, but among them were seed dispersal mode and geographic range size. For example, wind pollinated species of palms had lower population genetic structure, as measured with allozymes, than coexisting species with entomophilous pollination and lower seed dispersal abilities (Luna *et al.*, 2005).

Relationship between range size and probability of speciation/extinction

There is considerable evidence of species with larger ranges having a lower probability of extinction, but the relationship with probability of speciation is less clear. Most of this evidence is from the fossil record of marine invertebrates. The classic work of Hansen (1980) demonstrated that in lower Tertiary gastropods in the Gulf coast of North America, widespread species with planktonic larvae survived longer, a result that has been confirmed subsequently by different works (e.g. Jablonski, 1987; Gili and Martinell, 1994; Jeffery and Emlet, 2003; Foote *et al.*, 2007). Species without planktonic larvae could attain wide geographic ranges when barriers to dispersal were minimized, but could not maintain these wide distributions during periods of habitat fragmentation caused by delta formation within the Gulf, when the isolation of populations accelerated extinction (Hansen, 1980). Payne and Finnegan (2007) found that the geographic ranges of genera of fossil, benthic marine invertebrates were positively correlated with survival in 'normal' background extinction periods, irrespective of species richness and abundance, although not in periods of mass extinctions. Liow (2007) also reported a positive relationship between latitudinal and bathymetric range extension, and species longevity for marine Ostracoda. Based on extant species, higher probabilities of extinction have been linked with reduced geographical range in freshwater fishes (Rosenfield, 2002), primates and carnivores (Purvis *et al.*, 2000).

The relationship between geographical range size and speciation rate has been addressed more rarely. Gavrilets *et al.* (2000) used simulations to show that species with smaller range sizes (characterized by smaller local densities and reduced dispersal ability) should have higher speciation rates. Jablonski and Roy (2003) provided data for Late Cretaceous gastropod genera, which exhibit a strong negative relationship between the geographical ranges of constituent species and speciation rate per species per million years, showing that the factors promoting broad geographical ranges also tend to dampen speciation rates. Using data of extant species of Australian arid and semi-arid plants, Akwood *et al.* (1993) found that species adapted for long-range dispersal may have experienced lower speciation rates. Lester and Ruttenberg (2005) revealed a negative correlation between species richness and larval duration at the family level in Indo-Pacific tropical reef fishes, implying that speciation rate may be negatively related to dispersal potential. A negative relationship between speciation rate and range size is not always found, however (Rosenzweig, 1995). Cardillo *et al.* (2003) reported faster diversification rates for species with larger geographical ranges and larger litters among Australian mammals, although they attribute this difference to a decreased probability of extinction and not to an increased speciation rate.

Inheritability of habitat preferences ('niche conservatism')

The retention of ecological characteristics within species lineages ('niche conservatism') is well established (e.g. reviews in Wiens, 2004; Wiens and Graham, 2005), particularly for broad traits such as general habitat preferences. Although habitat shifts must occur, even among sister species (e.g. aquatic Coleoptera, Ribera and Vogler, 2000; Ribera *et al.*, 2003), species lineages, in general, tend to have a preferred or exclusive habitat type, allowing us to investigate the long-term macroevolutionary consequences of habitat constraints (e.g. Ribera *et al.*, 2001).

Inheritability of species-level traits (size of the geographic range, speciation rates)

The classic work of Jablonski (1987) has been until recently virtually the only published evidence of the possible inheritability of a species-level character such as the size of the geographic range. This finding has been contested by Webb and Gaston (2003, 2005) who, after re-analysing the same data set, found little support for the notion that species selection on geographic range sizes has played a significant role in shaping contemporary species–range size distributions, in disagreement with Hunt *et al.* (2005) and Jablonski and Hunt (2006). However, Mouillot and Gaston (2007), in a reappraisal of the question using a modelling approach, accept the possibility of significant heritability in the geographical range sizes of species, even without any biological trait differences. The heritability found was weaker than that observed in empirical studies, but suggests that a substantial component of heritability may not necessarily be associated with niche conservatism at the individual level. Waldron (2007) reviews the question of the heritability of geographical ranges, using a range of models and Nearctic birds as examples. In addition to reaffirming the non-randomness of the distribution of the size of geographical range in a phylogeny, the most relevant result is that current ranges of sister species are more symmetrical than expected at the moment of speciation. This means that biological or ecological characteristics of the species (kept through the cladogenetic event) constrained the subsequent evolution of the geographical range after speciation, increasing the observed similarity between sisters.

