Chapter 3
Dispersal by Aquatic Insects

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Abstract All habitats change over time, so most organisms must resist unfavorable conditions or disperse to more favorable localities. Typically, aquatic habitats are relatively short lived because of drying or infilling. Aquatic insects, then, often have adaptations for effective dispersal, sometimes over long distances and most often by flight. This chapter examines some of the environmental drivers and organismal responses that affect the nature of dispersal. These include consideration of how different habitats affect dispersal, especially some differences between lentic and lotic habitats. Dispersal characteristics may also have major effects on genetic structure of populations. Both selective forces and proximate cues affect when insects disperse and when and where they colonize new habitats; availability of space, presence of predators, and availability of food may all play a role, depending on species and circumstances. Adaptations for dispersal include, in addition to active flight, behaviors that promote passive movement by wind, dispersal polymorphism (i.e., changes in body structure, such as wing development, that enhance dispersal, usually hormonally controlled and incurring some cost in fecundity), increased body size, and timing of diapause and reproduction. In a few species dispersal extends to migrations of hundreds of kilometers and may have important seasonal effects on habitats of origin and of destination. Dispersal is also integral to the concept of metapopulations and in fact may be a major driver of community composition and dynamics. Simultaneous dispersal of very large insect populations can have an important effect on nutrient and energy flow to and from communities. Finally, dispersal may be a critical determinant of whether and how aquatic insects respond to climate warming.

Keywords Geographic range · Use of habitat · Habitat template · Community dynamics · Climate warming

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3.1 Introduction

Dispersal is one of the fundamental processes that influences the ability of organisms to reach suitable habitats, to find mates, and to avoid potentially disastrous disturbances. It can also have major effects on geographic range, genetic structure of populations, population persistence, and movement of energy and nutrients. Because the habitats of aquatic species are physically relatively well defined and cover broad ranges of size, permanence, and faunal complexity and because it is often relatively easy to maintain small populations and communities in the laboratory or under seminatural conditions they lend themselves to many sorts of observational and manipulative studies that are more difficult in many other animals. My hope is that this chapter will make clear some of the fascinating questions that have been and can be addressed using aquatic and semiaquatic insects as subjects.

3.2 The Evolution of Dispersal by Flight

The evolution of wings was the sine qua non of most insect dispersal, and one of the great morphological innovations of Metazoa—the first wings on earth. A brief discussion of that landmark therefore seems appropriate, especially since aquatic insects may have been the first to evolve proto-wings. For many years, most entomologists subscribed to the idea that insect wings developed from paranotal lobes, flattened extensions of the thoracic terga, and present on many Paleozoic insect fossils (Snodgrass 1935). The work of Kukalová-Peck (1978, 1983), however, based on detailed analysis of fossil morphology, turned the focus to aquatic taxa. She argued that wings originated as outgrowths of the insect pleura, possibly as modifications of movable gill covers that were found on the thoracic and abdominal segments of aquatic Paleozoic insect nymphs and that have a pattern similar to the inferred plesiomorphic pattern of veins in the wings. Although modifications of her scheme have been proposed (Trueman 1990; Elias-Neto and Belles 2016; Linz and Tomoyasu 2018), the main features seem likely to endure. Marden and Kramer (1994) suggested that the behavior like that of brachypterous stoneflies skimming across the water surface might have been a predecessor of flight, implying that flight may actually have originated in aquatic insects (but see Dudley et al. 2007). Wings then enabled insects to reach and exploit almost every nonmarine habitat on earth.

3.3 The Habitat Template

No habitat is perfectly stable, although change may occur at timescales ranging from hours to millennia. All eventually change owing to physical and/or biological processes, including human disturbance. Consequently, most organisms must be able to evade or resist unfavorable conditions. Aquatic insects, especially those inhabiting temporary ponds or pools, may resist periodic drought by, e.g., burrowing into mud or sheltering under vegetation or stones as adults or (rarely) larvae, diapausing in a drought-resistant form, or entering a terrestrial adult life stage (Batzer and Wissinger 1996). Most, however, have at some time in their life cycle the capacity to move from their area of birth or current residence to another, more suitable area. Many species that inhabit seasonal ponds and wetlands develop rapidly, with the resulting adults flying to permanent waters where they pass the dry season, in some cases reproducing there and in others returning to temporary waters for reproduction (Batzer and Resh 1992; Batzer and Wissinger 1996; Saijo 2001). Other insects may pass the dry season as adults in reproductive diapause (Corbet 1999). This movement from their birthplace or place of initial reproduction to other locations is dispersal, the subject of this chapter.

Dispersal of aquatic insects is not usually observed directly, and almost never from departure to arrival at a new habitat patch. Most often it is inferred from changes in populations in response to seasonal or other environmental changes. Sometimes direct observation of important portions of the dispersal process is possible and very useful, however. This is usually most feasible with large, diurnal species such as dragonflies (e.g., Russell et al. 1998; Wikelski et al. 2006; Anderson 2009; May 2013) or in cases of unusual dispersing swarms of smaller insects (e.g., Stevens et al. 2007). Mark-recapture methods have sometimes been useful, notably by using fluorescent powders to mark mosquitoes (e.g., Service 1993; Epopa et al. 2017; this technique does not allow discrimination of individuals) or paint marks or numbers on wings of Odonata (e.g., Michiels and Dhondt 1991) and on several species of water striders (Gerridae; Ditrich 2016), corixid bugs (water boatmen; Boda and Csabai 2009), and dytiscids (predaceous diving beetles. Davy-Bowker 2002). Medeiros et al. (2017) marked large numbers of the mosquitoes, *Culex quinquefasciatus and Aedes albopictus*, by adding small amounts of $^{15}KNO_3$ or ^{14}C-glucose to water in plastic tubs colonized by wild mosquitoes. Using light traps for recapture, they determined that *C. quinquefasciatus* females seeking oviposition sites often dispersed 1–2 km from the marking site while females of *A. albopictus* seldom went further than 300 m. Thus, despite the limitations of all mark-recapture techniques, a great deal has been learned through careful observation and experiment with both undisturbed and manipulated populations.

In general, dispersal increases in frequency and importance as habitat stability declines and habitat isolation increases (Southwood 1962). Some aquatic habitats are effectively permanent, including large, deep lakes, e.g., L. Baikal, estimated to be 20–25 million years old (Wikipedia 2018a), and a few river channels (Wikipedia 2018b; even if these estimates are correct, however, the habitats in these rivers have probably changed radically over the millennia). The vast majority of aquatic environments are of relatively short duration, and many still waters, such as shallow lakes, ponds, and wetlands, are seasonal or sometimes dry for several years at a time. Datry et al. (2014) estimated that ca. 30% of the total length of rivers globally are intermittent. Thus many aquatic habitats are relatively unstable and isolated from similar habitats by environments that are unsuitable for aquatic insects. Some aquatic species can survive desiccation in a state of diapause, commonly as eggs (e.g., Williams 1996; Corbet 1999), but for many dispersal is an essential, often urgent, adaptation that affects individual fitness, population and metapopulation dynamics, and community composition and persistence.

Intermittent rivers notwithstanding, still, or lentic, waters are much more likely to desiccate or suffer from other catastrophic events at relatively frequent intervals and will eventually be obliterated by sediment infilling. Moreover, lentic habitats are generally less interconnected than are lotic (running) waters, which normally are continuous with other streams and river systems. For that reason, insects of lentic waters are expected to have greater powers of dispersal than lotic species. Despite the difficulty of observing dispersal directly because of the small size of most insects and the difficulty of marking and recapturing large numbers, this expectation is supported indirectly by numerous studies.

For example, Arribas et al. (2012) studied sister species pairs of hydrophilids (water scavenger beetles) and showed that the member of each pair that lives in ponds had a substantially larger geographic ranges and longer wings than their stream-dwelling relative, both of which suggested greater powers of dispersal. Ribera and Vogler (2000) found that other aquatic beetles from lentic habitats had on average considerably larger ranges than lotic species in the Iberian Peninsula. On a wider geographic scale, Ribera et al. (2003) showed a similar difference, as well as higher species turnover, among lotic species throughout Europe. These differences were also present in each of the four independent beetle clades. Hof et al. (2008) presented evidence that in freshwater animals generally, not only insects, lotic species richness in Europe declines steadily with latitude, suggesting poor dispersal from southern Pleistocene refugia from glaciation, while lentic species richness showed a maximum at intermediate latitudes, and β-diversity (a measure of species turnover) was greater at any latitude for lotic than for lentic species, suggesting less mixing of populations among the former. Hof et al. (2012), using more detailed information on the European ranges of Odonata, found that lentic species usually occupy more of the projected suitable range, based on climatic characteristics, than do lotic species, again suggesting that the former disperse more readily into areas made suitable by a warming climate. Finally, many species of southern European Odonata have recently expanded their range northward, probably in response to climate warming, but this effect has been much stronger in lentic than in lotic species (Grewe et al. 2013). All these studies, however, measured presumed indicators of dispersal rather than dispersal directly, and comparable data apparently are not available from other continents.

Perhaps the most persuasive evidence of the correlation of range size with dispersal capacity is that of McCauley et al. (2014) for North American Libellulidae. These authors used data from McCauley (2007) on observed dispersal distance and rate from natural source populations to initially uninhabited artificial ponds. This was used along with two measures of niche breadth and several other variables as possible factors that might explain range in multiple regressions; only dispersal and niche breadth had significant effects, positive in both cases, on range size, which was extracted for each species from the web site, OdonataCentral (https://www.odonatacentral.org/) as of 2007.

Another indicator of the relative degree of dispersal is the genetic structure of populations. In species with high rates of dispersal, populations should experience a high level of genetic exchange, whereas if dispersal rates are low populations are more isolated and genetic differentiation among populations should be higher. This is commonly expressed in terms of F_{ST} (Wright 1951), which is a measure of the relative extent of genetic variation among subpopulations; the value ranges from 0, if the entire population is randomly mixed, to 1 if all variation is between, rather than within, subpopulations. Since the advent of allozyme frequency analysis, and especially of DNA sequence analysis, population structure of many organisms has been measured in this way. For example, Marten et al. (2006) compiled F_{ST} values for European aquatic molluscs, crustaceans, and insects. In all three cases, lotic species had, on average, significantly higher F_{ST}s. As might be expected, average F_{ST} values were lower in insects generally than in the other organisms, since among these only insects can fly.