The evidence supporting sustained differences in speciation rates, due to inheritance of species traits, is even more scarce and generally inconclusive (e.g. Duda and Palumbi, 1999; Jeffery and Emlet, 2003). Savolainen *et al.* (2002) explicitly addressed the inheritability of cladogenesis characteristics. By looking at the size of the branches in linearized trees, they found a pattern for most of the studied clades consistent with heritable net cladogenesis. These authors claim that heritability of cladogenesis may be a general phenomenon, detectable across a large number of lineages and a broad range of taxa. Gould (2002) also discusses extensively the macroevolutionary implications of sustained biases in cladogenetic processes, supporting the view that continuous habitat constraints (as would be landscape characteristics favouring the presence of either lotic or lentic habitats) could be determining factors in the macroevolutionary characteristics of whole lineages. In any case, the very existence of species radiations (i.e. lineages significantly more diverse than their sisters) may be taken as a proof of the maintenance in some lineages of 'higher than average' diversification rates across several cladogenetic events.

Testing the Predictions in Freshwater Ecosystems

This section reviews the work specifically addressing the macroecological or macroevolutionary implications of the lotic and lentic habitat constraints in freshwater invertebrates. The chain of inferences derived from the basic assumptions described above is used as a guide.

Predictions at the species/population level

Geographic range: overall size

Our research into the different constraints that lotic and lentic habitats could impose on organisms originated from observations that, in the Iberian peninsula, most of the species of aquatic Coleoptera with narrow distributions were exclusively found in running waters (Ribera and Vogler, 2000). Using data on range sizes for 490 coleopteran species, we found that lotic species had much smaller distributional ranges than lentic species, and that the association of habitat type and range size had independently arisen in at least four monophyletic coleopteran lineages and several more times within each of these main groups. Similarly, Hof *et al.* (2006) found that lentic Northern hemisphere odonates had larger latitudinal spans, and more northern distribution centres and range boundaries, than lotic species. Although the data were collected for a different purpose, Monaghan *et al.* (2005) observed that Madagascan mayflies associated with small lentic water bodies had the larger ranges, and showed the most recent, and presumably most frequent, transoceanic colonizations. Analysis of Illies' (1978) data on west European freshwater invertebrates also showed that lentic species of Hydracarina, Rotifera and Dytiscidae, but not Mollusca, had larger average ranges than lotic species (Fig. 15.1) (Meyer, 2000).

Geographic range: dynamics

The most direct way to test whether lentic species experience more frequent and intense range shifts than lotic species would be to examine the fossil record. Preliminary analysis of Late Quaternary beetle data shows that most of the species in the families Dytiscidae and Hydraenidae experiencing range shifts (i.e. known

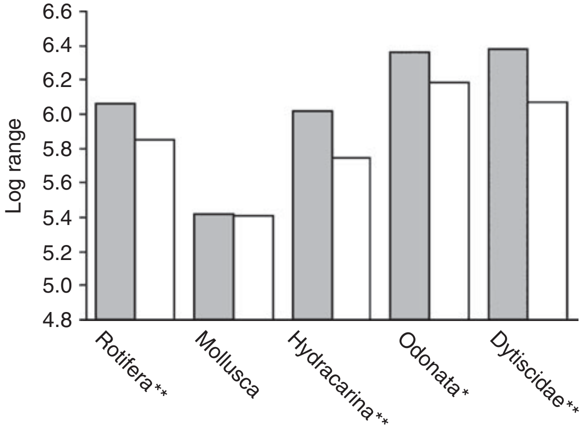

Fig. 15.1. Average range (in log km^2) of lotic and lentic European species of five taxonomic groups (data from Illies, 1978, compiled by Meyer, 2000; see text and Table 15.3 for details). **$P < 0.001$ in a two-tailed t-test comparison of averages; *$P < 0.1$.

as fossils from areas in where they do not currently occur) are mostly, or exclusively lentic (I. Ribera *et al.*, 2007 unpublished results). However, the fossil data has serious limitations, both temporal (covering in their vast majority only the last glacial cycle) and geographical (with virtually no records from the most species-rich areas in the Mediterranean). There are several other indirect ways of testing differences in range dynamics. In Ribera *et al.* (2001), two lineages of water beetles (family Dytiscidae) were compared: one with species living only in running waters (genus *Deronectes*), and one with species living only in standing water habitats (species of the *Ilybius subaeneus* group). Using species-level phylogenies, and assuming allopatric speciation, we tested the evolution of sympatry with node age: the prediction was that lotic species would keep allopatry longer than lentic species. When the degree of sympatry was plotted against relative node age, more allopatric splits were evident in the lotic *Deronectes*, suggesting a slower rate of range movement since speciation (medians of 0.5 and 0.8 in *Deronectes* and *Ilybius* respectively, where 0 is perfect allopatry and 1 fully overlapping ranges, Ribera *et al.*, 2001). However, differences were not significant when tested with the methodology of Barraclough and Vogler (2000).

Another set of predictions, derived from the greater hypothesized range movements of lentic species, pertain to latitudinal gradients and the different factors influencing the local and regional species richness of the two habitat types. Lentic species are expected to re-colonize recently glaciated areas faster than lotic species, the colonization success of the latter being more dependent on distance from glacial refugia. Ribera *et al.* (2003) collated species distributions for more than 800 species of water beetles in 15 regions across western Europe to test some of these predictions. Species number in any of these regions was related to three variables: total area, a measure of the geographic connectedness of the area and latitude. Pooled species numbers were, in general, accurately predicted based on these three simple measures (with correlations over 90% for the overall diversity), but correlations were different for lentic and lotic species. As predicted, lotic species were mostly correlated with latitude (as a surrogate of distance to refugia), while lentic species were only correlated with the measure of connectedness or with area size (Fig. 15.2, Table 15.2). Again, these differences were also observed in each of the four phylogenetically independent lineages of aquatic Coleoptera when analysed separately. The number of species of the five groups studied in Meyer (2000) in each of the 17 areas defined in Illies (1978) show similar differences among running and standing water habitats (Tables 15.3, 15.4). For molluscs, dragonflies and diving beetles, the only variable significantly correlated to the number of lotic species was southernmost latitude. For water mites the number of lotic species was not related to any of the variables studied, and only for Rotifera was connectivity the most significant variable, while latitude was not significant (Table 15.4). On the contrary, lentic species of Rotifera, dragonflies and water mites were highly correlated with area and connectivity, but not latitude. For molluscs and diving beetles there was no significant correlation (at $P < 0.05$) with any of the variables. Interestingly, the

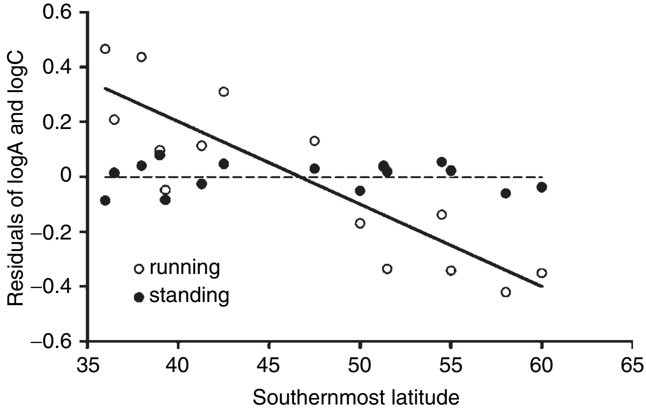

Fig. 15.2. Relationship between the number of lotic and lentic species of aquatic Coleoptera in 15 areas in western Europe and the southern most latitude of these areas, after controlling for area (A) and 'connectivity' (C) (see text and Table 15.2 for details, data from Ribera *et al.*, 2003). The regression line is significant for lotic species ($r^2 = 0.73$, $P < 0.001$), but not lentic species ($r^2 < 0.001$).

Table 15.2. Coefficients of determination (r^2) from multiple regression of the logarithm of the number of species of aquatic Coleoptera in each of 15 areas in western Europe with three geographical variables; Area (in km^2); southernmost latitude (sLatitude); and 'connectivity' (Con), a measure of the largest linear distance connecting each area with their neighbouring ones, intended to be a measure of the ease with which species could move through it.

Habitat	LogArea	sLatitude	LogCon	Combined	Sig.F
All	0.52	0.50	0.40	0.91	<0.00001
Running water	NS	0.56	NS	0.93	<0.000001
Standing water	NS	NS	0.84	–	<0.000001
Both	0.27	0.58	0.42	0.88	<0.0001

Sig. F indicates significance of variable based on an *F* test. Data from Ribera *et al.* (2003).