On the other hand, such broad generalizations may obscure a great deal of variation within and overlap among habitat types. Short and Caterina (2009), e.g., demonstrated that three largely sympatric, lotic beetles in southern California diverge markedly in genetic and phylogeographic population structure and corresponding variation in inferred population connectivity. They varied from practically unstructured, implying almost complete mixing throughout the entire population, to having an extremely close correlation of haplotype with geographic origin, thus presumably very little movement away from their place of origin. Likewise, Phillipsen et al. (2015) compared population genetic structure in three lotic species, *Abedus herberti* (a flightless bug), a stonefly, *Mesocapnia arizonensis* (males brachypterous, females fly), and *Boreonectes aequinoctialis* (a strong-flying beetle). All three showed precisely the genetic pattern that was predicted: *A. herberti* had high mean and variance in genetic distance among populations, and no indication that this was affected by geographic distance (i.e., almost no genetic mixing among its isolated populations); *Boreonectes* had very low mean and variance of genetic distance, and again no effect of geographic distance (populations all very similar because of great dispersal ability and intermixing); and in *Mesocapnia* the mean and variance increased smoothly with distance (i.e., so-called isolation by distance, consistent with intermediate dispersal; Fig. 3.1). Thus, while the broad patterns found by Marten et al. (2006) are probably correct, many individual exceptions surely exist.

Although streams are typically more stable than lentic waters, organisms in streams that dry up partly or entirely face many of the same problems as those of still waters. In some cases residual pools remain throughout the dry season and can provide refuges for at least some stream inhabitants, and a few species may shelter in the hyporheic zone (Stubbington 2012), but others must either disperse to running streams or diapause in a drought-resistant form (e.g., Corbet 1999; Garcia and Hagen 1987). A form of disturbance peculiar to streams is the occurrence of spates, or sudden floods may displace organisms far downstream. These may be avoided by movement into the hyporheic region, which seems to be a more common and

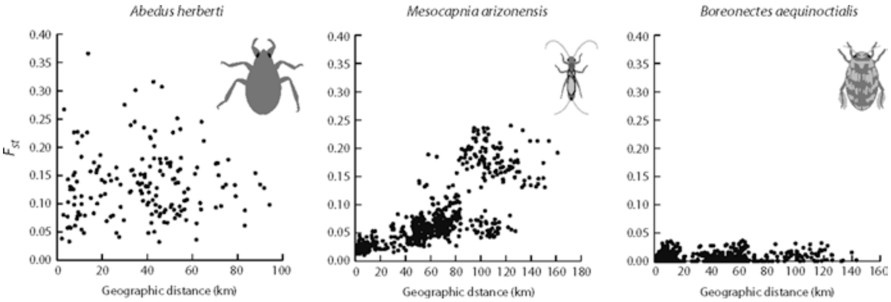

Fig. 3.1 Relationships between genetic distance (Fst) and geographic distance in three species of desert insects from the southwestern USA. The pattern for *Abedus herberti* shows highly variable genetic distance with virtually no relationship to distances between populations, suggesting that there is very little genetic exchange even between nearby populations. In *Mesocapnia arizonensis* nearby populations are more similar genetically than are distant populations, i.e., isolation by distance. *Boreonectes aequinoctialis* populations are all closely similar in genetic characteristics irrespective of distance between them, indicating that the regional population is essentially panmictic. Figure from Phillipsen et al. (2015), used with permission

successful strategy in the face of spates than in drought (Stubbington 2012), by sheltering under rocks or other in-stream objects, or, especially in univoltine species, by timing adult eclosion for the end of the dry season, so that most larvae have exited the stream just before the onset of flooding (Corbet 1999; Lytle 2008; pers. obs. 1994). In addition, many very small larvae may disperse short distances into the hyporheic zone, possibly to avoid predators as well as physical stresses (Mugnai et al. 2014; Williams 1981).

Lotic organisms also face another challenge that has received a great deal of attention over the years. Because of the persistent downhill flow of water in streams, their insect inhabitants, as well as other aquatic organisms, will tend to be displaced downstream; this is known as drift and has been documented in a number of lotic systems (e.g., Waters 1972). Thus headwater streams apparently would be depleted of aquatic fauna in the absence of substantial compensatory upstream movement. This process was first described explicitly by Müller (1954, 1982), who called it the "colonization cycle" (also known as "drift compensation" or "the drift paradox"). Müller presented data in support of his ideas, but subsequent tests of the phenomenon have been inconclusive; one study using stable isotope labeling with ^{15}N strongly supported the pattern of drift and return in arctic mayflies (Hershey et al. 1993), and Coutant (2008) used a similar technique to recover caddisflies up to 16 km upstream from a source of effluent of ^{65}Zn, but Briers et al. (2004), using ^{15}N as a label, showed little indication of preferential upstream movement in stoneflies in Wales. Several studies using malaise traps or sticky traps along a stream have obtained equivocal results (e.g., Svensson 1974; Bird and Hynes 1981; Williams and Williams 1993; Macneale et al. 2004; Winterbourn et al. 2007).

Anholt (1995) was probably the first to suggest that "drift compensation" by mass upstream movements of adults may be unnecessary if repopulation is density dependent; that is, under reasonable assumptions, if drift depletes larval populations upstream it is likely that the offspring of only a few adult pairs or gravid females can replenish the population, since few existing larvae will be present to compete with the newly colonizing individuals. This basic idea has been refined (Pachepsky et al. 2005; Mazzucco et al. 2015) and appears to provide a reasonable mechanism for maintenance of upstream populations, but without accurate measurements of insect movements it is difficult to verify in detail. It is also possible in some cases that movement of aquatic larvae, by swimming or crawling upstream, might partly reverse the effects of drift, and significant upstream crawling has been reported (Elliot 1971; Hershey et al. 1993; Williams and Williams 1993), although most investigators have found this to be of much less importance than adult flight (e.g., Graham et al. 2017). Humphries and Ruxton (2002), however, modified Anholt's model to show that, under some reasonable assumptions about population size and persistence, upstream crawling of less than 1 m might be sufficient to compensate for drift without reliance on adult flight. Substantial upstream crawling by larvae can occur (Graham et al. 2017) and may even facilitate independent habitat selection by larvae. Galatowitsch and Batzer (2011) observed large numbers of mayfly larvae moving upstream against strong currents into floodplain wetland, where they enjoyed faster growth than in the adjacent river channel.

Another fraught issue in the study of dispersal of insects in lotic habitats is the extent of overland movement away from natal streams that might indicate dispersal to separate streams or watersheds. It is clear that many insects do move along streams or stream valleys (e.g., Bogan and Boersma 2012). Most studies using passive traps have concluded that lateral movement away from streams is small, often less than 100 m (e.g., Collier and Smith 1998; Griffith et al. 1998; Briers et al. 2002; Petersen et al. 1999). In contrast, some genetic studies suggest substantial gene flow among separate watersheds at distances of up to tens or even hundreds of kilometers (Wilcock et al. 2003, 2007; Chaput-Bardy et al. 2008; Hughes et al. 2011). A possible reconciliation of these results is suggested by Didham et al. (2012), who placed arrays of passive interception traps at standardized distances from several streams, both at ground level and in the canopy of adjacent forest fragments approximately 15 m above ground. They collected more than three times as many adult aquatic insects in the canopy as at ground level, including at more than 1 km (the greatest distance of trap placement) from the nearest stream, although with some differences among taxa. Thus the apparent discrepancy between trapping and genetic results may stem, at least in part, from trapping schemes that failed to collect a majority of dispersing adults because traps were only placed at ground level.

Somewhat counterintuitively, several studies have demonstrated appreciably greater genetic uniformity across catchment basins than among reaches within streams (Bunn and Hughes 1997; Schmidt et al. 1995; Miller et al. 2002; Hughes et al. 2011). This could be explained by the so-called "patchy recruitment hypothesis" (Bunn and Hughes 1997). If each section of stream is colonized by offspring of only a few individual insects, then the allele complement in different reaches may differ strongly simply by the accident of which females oviposited there. If, at the same time, there is ample mixing of populations across catchments, the genetic profile of each catchment, which would include many individual reaches, should be similar to others in the region. This pattern may be common in many situations, although it seems less likely in taxa that emerge synchronously and oviposit quickly thereafter (Bunn and Hughes 1997) or that maintain large populations in very stable habitats (e.g., Krosch et al. 2011). Another pattern shown by some populations of insects confined to headwater streams, especially in mountains, is that populations in different catchments are more closely related to others on the same mountain than to lower portions of the same catchment. This suggests that such species are limited, possibly by temperature and stream gradient, to the uppermost reaches of streams but can disperse overland to nearby headwaters of other systems originating on the same mountaintop (Finn et al. 2007). Hughes et al. (2009) summarize the characteristics and predictions of these and several other models of genetic exchange.

3.4 Cues for Dispersal and Colonization

Given that dispersal allows organisms to anticipate and avoid deterioration of their habitat, what are the indicators of decline, currently or in the near future? Besides leaving a deteriorating habitat, dispersing individuals must locate and, often, assess the suitability of a new locale. This section examines some of the known solutions to these exigencies.

3.4.1 Initiation of Dispersal

Few experiments have addressed the direct effects of drying of water bodies on insect dispersal. Boersma and Lytle (2014) placed individuals of the giant water bug, *Abedus herberti*, which occurs in intermittent streams in the southwestern USA, into small tanks either with or without water and lined with screening so the insects could escape. These were placed into larger outer tanks that contained water. After 24 h, ten times as many bugs had left the dry small tanks as the small tanks with water. Velasco and Millan (1998) studied one hydrophilid and two dytiscid beetles and a corixid bug (water boatman), also from intermittent streams, and found that two of the beetles and the corixid left their aquaria if the water temperature was raised to about 40 °C. In addition, they found that, when they placed individuals of the same species in aquaria with different depths of water, from 10 cm deep to entirely dry, all of the beetles flew or crawled out of the aquaria when the depth was 1 cm or less; the corixid did not respond to water depth. In each replicate, 5–10 individuals of a single species were placed in the same aquarium, irrespective of depth, so it is possible that the beetles were responding to crowding rather than to water depth per se (Boersma et al. 2014). *Rhantus* spp. (Dytiscidae), which live primarily in temporary seepage pools, also respond to crowding with escape behavior (which would lead to dispersal), and to high temperature and to unsuitable substrate (smooth glass bottom in experimental containers; Smith 1973). Drummond et al. (2015) observed assemblages of insects in natural scour pools during progressive drying; emergence rates of most, but not all, taxa increased as drying progressed. Some larval mosquitoes from temporary pools accelerate development in response to drying (Chodorowski 1969; Schäfer and Lundström 2006); Chodorowski (1969) also observed slowing of development when pools were diluted with rainwater. On the other hand, De Block and Stoks (2005) found that damselfly larvae (*Lestes viridis*) from temporary ponds actually developed more slowly and emerged later than controls as water volume was reduced in outdoor tubs, although individuals that hatched late in the season did accelerate development (and see Johansson and Rowe 1999). The authors suggested that in this case crowding increased competition for food, which made rapid growth impossible. Jannot (2009) showed that development time in the caddisfly, *Limnephilus indivisus,* was unaffected by water depth but female size at eclosion was reduced. Some *Asynarchus* caddisfly larvae, which live in high-altitude snowmelt basins, become aggressive toward and may cannibalize conspecifics in response to high temperature, crowding, and lowered water level; this behavior may accelerate pupation and allow for successful dispersal by the resulting adults (Lund et al. 2016). Based on statistical analysis of field trap catches, Klečka (2008) concluded that dytiscids, hydrophilids, and scirtids (marsh beetles) in the Czech Republic made more dispersal flights when water in occupied pools was low. Finally, Lytle et al. (2008) observed large numbers of adult water beetles and dragonfly larvae displaying uncharacteristic positive rheotaxis and crawling upstream in a desert stream just ahead of the receding waterline of a drying stream reach.

An excess of water, at least in lotic habitats, can be nearly as harmful as the absence of water. Particularly in arid regions subject to occasional heavy rains, spates may represent a substantial danger to aquatic organisms, and several taxa, especially Hemiptera and Coleoptera, in the arid American southwest climb out the stream bed in response to rainfall and escape the danger of flash floods (Lytle 1999, 2001; Lytle and Smith 2004). Alternatively, some insects may time adult eclosion to just precede the onset of rains, thus avoiding spates (Lytle and Smith 2004). A number of other stimuli can induce dispersal, and their effect may depend in part on the phenotype of the dispersing insect.

One might imagine that the presence of predators would promote dispersal, but this has not often been demonstrated. The clearest evidence of a direct effect on dispersal behavior is probably the work of McCauley and Rowe (2010) and Baines et al. (2015, 2018) on the backswimmer, *Notonecta undulata*, in mesocosms (water-filled cattle tanks). In the first of these studies, the authors showed that in the presence of predators (caged fish that could not actually reach the insects), *Notonecta* dispersal increased dramatically in the presence of one fish, but there was no significant additional effect of adding a second fish. If one or more *Notonecta* were deliberately fed to the fish, however, there was a sharp increase in dispersal that increased further as additional *Notonecta* were eaten; therefore, these insects are sensitive not only to the presence of predators but also to some signal that conspecifics were consumed. The experiments of Baines et al. examined the effects of predators in combination with body condition adjusted by pre-experimental feeding regime (Baines et al. 2015), or conspecific density and predation (Baines et al. 2018). In the first experiment, emigration was higher in the presence of caged fish, irrespective of body condition. Better-conditioned bugs initially emigrated more rapidly than those in poorer condition, but the effect declined over time so the difference was marginal for the entire experiment. In the later study emigration increased across three levels of increasing density. Predation significantly increased emigration only at medium density for reasons that were not clear. Dispersal was also positively correlated with beetle density in dytiscids (Yee et al. 2009). Plant density was also manipulated and had a significant but small negative influence on dispersal.

The effect of predators on dispersal of mayfly (*Baetis* spp.) larvae has been investigated extensively by Peckarsky and her colleagues. *Baetis* usually coexist with insectivorous trout in mountain streams and in fact maintain higher densities in streams with trout than without (Peckarsky et al. 2011). They feed by drifting with the current until they encounter rocks with good patches of benthic algae, so they drift more in streams with less food available (Hernandez and Peckarsky 2014). Peckarsky and McIntosh (1998) placed larvae in one of the four mesocosms with flowing water and stones with roughly uniform growths of algae: (1) exposed to water dripping from a tank containing trout, (2) trout odor and predaceous stonefly larvae with mandibles glued so they could not prey on the mayflies, (3) stonefly larvae and odorless water, and (4) odorless water and no stoneflies. All *Baetis* were predominantly active at night, but fish odor reduced drifting sharply during the night. The presence of stoneflies increased crawling during the day in the absence of fish odor and drifting at night with or without fish odor. Thus fish tended to reduce dispersal while the presence of stoneflies increased dispersal even in the absence of actual predation (Peckarsky et al. 2008; Peckarsky et al. 2011). Wooster and Sih (1995) review earlier work on the effects of predators on drift in stream insects.

Because dispersal is a crucial part of the adaptation of an animal's life cycle to its environment, it must be coordinated with other facets of the life cycle, e.g., adult eclosion and timing of reproduction. Photoperiod supplies a cue that triggers many events in the lives of insects. Apparently no evidence has demonstrated a direct effect of photoperiod on dispersal, but certainly events that are closely coordinated with dispersal are strongly influenced by photoperiod. Lytle (2002, 2008) showed how photoperiodically controlled metamorphosis allows insects to time their adult eclosion, and thus their dispersal from the stream, before flooding is likely to occur. The trichopteran, *Phylloicus aeneus*, probably uses just such a strategy (Lytle 2002). In addition, photoperiod controls development of either winged or wingless forms in at least some wing-polymorphic species (Harrison 1980; Zera and Denno 1997), which clearly has profound effects on dispersal ability. Among related species, aptery is often more common in those that occupy more permanent habitats (e.g., Ditrich et al. 2008).

3.4.2 Colonization of New Habitats

Dispersal, i.e., moving away from a now or soon-to-be unsuitable place, also implies colonization, the occupation of a new and presumably more suitable environmental patch. How, then, do insects find appropriate habitats? At least part of the answer for aquatic species is by detection of polarized light reflected from water surfaces, a phenomenon demonstrated by Horváth and his associates (Bernath, et al. 2001; Horváth 1995a, b; Horváth and Kriska 2008). Several researchers have taken advantage of this phenomenon by using other polarizing surfaces, such as black plastic, as a means of attracting and collecting insects for study (e.g., Boda and Csabai 2009); this also explains the strange propensity for dragonflies to attempt oviposition on black gravestones and on the surface of cars (Horváth et al. 2007; Wildermuth and Horváth 2005).

More than likely some insects use other visual, tactile, or chemical cues to locate appropriate habitat, but few of these have been identified. Some aquatic insects can detect the presence of underwater predators without direct contact. Blaustein et al. (2004) showed that mosquitoes, *Culiseta longiareolata*, whose larvae are highly vulnerable to predation by notonectids (backswimmers), avoid ovipositing in artificial or natural pools containing *Notonecta*, apparently responding to chemical cues; midges, *Chironomus riparius*, have much less vulnerable larvae and do not avoid *Notonecta*. *Culiseta longiareolata* females also avoid laying eggs in pools containing a larva of the dragonfly, *Anax imperator* (Stav et al. 1999). Mosquitoes also apparently respond to other chemical and physical cues. Among tree hole-breeding mosquitoes in Florida, USA, drought-susceptible species chose more permanent holes that are larger and lower, with larger, more vertical openings, and contain darker water with higher conductivity, pH, and tannin-lignin content (Bradshaw and Holzapfel 1988). In coastal NSW, Australia, Mokany and Mokany (2006) studied larvae of *Ochlerotatus notoscriptus*, a relatively drought-resistant species, and the more drought-susceptible *Anopheles annulipes*, in small mesocosms with filtered pond water concentrated by evaporation by fivefold; mesocosms were filled with either 2 L or 4 L of either dilute or concentrated water. Larvae of *A. annulipes* were consistently recruited to higher volume containers, regardless of concentration, while *O. notoscriptus* favored higher concentration containers, regardless of volume. Thus *O. notoscriptus*, at least, responded to water chemistry.

Resetarits and Silberbush (2016) found that two species of *Culex* mosquitoes also avoid fish predators in arrays, each consisting of nine mesocosms constructed from plastic pools. In each array, the pools (“patches”) were arranged into three groups of three (“localities”). One locality contained no patches with fish, one a single patch with fish, and one two patches with fish. In this configuration, female mosquitoes exhibited a phenomenon called “compression” by these authors (Fig. 3.2). Mosquitoes laid fewer eggs in patches containing fish than in fish-free patches, but also laid fewer eggs in fish-free patches in localities also containing one and still fewer in those containing two patches with fish. That is, female mosquitoes were sensitive not only to the condition of individual patches but also to their

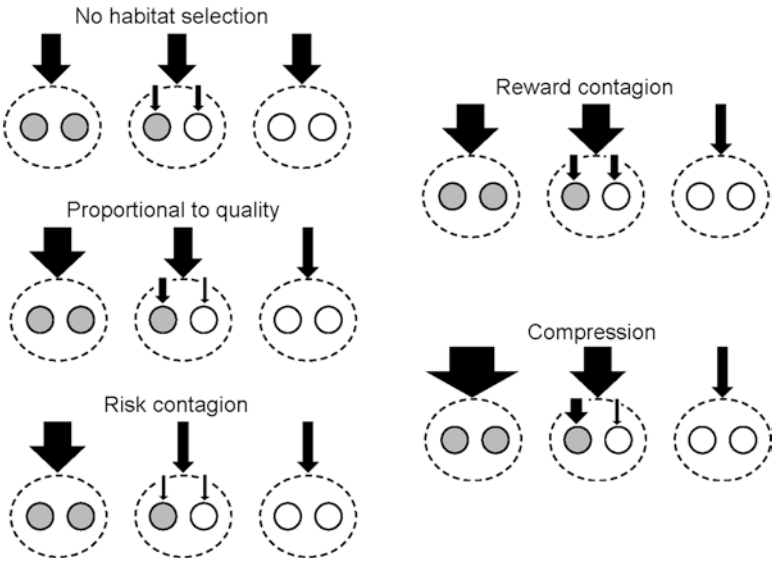

Fig. 3.2 Schematic illustration of effects of locality (dashed ovals) and patch (small circles) quality on colonization by dytiscid and hydrophilid beetles. Filled circles are patches of higher quality, e.g., lacking predators or with higher food quality, than open circles. Widths of vertical arrows are proportional to the number of beetles colonizing each locality or patch. Modified from Pintar and Resetarits (2017a), used with permission

context, i.e., the condition of each locality, so that more eggs were "compressed" into localities entirely without fish.

Similar experiments on dytiscid and hydrophilid beetles and some aquatic Hemiptera have examined several different contrasts among patches. Binkley and Resetarits (2007), e.g., found that these taxa were dramatically more likely to colonize mesocosms under an open tree canopy than under a closed canopy. The beetles also detected and avoided fish in mesocosms and even discriminated among fish species in a pattern that reflected the degree of threat they posed (Resetarits and Pintar 2016). Resetarits and Binkley (2009, 2013, 2014) arranged localities with variable numbers of patches (cattle tanks) with and without fish, resulting in three patch types: (1) fish free and distant from any fish-containing patches, (2) with fish, and (3) without fish but adjacent to patches with fish ("fish-associated" patches). In fish-free localities the number of colonists did not differ significantly among patches. Patches without fish always had more beetles than patches with fish, and the difference increased as the number of patches per locality increased, although the fish could not reach the beetles. Fish-associated patches had intermediate numbers. The difference in colonists between fish-free localities and localities with fish increased with locality size, even though the ratio of patches with and without fish was always 1:1 in mixed localities; beetles apparently perceived increasing rather than constant risk as the number of patches with fish increased ("spatial risk contagion"; Resetarits et al. 2005; Fig. 3.2). This response might lead to underutilization of some suitable natural habitats.