Table 15.3. The number of species, in five taxonomic groups, in 17 of the western European biogeographic areas defined in Illies (1978) (excluding islands and eastern areas with open boundaries), compiled by Meyer (2000).

					Rotifera				Odonata				Mollusca				Dytiscidae				Hydracarina			
No	Illies	Lat	Area	Con	R	S	B	T	R	S	B	T	R	S	B	T	R	S	B	T	R	S	B	T
1	1	36	689832	424	6	85	55	146	18	30	35	83	27	12	42	81	15	24	5	44	79	63	13	155
2	2	42.5	46768	424	3	42	34	79	9	18	28	55	20	7	35	62	14	17	1	32	63	28	8	99
3	3	38	227995	490	5	128	68	201	13	30	25	68	34	16	47	97	22	30	8	60	38	34	11	83
4	4	43	233841	953	27	184	100	311	14	37	30	81	39	17	46	102	18	31	4	53	147	86	21	254
5	5	42	175381	712	0	42	23	65	8	24	28	60	139	11	46	196	11	25	5	41	35	31	5	71
6	6	36.5	134459	307	1	47	35	83	10	24	31	65	40	82	45	167	13	20	4	37	41	22	6	69
7	7	40	192919	640	0	38	24	62	10	27	28	65	24	11	53	88	10	18	5	33	41	23	2	66
8	8	44	157843	751	6	82	51	139	13	35	29	77	30	10	43	83	14	28	4	46	100	61	18	179
9	9	48	292302	751	81	344	131	556	11	38	29	78	13	16	47	76	11	28	3	42	152	89	22	263
10	10	44.5	204611	738	34	221	98	353	8	37	29	74	16	12	44	72	5	21	2	28	140	21	11	172
11	11	44.5	192919	568	10	159	84	253	8	30	29	67	15	12	43	70	3	20	2	25	35	61	6	102
12	12	43.5	257225	1110	12	221	81	314	11	25	28	64	15	10	48	73	5	17	2	24	22	34	5	61
13	13	42.5	432606	914	10	150	75	235	17	30	27	74	28	14	49	91	15	36	6	57	79	85	19	183
14	14	50	572911	1130	61	412	137	610	9	38	30	77	9	16	48	73	7	32	3	42	75	148	23	246
15	15	53.5	227995	908	16	208	95	319	5	35	28	68	7	16	45	68	3	22	1	26	38	80	14	132
16	20	58	327378	496	5	149	62	216	3	22	0	25	5	13	34	52	4	22	2	28	19	43	7	69
17	22	60	280609	496	5	89	39	133	4	25	14	43	4	14	36	54	1	17	2	20	23	60	11	94

Species were categorized in running water (including springs, R), standing water (S) or both (B) according to the habitat preferences reported in Illies (1978). Illies = Number of the area as given in Illies (1978); Lat = latitude as measured at the southernmost point of the area; Area (in km^2), estimated through image analyses methods; Con = Connectivity of the area (see Ribera *et al.*, 2003 for details).

Table 15.4. Significance of the regression between the number of species, in five taxonomic groups, in 17 of the western European biogeographic areas defined in Illies (1978) (excluding islands and eastern areas with open boundaries) and each of three geographical variables (data from Meyer, 2000; see Table 15.3). Species were categorized in running water (including springs, R), standing water (S) or both (B) according to the habitat preferences reported in Illies (1978).

Habitat	Taxa	Lat	logArea	logCon
logR	Dytiscidae	<0.01	NS	NS
	Hydracarina	NS	NS	NS
	Mollusca	<0.01	NS	NS
	Odonata	<0.01	NS	NS
	Rotifera	NS	<0.1	<0.01
logS	Dytiscidae	NS	<0.1	NS
	Hydracarina	NS	<0.05	<0.05
	Mollusca	NS	NS	NS
	Odonata	NS	<0.05	<0.05
	Rotifera	NS	<0.05	<0.01
logB	Dytiscidae	<0.05	NS	NS
	Hydracarina	NS	NS	NS
	Mollusca	<0.05	NS	<0.05
	Odonata	<0.01	NS	NS
	Rotifera	NS	<0.1	<0.05
logT	Dytiscidae	<0.05	NS	NS
	Hydracarina	NS	NS	<0.1
	Mollusca	<0.05	NS	NS
	Odonata	<0.05	NS	NS
	Rotifera	NS	<0.05	<0.01