Vonesh et al. (2009) also reported that caged fish reduced the abundance and altered the composition of colonizing insects (mostly Diptera in their case). Subsequent exposure of the colonized containers to uncaged fish reduced abundance further due to predation. However, tanks that were fish free during the colonization phase still had more insects after actual predation than did the fish-associated tanks. Thus, differences in dispersal behavior can have long-lasting effects on community composition despite exposure to predators. Kraus and Vonesh (2010) showed that in their system the avoidance of fish by dytiscids was not strong if other colonizing species were allowed to accumulate but was much stronger if earlier colonizers were removed periodically. Hydrophylids and mosquitoes strongly avoided fish under all conditions, but, surprisingly, chironomid midges preferred to oviposit with fish, possibly because fish usually eliminate many invertebrate predators. Thus the responses of insect colonists may depend on subtle differences in patch characteristics. The presence of predators may also have other effects on life history and morphology, such as causing earlier metamorphosis, and, consequently, smaller size at metamorphosis, or development of defensive spines (Benard 2004).

The presence of food may also influence colonization of new habitat patches. Pintar and Resetarits (2017a, b, c) studied colonization by dytiscids (predators) or hydrophilids (predators as larvae, scavengers as adults). Hydrophilids preferred hardwood litter initially but later favored pools with pine needles, presumably due to changes in zooplankton composition. Dytiscids showed no significant preference. Individual species of both families mostly followed the same patterns, so the change among hydrophilids was not primarily due to species turnover. In separate experiments, dytiscids, but not hydrophilids, responded markedly to removal or addition of zooplankton to half the mesocosm containers (Pintar and Resetarits 2017b).

Aquatic beetles are subject to spatial contagion and compression in response to variation in resource level (Pintar and Resetarits 2017a). Beetles were as strongly attracted to localities with one high and one low resource patch as they were to localities with two high patches, and in the former case they compressed into the high-quality patch. As expected, localities with two low patches were less attractive. Finally, Pintar et al. (2018) compared the effects of three levels of predatory fish combined with three nutrient levels (i.e., nine possible combinations). In all cases they found that the presence of predators depressed colonization but, in these circumstances, the effect of nutrient level was not significant for any one species of beetle, although it was significant for all beetles taken together. They also counted egg rafts of *Culex* mosquitoes, which responded to both nutrients and presence of predators. Overall, they concluded that predators had a stronger effect than nutrient level on immigration. The giant water bug, *Lethocerus deyrollei*, however, emigrates more readily if deprived of food (Ohba and Takagi 2005).

3.4.3 *Timing of Dispersal*

The daily and seasonal peaks of dispersal may be responses to specific environmental cues, although this has received less attention than the questions of whether and where to disperse. As seen in the next section, seasonal timing is often a crucial adaptation for dispersal, especially when the latter is necessary to avoid seasonally unfavorable conditions. The timing of dispersal, however, may also serve more quotidian ends and may respond to several immediate cues. In some cases, as with many Odonata, adult emergence occurs at night or near dawn and is followed by dispersal away from the natal site as soon as hardening of the exoskeleton allows for flight (e.g., Corbet 1957; Michiels and Dhondt 1991; Geenen et al. 2000). This probably reduces predation and also spares the still rather fragile new adults from attack and injury by mating attempts from mature conspecific males at the water before their muscles are fully developed and their exoskeleton is fully hardened.

In other insects various physical cues may stimulate and assist dispersal. These are summarized exhaustively by Johnson (1961). More recently Boda, Csabai, and colleagues in Hungary have investigated conditions favoring or inhibiting dispersal by aquatic beetles and bugs. One important factor is wind. Dispersal flights were most common at wind speeds of <6 km h^{-1} and was completely inhibited by wind speeds of >12 km h^{-1} (Bota and Csabai 2005). Csabai et al. (2012) found that most of species of Coleoptera and Hemiptera flew during one or more of three distinguishable daily intervals: mid-morning, near noon, or at nightfall. In the spring, however, a few species flew throughout the day, and a number of others had different activity patterns in different seasons. Nearly all had a distinct seasonal peak, although relatively few were confined strictly to a single season. The authors concluded that the seasonal variation was driven by changes in air temperature in relation to the minimum temperature for flight and the (higher) minimum for mass dispersal although they did not report measurements of minimum or routine body temperatures. Certainly, however, wind and temperature are likely to have marked effects on dispersal in these and other insects.

3.5 Adaptations for Dispersal

The division between this section and the last is somewhat artificial. Clearly the responses to the various “cues” that stimulate dispersal and colonization ordinarily are adaptive, so I have made some arbitrary decisions about how to allocate information to one or the other topic. Here we will be concerned with characteristics that have evolved to favor successful dispersal rather than the circumstances that dictate when and where dispersal begins or ends. However, the sources of many cues for dispersal and colonization, such as food sources or presence of predators in a habitat patch, are the immediate result of features that make avoidance or exploitation of those patches adaptive, as shown clearly in the preceding discussion.

3.5.1 Passive and Active Dispersal

An important distinction is that between passive and active dispersers, i.e., between those that are propelled entirely by wind or water or that attach themselves to other animals, and those that move primarily under their own power. Most insects, because they can fly, fall into the latter category. Nevertheless, a number of insects, especially small Diptera, including mosquitoes, ceratopogonid midges, and blackflies, are dispersed by wind (Elbers et al. 2015; Jones et al. 1999; Service 1980). Japanese encephalitis is thought to have been introduced to Australia by wind-blown *Culex* mosquitoes from Papua New Guinea (Chapman et al. 2003), and genetic analysis suggested a panmictic population of these mosquitoes throughout western PNG and the Australian Cape York Peninsula. So-called aerial plankton—small organisms that are transported passively by winds, usually at hundreds to thousands of meters altitude—includes small insects of many orders, including a number of aquatic groups (Compton 2002). *Ischnura aurora*, a tiny zygopteran, also probably migrates passively on the wind while teneral (Rowe 1978). All these insects have little control of their direction except during takeoff and landing, and their movements may not always be either intentional or adaptive.

Of course not all insects are airborne dispersers. Many aquatic insects can walk or swim for some distance to reach emergence sites, escape drying habitats (Lytle et al. 2008), or compensate for downstream drift (as discussed above). Among terrestrial species nymphs of some locusts (Acrididae) and Mormon crickets (Tettigoniidae), e.g., walk for long distances to find food (Reynolds et al. 2014). In many Lepidoptera first instar caterpillars "balloon" by spinning out long silk threads that catch the wind. Some small Hemiptera nymphs can position themselves at the edge of leaves to launch themselves into the wind (Washburn and Washburn 1984). These methods are mostly unavailable to aquatic insects, however. Several semiaquatic insects and Collembola are also propelled by wind or currents on the surface of water, and this may effect successful dispersal but probably is often maladaptive (Reynolds et al. 2014). One known case of adaptive dispersal in this manner is that of the aphid, *Pemphigus trehernei*, for which the sea aster, a plant of tidal salt marshes, is secondary host. First instar larvae are initially photopositive and crawl to and walk on the soil surface until they encounter the incoming tide. They are small enough to remain on the surface due to surface tension and often are blown along the surface by wind until they reach their host, at which time they become photonegative and descend through cracks in the soil to the aster roots where they feed (Foster and Treherne 1978).

Darwin (1859) famously observed that newly hatched larval snails readily attached themselves to a duck's feet. He conclude that small aquatic animals might easily be dispersed on the feet and legs of water birds, and this has been confirmed in a number of cases for some small crustaceans and other zooplankton (Figuerola and Green 2002). Desiccation is a danger in such circumstances, but it should be possible for desiccation-resistant resting stages, including diapausing insect eggs. Apparently, though, this has never been definitely confirmed for insects.

3.5.2 Dispersal Polymorphism

A dramatic example of adaptive morphology is that of dispersal polymorphism, in which some individuals are adapted for dispersal and have fully developed wings while others do not disperse and usually have reduced or absent wings (brachyptery or aptery). For non-dispersing individuals there can be a considerable advantage to reduced or absent wings and flight muscles because in most insects these structures represent a considerable investment of energy and material, which may slow development and reduce fecundity compared to individuals without them (Harrison 1980; Zera 1984; Zera and Denno 1997).

Among aquatic taxa, this has been studied extensively in Gerridae, or water striders (summarized by Vepsäläinen 1978). Wing development varies among species, often geographically within species, and often between diapausing (usually wintering as inactive adults) and non-diapausing (summer, actively breeding) generations. Some species of *Gerris* are not dimorphic at all, while in others the diapause generation is long-winged, since they need to find sheltered sites for diapause and then return to habitats suitable for reproduction. The non-diapause generation generally does not disperse, sacrificing the ability for higher fecundity. In some species, populations in certain areas retain functional wings in summer, perhaps to avoid drying of their habitat. In some species dimorphism is seasonal, as described above, and probably is controlled by photoperiod, while in others dimorphism is genetically determined. Several other combinations of diapause and wing development have been identified. Zera et al. (1983) found in the North American genus *Limnoporus* that both genetic factors and photoperiod affect wing development, with short and declining photoperiod favoring production of long-winged morphs. Harada and Nishimoto (2007) reported that in *Aquarius paludum*, adults held under a long-day photoperiod regime and fed daily quickly broke reproductive diapause and matured ovaries while also histolyzing their flight muscle; others on the same photoperiod but fed only once every 3 days remained in diapause and retained functional flight muscles and their ability to disperse by flight. Thus the underfed individuals could disperse and possibly colonize a more favorable patch, while those with ample food diverted resources to gamete production and were ready to reproduce in situ (see Dingle and Arora 1973 for a more detailed study of a similar phenomenon in terrestrial bugs).

In the closely related and ecologically similar family Veliidae (riffle bugs), somewhat similar patterns are found (Ditrich 2016; Ditrich et al. 2008). As an interesting aside, at least one species of *Velia* is mostly flightless and is dispersed overland by walking (Ditrich and Papáček 2009).

A diverse group of other aquatic taxa also exhibits flight polymorphism. These include at least one mayfly (Ruffieux et al. 1998), a number of stoneflies (Brittain 1990; Lillehammer 1985; Zwick 2000), several Hemiptera in addition to gerrids and veliids especially corixids and notonectids (Young 1965; Baines et al. 2018), a few Trichoptera (Giudicelli and Botosaneanu 1999), and a few Diptera (Byers 1969;

Berendonk and Bonsall 2002). Whether reduced wings and/or flight muscles are genetically determined or induced by environmental circumstances is mostly unknown. The selective pressures that might lead to this condition may include the trade-off between flight and rate of development, fecundity, or longevity, or they could be in response to the danger of being permanently transported away from suitable habitat (Bilton 1994), as might be the case for species living on oceanic islands (e.g., Short and Liebherr 2007); these authors questioned the "island effect" as an explanation in this case, however, as did Roff (1990) more generally.

One other taxon deserves brief mention here. Although not truly aquatic, several species of planthoppers in the family Delphacidae are restricted to intertidal salt marshes. These were extensively studied by Denno and his collaborators (Denno and Roderick 1990) and subsequently reviewed in a broader context by Zera and Denno (1997). This is one of the most thorough studies of flight polymorphism to date, including ecological, physiological, and evolutionary aspects such as the close correlation of brachyptery with stable habitats. This correlation is also supported by Roff (1990) based on data from a very wide array of aquatic and terrestrial insects.

Aside from physical polymorphism, more subtle changes in the flight system affect dispersal. Dispersal behavior is usually accompanied by hormonal and other physiological changes. Modulation of juvenile hormone (JH) is probably the most pervasive of these. JH probably plays a major role in determining whether individuals develop normal or reduced wings, as well as muscle histolysis, although ecdysone, the molting hormone, is also important. The interplay of these hormones also largely controls the ultimate body size of individuals. In addition, a suite of hormones, most prominently adipokinetic hormone (AkH), but also including octopamine, regulate the deposition and mobilization of fat and the relative utilization of fat, carbohydrate, and, in some taxa, amino acids as fuel for energy metabolism. Fat is the normal fuel for all but very-short-range dispersers because it contains the largest amount of metabolic energy per unit mass (Dingle 2014).

Body size is influenced by many selective and life history factors (e.g., Peters 1986), but requirements for dispersal are often among these. Although not thoroughly investigated, a number of instances are known in which dispersers are larger on average than non-dispersers (reviewed by Benard and McCauley 2008). These include several cases among Odonata (e.g., Angelibert and Giani 2003; Conrad et al. 2002; Anholt 1990; and Michiels and Dhondt 1991). Roff (1991) found similar relationships in intraspecific comparisons. Larger body size may benefit active migrants because the mass-specific metabolic cost of flight tends to be smaller at larger body size. Flight speed and hence the ability to control flight direction at higher wind velocity are usually greater. Larger size might also tend to increase fecundity and make successful colonization of new habitats more likely. On the other hand, Thompson (1991) found no size difference among resident and dispersing individuals of a coenagrionid damselfly. McCauley (2005, 2010) also very carefully investigated males of two species of libellulid Anisoptera, *Leucorrhinia intacta* and *Pachydiplax longipennis*, both of which are highly territorial and aggressive, dispersing from permanent to recently refilled temporary ponds. In both cases, dispersing males were smaller than non-dispersers. The large males dominated smaller ones in territorial interactions, and the latter may disperse because of their greater difficulty in establishing new territories at the occupied ponds.

Since variation in body size does not necessarily prevent dispersal, it is often said to influence the propensity to disperse, i.e., a behavioral effect rather than a physical barrier to dispersal like aptery. Another such adaptation is subtle variation in wing size or shape. For example, Rundle et al. (2007) found that in *Enallagma* damselflies in North America wing length was positively correlated with range size, even when controlling for body length. In three species of *Libellula* dragonflies McCauley (2013) showed that two species with a broader habitat range and that dispersed further and more frequently had larger wings with a higher aspect ratio than a third species that had a narrow habitat range and was less dispersive. Suarez-Tovar and Sarmiento (2016) found that, when corrected for phylogenetic relatedness, migratory South American Libellulidae had larger and more deeply corrugated wings and a more expanded hindwing anal lobe than in nonmigratory species. In Swedish mayflies and stoneflies wing length was positively correlated with range size and in mayflies also with occupancy (the proportion of sampled sites actually occupied by a species) (Malmqvist 2000), and a similar, although not entirely consistent, correlation with habitat predictability occurs in chironomids (McLachlan 1985). Adaptive changes in dispersal propensity need not depend only on morphological features—physiology and behavior are clearly involved and may be of greater importance. Iversen et al. (2017), e.g., argued that the difference in flight tendency and distance in two genera of dytiscids are purely behavioral, since the wings and flight muscles remained intact in both.

McPeek (1989) found that larvae of two species of *Enallagma* damselflies only inhabit permanent lakes with predatory fish (which usually extirpate large invertebrates) and two others occur only in fishless lakes, dominated by invertebrate predators and generally less permanent than fish lakes. One species, *E. ebrium*, mostly inhabited “winterkill” lakes, which normally have fish but where winter oxygen levels may drop below lethal levels for fish, allowing large invertebrate predators to take over. *Enallagma ebrium* can coexist with fish but not with invertebrate predators, so adults disperse temporarily to lakes with fish only. The four species that coexist only with fish or with predatory invertebrates but not both are very philopatric. *Enallagma ebrium*, however, is adapted to lakes in which predator populations change radically and thus is much less philopatric. McCauley (2006), in another mesocosm experiment, showed that connectivity to other tanks explained a high proportion of the species richness of Odonata adults, and a still higher proportion of larvae, in the focal tank. The identities of adults seen nearby natural habitats and fields without cattle tanks were also extremely similar to those of adults and larvae at or within the tanks, suggesting that no physical barriers to dispersal existed. McCauley concluded that dispersal behavior alone limited colonization and largely determined community composition of these odonates.

3.5.3 Diapause, Reproduction, and Dispersal

As suggested in several examples already described, diapause, reproduction, and dispersal, with or without morphological changes, are intimately coordinated (Southwood 1962). The case of *Aquarius paludum* females (Harada and Nishimoto 2007) was described above. Other examples include several Odonata. In Japan, most *Sympetrum frequens* disperse from emergence sites in lowlands, often rice paddies, into highland areas during the summer, where they undergo partial reproductive diapause, although gametes slowly mature and mature coloration develops (Corbet 1999, pp. 390–394; Ueda 1988), and a very similar phenomenon occurs in *Sympetrum meridionale*, *S. striolatum*, and *Aeshna mixta* in Algeria (Samraoui et al. 1998). In many tropical dragonflies in areas with a distinct dry season, prereproductive adults may move from bodies of water where they reproduce into forest where they remain in reproductive diapause, often until the onset of rains, then quickly mature gametes, and develop mature coloration (Corbet 1999, pp. 261–262; pers. obs. 1974, 1994).

Because dispersal and diapause are intimately related, it may be difficult to distinguish independent environmental conditions that induce the two states, and in fact the cues may be the same. It is commonly assumed that photoperiod usually affects both, and Goehring and Oberhauser (2002) showed that in Monarch butterflies diapause induction and readiness to migrate are closely parallel. In other cases, it has been implicitly assumed that one effect of diapause induction (and sometimes also termination) is to initiate migration (Saunders 2010), but I know of no comparable studies on aquatic insects.

The close connection among dispersal, diapause, and reproduction led Johnson (1969) to propose the "oogenesis-flight syndrome," that is, female insects have hypertrophied fat bodies and maintain their gametes in an immature state until dispersal is accomplished, after which JH titer increases, mature eggs develop, and oviposition ensues. This should allow them to begin dispersal with maximum energy stores and possibly reduced flight costs, and arrive at their destination with maximal reproductive value. This syndrome does apply to many dispersing insects. Rankin (1978) showed that in the large milkweed bug, *Oncopeltus fasciatus*, migration is stimulated by an intermediate level of JH and maturation of gametes by a high level. Instances of oogenesis-flight syndrome have not been studied in detail in aquatic insects but seem likely in the hydrophilid, *Helophorus brevipalpis* (Landin 1980), and dytiscids in the genus *Graphoderus* (Iversen et al. 2017). There is also good evidence for the syndrome in belostomatid bugs (Cullen 1969; Lytle and Smith 2004), and it is likely in Gerridae and probably numerous other taxa, although its hormonal control has not been shown definitively in either aquatic Hemiptera or Coleoptera. On the other hand, it certainly is absent, or present in abbreviated form, in some migrating dragonflies. These normally begin migration when sexually immature (Corbet 1999, pp. 395–396), but they mature gametes and may mate and oviposit long before reaching their final destinations (May and Matthews 2008; May 2013; May et al. 2017).

3.6 Long-Distance Migration

Many authors have used the terms migration and dispersal interchangeably or ambiguously (Johnson 1969, pp. 3–8). Here, I consider migration to be a category of dispersal, more or less equivalent to Corbet's (1999, p. 394) interhabitat displacement, that is, usually a movement over multiple tens to hundreds of kilometers. Typically it entails a later return to the original habitat, although, in insects, not usually by the same individuals that migrated initially. Among terrestrial insects, this would include the famous migrations of monarch (e.g., Agrawal 2017) and painted lady butterflies (Stefanescu et al. 2012), the bug, *Oncopeltus fasciatus* (e.g., Dingle 1996), or plague locusts such as *Schistocerca gregaria* (Rainey 1951, 1976). Only a few aquatic insects, notably Anisoptera, undertake similar migrations under their own power, although a number of taxa may be dispersed passively for long distances, as noted above. Kennedy (1985) defined migration in behavioral terms as "… persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence." This is still a useful and insightful definition and is widely used, although it does not include purely passive dispersal (but does include, e.g., cases in which insects actively fly high into the air so as to become entrained in air currents—a "vehicle"—which thereafter carry them passively). It also does not depend on any particular adaptive advantage accruing or even require that dispersal be adaptive, although Kennedy certainly recognized the advantages and trade-offs involved.

Although butterflies, locusts, and dragonflies perform the most visually spectacular migrations, recent attention has been focused on vast migrations at hundreds of meters aloft by a variety of smaller insects at night across Britain and northern Europe (Hu et al. 2016). These fly well above their flight boundary layer (Taylor 1958), so they depend largely on the wind for propulsion and have been shown to actively seek out altitudes where wind direction matches their intended flight direction. They have been studied partly by aerial sampling e.g., (Chapman et al. 2004) but mainly by upward-looking radar that reveals patterns, velocities, and even headings, of insects as small as 10 mg. Upwards of 3×10^{12} insects (including many <10 mg, estimated from high-altitude net captures) may pass over southern Britain during the autumn, always on northerly winds. The smallest species are carried passively, but even slightly larger insects can modify their course by shifting their heading if wind is not blowing within 20° of the preferred flight direction (Chapman et al. 2015). The vast majority of these are terrestrial species, although a small number of aquatic insects—Corixidae, Dytiscidae, and Hydrophilidae—are included. These flights illustrate, however, the extent and importance of long-distance insect migration.