Area (in km^2) estimated through image analyses methods; Lat = latitude as measured at the southernmost point of the area; Con = Connectivity of the area (see Ribera *et al.*, 2003 for details).

only group in which lotic and lentic species show a similar pattern (i.e. no relation with latitude and both related with the measure of connectivity) was Rotifera, a group in which most species are good dispersers and have resistant forms (e.g. De Meester *et al.*, 2002). In any case, even for this group and using the same data set, lentic species have significantly larger ranges than lotic species (Fig. 15.1). The higher beta diversity of lotic species is a direct consequence of their smaller ranges and latitudinal gradient in species richness (Hubbell, 2001), and has been documented for European water beetles (Ribera *et al.*, 2003) and Holarctic dragonflies (Hof *et al.*, 2006).

Genetic flow among populations

Using a compilation of published allozyme data on more than 150 species of freshwater molluscs, insects and crustaceans from all over the world, Marten *et al.* (2006) analysed the genetic population differentiation of lentic and lotic species. They concluded that lentic invertebrates exhibit on average lower genetic population differentiation than lotic species, in a consistent way across the three studied groups. Abellán *et al.* (2007) reported high levels of genetic divergence among populations of *Ochthebius glaber*, a species of Coleoptera exclusive to hypersaline running waters in south-east Spain. Although the comparative data were preliminary, nucleotide diversity within *O. glaber* was an order of magnitude higher (0.026 and 0.004, respectively) than a closely related species, *O. notabilis*, which is exclusive to hypersaline standing waters, despite the larger area occupied by populations of *O. notabilis* (from the Pyrenees to the south of the Iberian Peninsula).

Predictions at the level of lineages

In the comparison of species-level phylogenies based on mitochondrial sequences for the lentic *Ilybius* and the lotic *Deronectes*, Ribera *et al.* (2001) found no significant difference in the lineage through time (LTT) plots of the linearized trees, intended to reflect the diversification pattern of a lineage (Barraclough and Nee, 2001). *Deronectes* displayed a higher frequency of recent splits than *Ilybius*, consistent with a higher evolutionary turnover and a higher frequency of recent species. The difference, however, was not significant compared with expected patterns under a constant speciation rate null model. Ribera *et al.* (2001) argued that current methods for analysing species-level phylogenies may not be powerful enough to discriminate contrasting cladogenetic patterns. A different possibility is that lentic and lotic clades may indeed display similar levels of species turnover, but the evolutionary processes take place at very different spatial scales—a Holarctic distribution for *Ilybius*, with some species spanning the whole realm, and a more restricted Mediterranean distribution for *Deronectes*, with abundant endemics with local distributions. In an attempt to find new approaches to compare cladogenetic processes based on linearized trees, I plotted both the distance between nodes in the LTT plot and the estimated length of the branches in decreasing order of magnitude. The distance between nodes in the *Ilybius* tree (lentic) follows an almost perfect logarithmic decrease, while the *Deronectes* tree shows a hollow curve with an excess of very large and small values (Fig. 15.3). This difference is not reflected in the standard deviation (0.01 in both cases), but in the kurtosis (10.4 and 0.6 for *Deronectes* and *Ilybius* respectively). The biological interpretation of the kurtosis is less straightforward than more commonly used statistics, but it can be taken as a measure of the high-level heterogeneity of the data (i.e. the way variance is distributed, Sokal and Rohlf, 1995).

The situation is similar when plotting the logarithm of the length of the branches (Fig. 15.4). The branches of the tree of *Ilybius* follow a linear trend, without apparent outliers, when plotted in decreasing order, suggesting that the logarithm of the time between cladogenetic events (as reconstructed in the phylogeny, i.e. with missing data and including extinctions) has a uniform random distribution. The distribution of branch lengths for the *Deronectes* tree is very similar, other than the presence of an excess of branches at the shorter end of the spectrum (Fig. 15.4). Again, this difference is mostly reflected in the kurtosis of the distribution: 7.4 for *Deronectes* and −0.2 for *Ilybius*.

The results of the comparison of the distribution of branch lengths and internodal distances in the LTT plots suggest a higher irregularity or unpredictability

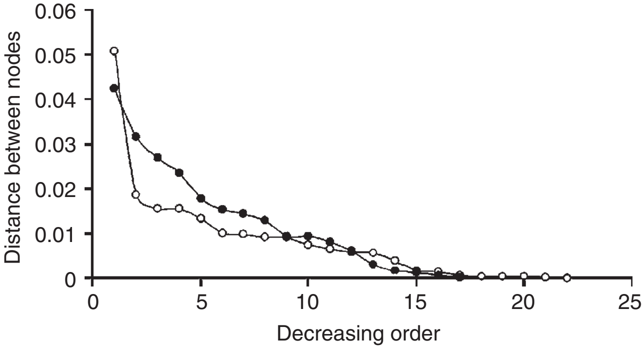

Fig. 15.3. Distance between nodes in the lineage through time plot (LTT) of the linearized phylogenies of the genus *Deronectes* (lotic, white circles) and *Ilybius* (lentic, black circles), sorted in decreasing order (data from Ribera *et al.*, 2001). The distances between nodes in the lentic tree follows an almost perfect logarithmic decrease ($r^2 = 0.99$), while those of the lotic tree have an excess of extreme high and low values ($r^2 = 0.85$) (higher kurtosis, see text).

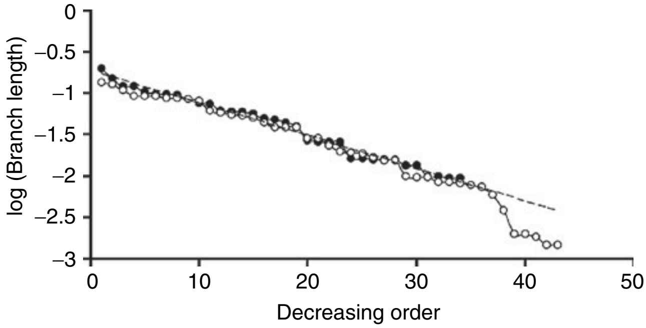

Fig. 15.4. Logarithm of the branches in the linearized phylogenies of the genus *Deronectes* (lotic, white circles) and *Ilybius* (lentic, black circles), sorted in decreasing order (data from Ribera *et al.*, 2001). The branch lengths in the lentic tree follow an almost perfect straight line ($r^2 = 0.98$), while those of the lotic tree have an excess of extreme low values (higher kurtosis, see text).

of the cladogenetic processes in the lotic lineage. To what extent this is a general result, and if this can be taken as evidence of a higher evolutionary turnover, are still open questions.

What's Next?

Alternative explanations

Initial objections that could be levelled at the framework outlined in this chapter include the possibility of artefacts due to idiosyncratic factors of the groups studied, or a biased distribution of habitat types in the studied areas. These types of alternative explanations lose strength when other geographical areas and taxonomic groups match the predictions (e.g. North American dragonflies, Hof *et al.*, 2006; Madagascan mayflies, Monaghan *et al.*, 2005; or a wide variety of aquatic macroinvertebrates, Meyer, 2000; Marten *et al.*, 2006). More difficult to address is the possibility that the factor driving the observed differences is not the contrasting long temporal stability of the habitat, but its ecological heterogeneity at shorter temporal scales. If lentic environments were ecologically more variable than lotic habitats at temporal scales much smaller than the lifespan of some organisms (e.g. daily variations on temperature, oxygen concentration; or seasonal variations in water level, amount of vegetation, temperature, etc.), the need to withstand wider ecological conditions may result in a wider geographical range (a similar mechanism to that used by Stevens, 1989, to explain Rappoport's rule). Once differences in the size of the geographic range are established, some of the processes detailed above will start to take place and, consequently, the observed patterns will also be similar (Dynesius and Jansson, 2000; Harley *et al.*, 2003; Jablonski and Roy, 2003; Qian and Ricklefs, 2007).

Under this alternative scenario, there does not need to be any difference in dispersal ability. Consequently, there should be no differences in genetic geographical structure among populations at the same geographical scale, and latitudinal gradients should not be related to post-glacial colonization. While the presence of latitudinal gradients could be related indirectly to ecological tolerance (Stevens, 1989), the observation of clear differences in the genetic structure of populations at the same geographic scale does not seem to support this interpretation. These two possibilities (differences in ecological heterogeneity at short temporal scales and differences in long-term stability) are compatible and it is possible that both may contribute, in a different proportion depending on the circumstances, to the global patterns reported here.