Odonata are probably the most flight-worthy of aquatic or semiaquatic insects and rank high among all insects. Several species are known to make long migrations, in at least two cases over thousands of kilometers. Although they do fly under their own power, they also depend, at least to some extent, on favorable wind for propulsion. One species that has been studied extensively, *Pantala flavescens* (the "Wandering Glider" or "Globetrotter"), has been shown to fly some 500–1000 km from India to the Maldives archipelago and thence on to east and southeast Africa, a total distance of around 3500 km (Anderson 2009). Based on observations in the Maldives and literature reports from southern India and east to southeast Africa, Anderson inferred that *P. flavescens* adults emerging in India during late summer fly southwest at high altitude on winds associated with the Intertropical Convergence Zone (ITCZ) to Africa. Corbet (1962) noted that adults are at various latitudes in Africa in synchrony with the ITCZ, and they may breed continuously within the continent. During the northern spring, however, a strong westerly upper air current, the Somali Jet, develops off the Horn of Africa and blows across the Arabian Sea and northern Indian Ocean, also bringing moisture that helps initiate the southwest monsoon in south Asia. This jet probably enables a reverse movement of *P. flavescens* back to northern India. Hobson et al. (2012), using stable hydrogen isotope ratios in wing samples of *P. flavescens*, showed that the most probable origin of specimens collected on the Maldives in October was in northeasternmost India, Nepal, and Bangladesh. This confirms Anderson's proposed route from India to the Maldives and is strongly supportive of a circuit very much as he suggested.

Pantala mostly breed in ephemeral pools created by rains along the ITCZ and consequently have very rapid larval development (Corbet 1999, p. 227). It is very likely that they never diapause as larvae and are obligate migrants in most places where they occur. Some other migrant odonates may diapause as larvae and thus could have two options for surviving conditions unsuitable for development. The common North American migrant, *Anax junius* (Fig. 3.3), is one such species. It has

Fig. 3.3 Photograph of male *Anax junius* in flight, as during migration. Used with permission of the photographer, Dennis R. Paulson

attracted attention since the nineteenth century because of its sometimes spectacular mass migrations (Russell et al. 1998). It was long thought (Trottier 1971) that two temporally separate cohorts exist, one emerging in early summer and breeding in the neighborhood of its natal site, and the other emerging in late summer and migrating south. Freeland et al. (2003) showed that migrant and nonmigrant individuals could not be distinguished genetically. Thereafter Matthews (2007a) and Hobson et al. (2012), again using stable hydrogen isotopes, confirmed that late summer-autumn migrants collected in Texas and Mexico had very likely emerged in the northern USA or southernmost Canada. Matthews (2007a) also found that *A. junius* population show very little genetic differentiation across their entire eastern North American range. Stable isotope studies indicate, as expected, that individuals collected in the northern USA in early spring emerged far to the south (Matthews 2007a; Macfarland K, pers. comm. 2015). Most recently May et al. (2017) examined developmental phenology of *A. junius* at several sites in the eastern USA. Two emergence groups of larvae could usually be distinguished, but they overlapped broadly both in larval size and adult emergence, making genetic differentiation unlikely. Larval growth and timing of eclosion suggest that the early emerging group are largely individuals that overwintered as late instar diapausing larvae and probably will lay eggs locally, most of which will hatch as larvae that again overwinter in diapause. Late emerging adults are thought to be the offspring of adults that migrated from the south and laid eggs in early spring. The resulting larvae develop directly, emerging in late summer or autumn, and migrate south. However, because of the genetic evidence already cited and the broad overlap of larval size groups and adult emergence, it is probable that the timing of emergence and hence the likelihood of migration are determined by the effect of some environmental cues such as photoperiod on early larval instars (Matthews 2007b). Other known but less studied migrants among Odonata include *Aeshna mixta, Anax ephippiger, A. parthenope, Libellula quadrimaculata, Pantala hymenaea, Rhionaeschna bonariensis, Tramea lacerata*, and several species of *Sympetrum*, among others (Corbet 1999).

Long-distance migrants are likely to face some challenges that are absent or much less acute for insects that disperse short distances. One of these may be the necessity for navigation over hundreds of kilometers—the mere fact that it is far away makes a remote habitat patch harder to find than a comparable nearby patch. Presumably these and other long-distance migrants recognize suitable habitat using cues similar to those already described after arrival in the appropriate region, although it is not always clear how they recognize the latter. In the case of *Anax junius*, and probably some other migrants, migrating adults may mate and oviposit several times before reaching their final destination (May and Matthews 2008; May 2013).

Monarch butterflies have been studied extensively and have a complex, multifaceted navigation system (Reppert et al. 2016; Shlizerman et al. 2016) that allows individuals from all over the eastern USA to find a few patches of forest in a limited area in the mountains of Mexico. Comparable information is not available for any aquatic insect. On the other hand, most migrants are much less constrained than Monarchs as to their destination. May and Matthews (2008) suggested that *A. junius* might find suitable habitats, because the latter are quite widespread, simply by orienting very generally southward and avoiding dangerous areas such as open sea. It seems unlikely that *Anax* navigation is quite that simple, since they do preferentially fly when tailwinds are available (Wikelski et al. 2006) and may follow landmarks such as roadways (pers. obs. 1992). Other migrants have also been observed flying along river courses (Dumont and Hinnekint 1973) and probably dry wadis in the northern Sahara (Dumont and Desmet 1990).

In the case of ITCZ migrants or others that rely mostly on flying downwind to more favorable regions, usually where sustained rainy periods are starting, navigation problems are considerably less, since they need, for the most part, simply to maintain a flight heading that takes best advantage of the wind. Recognition of suitable habitat may also be simplified, because the downwind flight automatically brings them to areas where suitable pools are available, although they must still, of course, recognize specific sites for reproduction. Also, most, and probably all, animals that migrate by flight depend to a significant degree on wind to assist and guide their flight. For example, visible migration of *Anax junius* usually takes advantage of northerly winds associated with cold fronts that appear to stimulate flight and typically also strongly influence its direction (e.g., Russell et al. 1998; Wikelski et al. 2006). During fall migration, dragonflies, like many birds, take advantage of updrafts over mountain ridges to reduce flight cost and gain altitude.

The stimuli that prompt Odonata to begin or end migration are not well known but are more likely to be related primarily to seasonal changes and weather than immediate responses to predation, competition, or food supply because predation probably is often more intense during migration than during other periods (Nicoletti 1997), and long-distance migration is generally initiated before food availability deteriorates. Some other migrants such as *Oncopeltus* may respond to restriction of their food supply (Dingle 1968). Among so-called obligate migrants (Corbet 1999, pp. 408–418), migration may be initiated endogenously shortly after the teneral period (i.e., as soon as the cuticle has become sufficiently hardened); this appears to be the case in many Odonata, in which dispersal begins shortly after adult emergence with the so-called maiden flight (Corbet 1957). Alternatively, in ITCZ migrants it could be triggered by the onset or the cessation of rains or in response to habitat drying. In North America southward migration often is associated with cold fronts (Russell et al. 1998; Wikelski et al. 2006). As suggested above for *A. junius*, photoperiod might trigger developmental processes that determine whether eclosing individuals are prone to migrate or not. In principle, photoperiod might directly inhibit or stimulate migratory behavior, as it does in birds (Dingle 1996, 2014). In addition, conditions that prompt shorter dispersal episodes, described above (e.g., drying of natal ponds, crowding, high or low temperature, food supply, or availability of local oviposition sites), may stimulate or modulate long-distance migration in some species (Johnson 1969, pp. 203–239). Regardless of the specifics, it is likely that bouts of migration alternate with intervals of maintenance behavior such as feeding, probably at least in part because of reciprocal inhibition of flight and maintenance; for example, at the beginning of migratory flight, stimuli that would ordinarily elicit feeding are inhibited, but as flight is prolonged, feeding stimuli become more salient and eventually inhibit flight, and vice versa. This general pattern was first described by Kennedy (1961, 1985) in "migrating" aphids, but it appears to apply to many migratory organisms (e.g., Wikelski et al. 2006). The separation of migration and maintenance activity is not absolute, however, as I have watched migrating dragonflies divert from their flight path to grasp prey, albeit much less frequently than during nonmigratory feeding aggregations (Russell et al. 1998).

3.7 Population, Community, and Ecosystem Consequences

3.7.1 Metapopulations

We often think of populations and communities as existing as isolated and self-contained entities (Forbes 1887). Many organisms, however, exist not in isolated populations but rather in groups of subpopulations, each within a restricted area (a "patch"), so that population dynamics of these subpopulations may strongly influence one another. They may, e.g., experience fairly frequent stochastic extinctions within a patch but with the possibility of "rescue" by dispersal from other nearby patches. This led Levins (1969) to propose the concept of a metapopulation, i.e., a group of these interacting populations, and to analyze how their dynamics might differ from those of larger but more remote populations. These ideas have been tested, modified, and expanded by a number of authors (e.g., Hanski 1998; Bohonak and Jenkins 2003), for instance by explicitly incorporating variation in patch characteristics and isolation; by allowing for priority effects, including local adaptation, that may give initial colonizers an advantage in exploiting the patch; or by considering assemblages of species within patches (a metacommunity; Wilson 1992; Hanski 1998). These metapopulation models seem particularly appropriate for understanding the dynamics of small ponds scattered through a landscape, isolated from one another by variable stretches of terrestrial habitat. The general concept has also been modified (Hanski 2001) to include circumstances similar to those envisaged by MacArthur and Wilson (1967), with a single large and relatively stable population, e.g., in a lake, with a number of smaller ponds nearby containing populations that might show local adaptation or even become extinct but could be rescued by dispersal from the lake; the large, stable population would presumably be little changed. Metapopulation analyses have also been extended to include population along different reaches in a single stream catchment (Fagan 2002; Downes and Reich 2008). There is general agreement that the model is applicable to many organisms and that interchange among subpopulations can stabilize the wider population of a species, depending on the size, number, and connectivity (i.e., the ease of moving among subpopulations).

A number of studies described above, including most mesocosm experiments in which initial conditions are very similar among widely separated patches, probably fit the assumptions of metapopulation models reasonably well, although few, if any, have continued long enough to observe extinction and rescue. Nevertheless, they do illustrate that dispersal ability can have an important influence on population and community dynamics. For example, McCauley (2006) showed that dispersal was probably the primary determinant of species richness of Odonata larvae in tanks placed at varying differences from source populations of adult odonates, and in fact the more distant tanks contained, for the most part, a nested subset of the species found in the closer tanks. Most of the experiments of Resetarits and colleagues, cited above (pp. 11–13), directly show the effects of dispersal and colonization but not subsequent population and community development, because colonizing insects were completely removed each week. Recruitment varied among treatments, often among taxa, over time, and in response to conditions in neighboring patches, e.g., presence of predators. All these effects were dependent on dispersal followed by acceptance or rejection of patches at close range and made large differences in the sizes of populations and community composition. A frequent assumption in modeling dispersal in metacommunities is either that (1) dispersal is random and selection of dispersing organisms occurs after entering a habitat patch, e.g., by competition or predation, or (2) populations are philopatric, i.e., they rarely disperse from their natal patch (McPeek 1989). Resetarits et al. (2005) argued that nonrandom dispersal and subsequent individual habitat selection (IHS) based on perceived patch quality are likely to be frequent, and they showed experimentally that this, rather than random dispersal or philopatry, is the rule among water beetles (Binckley and Resetarits 2005; Resetarits and Binckley 2013). In turn, habitat selection makes possible the phenomena of compression and contagion, discussed above. These authors argue that IHS is likely to provide a better description than truly random dispersal of population changes and species assembly for many active dispersers. Philopatry may be common principally among species inhabiting extremely stable habitats, perhaps including large, deep lakes, or organisms that cannot detect potential predators in a new habitat, as may be the case for many adult Odonata in habitats with larval predators (McPeek 1989; pers. obs.).

3.7.2 Dispersal and Genetic Change

Dispersal may also influence species characteristics or speciation since it strongly affects the extent of genetic interchange among (sub)populations. In general it is assumed that greater dispersal results in more gene exchange and thus increases the genetic similarity among populations and reduces the opportunity for speciation. Bohonak (1999) found a general, albeit weak, tendency for this to be true in a wide variety of animals. It is particularly evident in very mobile and widespread taxa like the dragonflies, *Anax junius* (Matthews 2007a) and *Pantala flavescens*, which Troast et al. (2016) suggested may be panmictic throughout its nearly global range (but see Pfeiler and Markow 2017). Several possible mechanisms, however, could alter this outcome. Rapid population growth and local adaptation (De Meester et al. 2002) or low dispersal rates (Bohonak and Jenkins 2003) might make it difficult for genes from individuals dispersing from outside to invade an existing population, thus increasing the likelihood of divergence of populations, and possibly speciation. On the other hand, if dispersal leads to a suitable patch with few or no conspecifics or allows the disperser to successfully establish itself in an occupied patch, new alleles will be introduced that may, if they spread initially, result in an altered genetic landscape within that patch. Finally, if dispersal propensity is contingent on properties of dispersing individuals (e.g., body size) or of their natal patch (e.g., crowding), the chances are increased of the same contingent behavior being spread (Arendt 2015).

3.7.3 Dispersal and Community Dynamics

Dispersal might be important in determining community composition and dynamics even in the absence of niche-based interactions such as competition or predation. Hubbell (2001) introduced the so-called neutral theory of biodiversity, which suggests that similar organisms' coexistence does not depend on differences in niche, but rather that they enter a community via dispersal until resource availability is limiting and then are extirpated or fail to invade purely by chance. In such a case, the existing assemblage of species depends largely on their probability of immigrating into the community. A likely example applying to aquatic insects is a study by Siepielski et al. (2010), who investigated *Enallagma* damselfly larvae that coexist with fish. These clearly occupy a different niche than their congeners that cannot coexist with fish, as well as non-congeneric Odonata, but among themselves they are ecologically extremely similar. Siepielski et al. compared growth and mortality of seven species of *Enallagma* larvae, with special emphasis on two species, across a range of primary production, macrophyte abundance and diversity (as refugia for the larvae), and abundance and diversity of potential predators. They found that the species appeared to be ecologically equivalent, i.e., to share a single niche. This led to the conclusion that coexistence of these species depended on stochastic immigration and local extinction. It should be borne in mind, however, that dispersal is assumed to be stochastic here, but this is rarely known to be the case. Other studies have suggested that adaptations to particular aquatic niches are, in some habitats, the principal determinants of insect distribution (e.g., Heino and Mykrä 2008).

Immigration may increase intraspecific competition for resources and for mates (if the sex ratio of the newcomers is not 1:1), while emigration could have the reverse effects, and might also ameliorate the effects of kin selection, if this exists. Profound effects on other organisms occupying the patch could occur. In fish-free bodies of water, the top predators are often dragonfly or dytiscid and hydrophilid larvae. If large numbers of these insects invade a habitat where none or only a few lived before, it is conceivable that they could seriously compete with native species or decimate their prey, with effects throughout the food web. This has never been investigated, but would surely be worth examining. Conversely, if their progeny later leave the habitat, as probably occurs in long-distance migrants, a substantial relaxation of competition or predator pressure, or a reduction of food resources, might occur. The potential for nutrient and energy transfer by migrating insects in general is quite large. Hu et al. (2016) estimated that the nocturnal fall migration of insect over England transports as much as 5.78×10^{12} Joules of energy, 100,000 kg of nitrogen, and 10,000 kg of phosphorus annually. Over the long term quantities transferred southward are very close to those transferred northward in spring, but in some years amounts are markedly unbalanced, resulting in substantial net movement of nutrients and energy in one direction or the other.

3.7.4 Dispersal and Nutrient Subsidies

Although little is known about the effects of mass long-distance migration of aquatic insects on the ecosystems they enter or leave, the effects of nutrient and energy flux from aquatic to terrestrial habitats have been studied rather extensively on a smaller scale and can be impressive (reviewed by Polis et al. 1997; also more briefly by Schindler and Smits 2016). It must be said at the outset that energy and nutrient subsidies are nearly always greater from terrestrial to aquatic systems than vice versa, simply because of gravity—mineral nutrients either in solution or as suspended material, and carbon and energy from detritus and dissolved organic solids, are all brought in by runoff from the surrounding land. In many headwater streams energy from this source substantially outstrips in-stream primary production (Fisher and Likens 1973). Nevertheless, the energy and nutrients from the bodies of dispersing insects can provide a substantial subsidy downstream or to nearby terrestrial habitats. Among the more impressive reported instances are at Lake Mỳvatn (Lake of Midges) in Iceland, where huge numbers of midges emerge in summer. Dreyer et al. (2015) estimated that some 290 kg ha^{-1} yr^{-1} of midges were deposited within 450 m of the lake edge (mostly within the nearest 100 m) during the most prolific of 4 years of study, although the amount was less than 10% of this during the least prolific year. This was equivalent to about 10 kg N ha^{-1} yr^{-1} and 1 kg P ha^{-1} yr^{-1} during the best year. Thus the nutrient subsidy was very significant, at least during good midge years.

Jackson and Fisher (1986) measured production of aquatic insects in Sycamore Creek, Arizona, during April to November, spread over part of two calendar years. In-stream secondary productivity was about 1200 kg ha^{-1} yr^{-1} and biomass of emerged insects was 230 kg ha^{-1} yr^{-1}, i.e., similar to the Lake Mỳvatn values, although in a starkly different habitat. Both of these results are unusually high for productivity of aquatic insects, but they illustrate the potential for nutrient transfer as a result of dispersal away from the immediate site of emergence. Paetzold et al. (2006) artificially subsidized small plots along a stream with about 75 mg day^{-1} of dried aquatic insects, i.e., approximately 3 kg N ha^{-1} yr^{-1}, assuming that the insects were ca. 10% N (Fagan et al. 2002), and recorded slightly more than twice the abundance of aquatic arthropods in the enriched plots as in control plots. Thus the natural subsidies at Lake Mỳvatn and Sycamore Creek cold have quite a significant effect on the later abundance of aquatic insects.

Export of insect biomass from aquatic habitats may also have marked effects on predators of flying adults of aquatic insects. For example, Fukui et al. (2006) used netting to prevent emergence of insects along a 1.2 km reach of a forest stream in Japan and measured bat foraging activity along that reach and an undisturbed adjacent control reach. They found that bat activity was dramatically reduced along the experimental reach compared to the control reach in May and June; thereafter, the abundance of aquatic adults decreased in both reaches while flying terrestrial insects increased throughout, and bat foraging increased, apparently because bats then depended on terrestrial prey.

3.7.5 Dispersal and Climate Warming

As the most recent report of the IPCC (2018) makes clear, climate warming is proceeding rapidly and is likely to continue for some time even under the most optimistic scenarios. These changes already are affecting aquatic insects. For many this means that to avoid extinction, they must quickly evolve resistance to the rapidly changing conditions or be able to disperse to more a favorable climate; in other cases, northward expansion may enable species to exploit otherwise suitable habitats from which they had been excluded by low temperature. Indications that this has happened during and since postglacial warming (Grewe et al. 2013) and probably still is occurring (Hof et al. 2012) have already been cited. Additional studies, especially in the UK, suggest that the pace of northward expansion has accelerated in recent decades. Hickling et al. (2006) showed that the northern limit of the ranges of both aquatic bugs and Odonata on average moved northwards about 75 km from 1970 to 2000 and 1960 to 1996, respectively. Hassall and Thompson (2008), in a general review of effects of climate change in UK Odonata, reported that emergence periods have shifted to earlier dates in many species, an ability that might improve their success if moving north but is complicated by its interaction with photoperiod as well as temperature. Considerable anecdotal evidence suggests that some tropical and subtropical odonate species have expanded their ranges northward (e.g., Paulson 2011), although this has not yet been supported by formal studies. Odonata are, among aquatic taxa, among the best adapted for dispersal, but they are also relatively easily detected and identified. It is likely that members of other orders have also moved northward.

Hering et al. (2009) estimated the sensitivity of European Trichoptera to climate change, based on current habitat requirements. Perhaps counterintuitively, they predicted that southern taxa would probably be more vulnerable to adverse effects of warming. Southern species lived in more restricted habitats and had smaller ranges, probably because they occupied areas south of the limit of Pleistocene glaciation and had been present in their current ranges for longer and become more specialized. These authors also, as expected (e.g., Laurance et al. 2011), found that high-altitude species are at rather high risk. Similarly, De Knijf et al. (2011) estimated that the range of two boreo-alpine *Somatochlora* dragonflies in the mountains of

Romania were predicted to be forced upward by at least 200 m and thus to lose ca. 40% of their current range by a temperature increase of 1.5 C. *Epiophlebia laidlawi*, a relict odonate from the Himalayas, is predicted to lose around 60% of its current potential range by 2050 under even a moderate warming regime (Shah et al. 2012).