The paradox of the 'living-dead'

If the scenario outlined here is accurate, species living in running waters have similar characteristics to those considered 'super specialists': reduced size of the geographical range, genetic isolation and fragmentation of populations, and high probability of extinction. When habitat characteristics are kept through successive cladogenetic events (either for phylogenetic inheritance or *de novo* habitat constraints due to a specific geographical setting), the question becomes how could these lineages survive despite the high probability of extinction, i.e. why do old running-water clades occur at all? Other than by chance (given enough of them, some will survive), an obvious possibility is the regular renewal of the clade by the appearance of a widespread lotic species, which could start a new cycle of differentiation and fragmentation (and eventually extinction). It is important to remember that the habitat constraints are not symmetrical: while lentic species *have to* move when the habitat disappears, lotic species *do not need* to move that frequently. Thus, while among lentic species the frequency of outliers (i.e. species with small ranges) is expected to be low, within lotic lineages it is not rare to find widespread species (Ribera and Vogler, 2000). The possibility exists that these widespread lotic species act as 'diversity pumps', extending the range of existing clades and keeping a constant supply of new species, in a similar case to the 'taxon cycle' or 'taxon pulse' (e.g. review in Liebherr and Hajek, 1990). The situation will be similar to that described by Janz *et al.* (2006) with butterflies, in which high diversity may be kept through cycles of range expansion by host switching and subsequent diversification by fragmentation. Specialization alone cannot generate diversity as it is only a 'pruning' process; to generate diversity, consecutive cycles of generalists (by incorporating new hosts) and subsequent specialization would be necessary (Janz *et al.*, 2006). The question remains as how these 'generalist' (i.e. widespread) species appear in the first place, that is, how the constraints that act on most species in the same habitat (so that patterns are highly significant statistically) are not relevant in some particular cases.

Disregarding the possibility of taxonomic artefacts, there are different possibilities as to why a lotic species may have a widespread geographic range.

(i) *Ecological particularities*. Some taxa may be tied to particular microhabitats, or habits, that select for high dispersal abilities, even if they are usually found within a general lotic setting. For example, some of the species traditionally considered as 'aquatic' are in fact riparian. Among aquatic Coleoptera, this is the case with many species of Dryopoidea that have widespread distributions despite being exclusively associated with running waters (e.g. there are no presently recognized Iberian endemics among Limnichidae, Heteroceridae or Dryopidae). It is likely that riparian species are constrained by different factors than those affecting true aquatic species (e.g. most of them are good fliers, with very good dispersal abilities).

(ii) *Relative age of the species*. There may be a 'species life cycle', with young species originating in a small area, dispersing to reach a maximum stable distribution and then contracting again on the way to extinction (e.g. Taylor and Gotelli, 1994; Gaston, 1994, 2003; Webb and Gaston, 2000; Vrba and DeGusta, 2004; Foote *et al.*, 2007). Under this scenario, the average shorter duration of lotic species would be a contributing factor to their smaller ranges, as they would have little time to reach their full potential distribution. Species that, for any reason, escape extinction could reach a wider geographical range.

If this was the case, young species will have restricted distributions around their centre of origin, 'mature' species will have widespread distributions and old species will have restricted relict distributions, not necessarily close to their centre of origin. To distinguish between restricted distributions around the centre of origin and relict distributions (in the sense of remains of a former wider geographical range), the relative geographical position of the species in the clade could be studied. It is expected that, in species remaining in their centre of origin, geographically close species will also be phylogenetically close. On the contrary, species with relict distributions will not necessarily have their closest relatives in geographically close areas.

(iii) *Privileged geographical position.* In the Western Palaearctic, widespread lotic species tend to have a central and north European distribution, i.e. including the areas most affected by the Pleistocene glaciations. Among the water beetles, in these areas there are few, if any, species with restricted distributions (Ribera *et al.*, 2003). Two main hypotheses have been put forward to account for this pattern.

First, the Mediterranean as a refuge (e.g. Hewitt, 2000): During the glacial maxima, the populations of most European species were confined to refuge areas in the southern peninsulas, from where they would have re-colonized the continent in the interglacials. The flow of migration would be mostly south to north, with southern peninsulas acting as a 'melting pot' in which genetic diversity is maximal, and northern populations being a subset of the southern genetic diversity. Widespread species will be those that could re-colonize Europe after the glaciations; species with restricted distributions, those that would remain in one of their refuges, having (for any reason) being unable to re-expand.

Second, the Mediterranean as an area of endemism (Bilton *et al.*, 1998; Ribera and Vogler, 2004): Rather than a source of re-colonizers, the southern peninsulas are a source of endemism: the isolation during the glacial cycles was enough to prevent genetic flow among the peninsulas and mainland Europe. These southern endemics would not re-colonize the European mainland, but remain confined as species with restricted distributions in the southern areas. The flow of migration was mostly east–west, rather than north–south. Only the species/populations in the areas at the edge of the southern peninsulas (e.g. Pyrenees, Alps, Carpathians) would be able to expand their ranges to the north, with most of the species/populations in the south being isolated and genetically homogeneous, but distinct from those in mainland Europe. Widespread species will be those that remained in, or next to, mainland Europe; species with restricted distributions those that were geographically isolated in the southern peninsulas.

Under the first scenario, the genetic diversity of the southern populations of the widespread species will be maximal, and the species with restricted distribution will not follow a clear geographical pattern (i.e. species geographically close will not necessarily be phylogenetically close). Under the second scenario, the genetic diversity of the widespread species does not need to be larger in the southern populations, and species with restricted distributions will have a clear geographical pattern (phylogenetically close species will be geographically close).

(iv) *Differences in the ecological tolerance of the species*. Species with restricted distributions may have a limited physiological tolerance, whereas widespread species may be able to cope with a wider range of environmental or habitat conditions. To be considered an explanation of the differences in the size of the geographical range of closely related species, the physiological differences must precede the range expansion of the widespread species, and not result from a subsequent adaptation to the local conditions. The range of the widespread species also has to be ecologically and climatically more diverse than that of the species with restricted distributions.

(v) *Stochastic processes*. Gaston and He (2002) found that a stochastic null model fits several range size distributions well, so the question is whether there is even a pattern to explain. Given enough species, and assuming there is some variance in the distribution of size ranges, there will always be some widespread species among lotic lineages that, on average, may still have much smaller ranges than their lentic counterparts.

Further Work

Although most evidence so far supports the model presented here, there are areas in need of further study. The most prominent among them is perhaps to test some of the macroecological patterns in less well-studied southern areas, as well as in a wider range of macroinvertebrates. Obvious candidates, for which enough information is available for several groups, include Australia, Southern Africa or austral South America. The study of the same groups (e.g. aquatic Coleoptera) will allow the direct comparison with areas in the northern hemisphere, but the inclusion of other groups will allow wider conclusions – especially if there are differences among them that could be interpreted in terms of differences in ecology, life cycle or other biological characteristics.

Some of the straightforward predictions of the model are untested, although in many cases work is in progress. Thus, the Quaternary beetle record offers an untapped possibility of comparative studies, despite the limitations outlined above. Similarly, the wealth of descriptive methods to model distributions and potential niches could be used to compare the match between potential and realized niches in lotic and lentic species, or to introduce habitat as a predictive factor in models of global change or habitat alteration.

More complex are tests of the predictions of differences in the probability of habitat shifts, and in the evolutionary turnover of lineages. In the later case, it is expected that this high turnover will leave a signal in both the topology of the tree and the distribution of branch lengths or internodal distances (as measured with LTT plots), but these are notoriously difficult to characterize and to compare in a statistical framework (see above). Simulations are a potential powerful tool for these kind of comparisons, although the risk exists of oversimplification, which could lead to a decrease in statistical power.

There is also the problem of how to integrate differences in geographical scale in the comparison of phylogenetic trees. When confined to the same geographical space, the prediction is that two lineages of contrasting habitat types will develop according to the model outlined here. However, if space is not a limiting factor, the outcome may be less clear: the genetic/evolutionary processes may result in the same topological or diversification patterns, but at very different geographical scales (Ribera *et al.*, 2001). More specifically, it could be that two species have the same metapopulation dynamics over their whole range, with a given level of geographic isolation among populations, amount of genetic variation and geographic structure, as measured, for example, by haplotype distribution and divergence, degree of isolation by distance, etc. In a scale-less geographical matrix, both species may be indistinguishable when looking only at haplotype trees, networks or other measures of population genetic structure, but may have contrasting absolute sizes of the geographical range—which implies that, if confined to a similar space, both would have very different dynamics.

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