References

Agrawal A (2017) Monarchs and milkweed: a migrating butterfly, a poisonous plant, and their remarkable story of coevolution. Princeton University Press, Princeton, NJ, p 296

Anderson RC (2009) Do dragonflies migrate across the western Indian Ocean? J Trop Ecol 25:347–334

Angelibert S, Giani N (2003) Dispersal characteristics of three odonate species in a patchy habitat. Ecography 26:13–20

Anholt BR (1990) Size-biased dispersal prior to breeding in a damselfly. Oecologia 83:385–387

Anholt BR (1995) Density dependence resolves the stream drift paradox. Ecology 76:2235–2239

Arendt JD (2015) Effects of dispersal plasticity on population divergence and speciation. Heredity 115:306–311

Arribas P, Velasco J, Abellán P, Sánchez-Fernandez D, Andújar C, Calosi P, Millán A, Ribera I, Bilton DT (2012) Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). J Biogeogr 39:984–994

Baines CB, McCauley SJ, Rowe L (2015) Dispersal depends on body condition and predation risk in the semi-aquatic insect, *Notonecta undulata*. Ecol Evol 5:2307–2316

Baines CB, McCauley SJ, Rowe L (2018) The interactive effects of competition and predation risk on dispersal in an insect. Biol Lett 10:20140287

Batzer DP, Resh VH (1992) Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. Wetlands 12:1–7

Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Annu Rev Entomol 41:75–100

Benard MF (2004) Predator-induced phenotypic plasticity in organisms with complex life histories. Ann Rev Ecol Evol Syst 35:651–673

Benard MF, McCauley SJ (2008) Integrating across life-history stages: consequences of natal habitat effects on dispersal. Am Nat 171:553–567

Berendonk TU, Bonsall MB (2002) The phantom midge and a comparison of metapopulation structures. Ecology 83:116–128

Bernath B, Szedenics G, Molnar G, Kriska G, Horváth G (2001) Visual ecological impact of ‘shiny black anthropogenic products’ on aquatic insects: oil reservoirs and plastic sheets as polarized traps for insects associated with water. Arch Nat Cons Landsc Res 40:89–109

Bilton DT (1994) The flight apparatus and flying ability of *Hydroporus glabriusculus* (Coleoptera, Dytiscidae) with a brief review of structural modifications in flightless beetles. Entomol Tidskr 114:23–32

Binckley CA, Resetarits WJ (2005) Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. Biol Lett 1:370–374

Binkley CA, Resetarits WJ (2007) Effects of forest canopy on habitat selection in tree frogs and aquatic insects: implications for communities and metacommunities. Oecologia 153:951–958

Bird, BA, Hynes HBN (1981) Movements of adult aquatic insects near streams in southern Ontario. Hydrobiologia 77:65–69

Blaustein L, Kiflawi M, Eitam A, Mangel M, Cohen JE (2004) Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. Oecologia 138:300–305

Boda P, Csabai Z (2009) Seasonal and diel dispersal activity characteristics of Sigara lateralis (Leach, 1817) (Heteroptera: Corixidae) with special emphasis on possible environmental factors and breeding state. Aquat Insects 31:301–314

Boda P, Csabai Z (2013) When do beetles and bugs fly? A unified scheme for describing seasonal flight behaviour of highly dispersing primary aquatic insects. Hydrobiologia 703:133–147

Boersma KS, Lytle DA (2014) Overland dispersal and drought-escape behavior in a flightless aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). Southwest Nat 59:301–302

Boersma KS, Bogan MT, Henrichs BA, Lytle DA (2014) Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. Freshw Biol 59:491–501

Bogan MT, Boersma KS (2012) Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Freshw Sci 31:1131–1144

Bohonak AJ (1999) Dispersal, gene flow, and population structure. Q Rev Biol 74:21–44

Bohonak AJ, Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett 6:783–796

Bradshaw WE, Holzapfel C (1988) Drought and the organization of tree-hole mosquito communities. Oecologia 74:507–514

Briers, RA, Cariss, HM, Gee, JHR (2002) Dispersal of adult stoneflies (*Plecoptera*) from upland streams draining catchments with contrasting land-use. Arch.Hvdrobiol. 155: 627–644

Briers RA, Gee JHR, Cariss HM, Geoghegan (2004) Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. Freshw Biol 49: 425–431

Brittain JE (1990) Life history strategies in Ephemeroptera and Plecoptera. In: Campbell IC (ed) Mayflies and stoneflies: life histories and biology. Springer, Dordrecht

Bunn ES, Hughes JM (1997) Dispersal and recruitment in streams: evidence from genetic studies. J N Am Benthol Soc 16:338–346

Byers GW (1969) Evolution of Wing Reduction in Crane Flies (Diptera: Tipulidae). Evolution 23: 346–354

Chapman HF, Hughes JM, Ritchie SA, Kay BH (2003) Population structure and dispersal of the freshwater mosquitoes *Culex annulirostris* and *Culex palpalis* (Diptera: Culicidae) in Papua New Guinea and northern Australia. J Med Entomol 40:165–169

Chapman JW, Reynolds DR, Smith AD, Smith ET, Woiwod IP (2004) An aerial netting study of insects migrating at high altitude over England. Bull Entomol Res 94:123–136

Chapman JW, Reynolds DR, Wilson K (2015) Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. Ecol Lett 18:287–302

Chaput-Bardy A, Lemaire C, Picard D, Secondi J (2008) In-stream and overland dispersal across a river network influences gene flow in a freshwater insect, *Calopteryx splendens*. Mol Ecol 17:3496–3505

Chodorowski A (1969) The desiccation of ephemeral pools and the rate of development of *Aedes communis* larvae. Pol Arch Hydrobiol 16:79–91

Collier KJ, Smith BR (1998) Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. Hydrobiologia 361:53–65

Compton SG (2002) Sailing with the wind: dispersal by small flying insects. In: Bullock JM, Kenward RE, Hails RS (eds) Dispersal ecology. Blackwell Science, Oxford, pp 113–133

Conrad KF, Willson KH, Whitfield K, Harvey IF, Thomas CJ, Sherratt YN (2002) Characteristics of dispersing Ischnura elegans and Coenagrion puella (Odonata): age, sex, size, morph and ectoparasitism. Ecography 25:439–445

Corbet PS (1957) The life-history of the emperor dragonfly Anax imperator leach (Odonata: Aeshnidae). J Anim Ecol 26:1–69

Corbet PS (1962) A biology of dragonflies. E.W. Classey, Faringdon, p 247

Corbet PS (1999) Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca, NY, p 829

Coutant CC (2008) Evidence for upstream dispersion of adult caddisflies (Trichoptera: Hydropsychidae) in the Columbia River. Aquat Insects 4:61–66

Csabai Z, Kálmán Z, Szivák I, Boda P (2012) Diel flight behaviour and dispersal patterns of aquatic Coleoptera and Heteroptera species with special emphasis on the importance of seasons. Naturwissenschaften 99: 751–765

Cullen MJ (1969) The biology of giant water bugs (Hemiptera: Belostomatidae) in Trinidad. Proc R Entomol Soc Lond A 44:123–136

Darwin C (1859) On the origin of species by means of natural selection. J. Murray, London

Datry T, Larned ST, Tockner K (2014) Intermittent rivers: a challenge for freshwater ecology. Bioscience 64: 229–235

Davy-Bowker J (2002) A mark and recapture study of water beetles (Coleoptera: Dytiscidae) in a group of semi-permanent and temporary ponds. Aquat Ecol 36:435–446

De Block M, Stoks R (2005) Pond drying and hatching date shape the tradeoff between age and size at emergence in a damselfly. Oikos 108:485–494

De Knijf G, Flenker U, Vanappelghem C, Manci CO, Kalkman VJ, Demolder H (2011) The status of two boreo-alpine species, *Somatochlora alpestris* and *S. arctica*, in Romania and their vulnerability to the impact of climate change (Odonata: Corduliidae) Int J Odonatology 14: 111–126

De Meester L, Gómez A, Okamura B, Schwenk K (2002) The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. Acta Oecol 23:121–135

Denno RF, Roderick GK (1990) Population biology of planthoppers. Annu Rev Entomol 35:489–520

Didham RK, Blakely TJ, Ewers RM, Hitchings TR, Ward JB, Winterbourn MJ (2012) Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundam Appl Limnol 180: 27–40

Dingle H (1968) The influence of environment and heredity on flight activity in the milkweed bug *Oncopeltus*. J Exp Biol 48:175–184

Dingle H (1996) Migration: the biology of life on the move, 1st edn. Oxford University Press, Oxford, p 480

Dingle H (2014) Migration: the biology of life on the move, 2nd edn. Oxford University Press, Oxford, p 326

Dingle H, Arora G (1973) Experimental studies of migration in bugs of the genus *Dysdercus*. Oecologia 12:119–140

Ditrich T (2016) Migration and dispersal patterns of semiaquatic bugs from lentic and lotic freshwater habitats. In: Abstracts of the 25th International Congress of Entomology, Orlando, FL, pp 25–30

Ditrich T, Papáček M (2009) Correlated traits for dispersal pattern: terrestrial movement of the water cricket Velia caprai (Heteroptera: Gerromorpha: Veliidae). Eur J Entomol 106:551–555

Ditrich T, Papáček M, Broum T (2008) Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohořský Potok stream spring area (Novohradské Hory Mts.). Silva Gabreta 14:173–178

Downes BJ, Reich P (2008) What is the spatial structure of stream insect populations? Dispersal behaviour at different life-history stages. In: Lancaster J, Briers RA (eds) Aquatic insects challenges to populations. CABI, Wallingford, pp 184–203

Dreyer J, Townsend PA, Hook JC III, Hoekman D, Vander Zanden MJ, Gratton C (2015) Quantifying aquatic insect deposition from lake to land. Ecology 96:499–509

Drummond LR, McIntosh AR, Larned ST (2015) Invertebrate community dynamics and insect emergence in response to pool drying in a temporary river Freshw Biol 60: 1596–1612

Dudley R, Byrnes G, Yanoviak SP, Borrell B, Brown RM, McGuire JA (2007) Gliding and the functional origins of flight: biomechanical novelty or necessity? Ann rev Ecol. Evol Syst 38:179–201

Dumont HJ, Desmet K (1990) Transsahara and transmediterranean migratory activity of *Hemianax ephippiger* (Burmeister) in 1988 and 1989 (Anisoptera: Aeshnidae). Odonatologica 19:181–185

Dumont HJ, Hinnekint BON (1973) Mass migration in dragonflies, especially in *Libellula quadrimaculata* L. a review, a new ecological approach and a new hypothesis. Odonatologica 2:1–20

Elbers ARW, Koenraadt CJM, Meiswinkel R (2015) Mosquitoes and *Culicoides* biting midges: vector range and the influence of climate change. Rev Sci Tech 4:123–137

Elias-Neto M, Belles X (2016) Tergal and pleural structures contribute to the formation of ectopic prothoracic wings in cockroaches. R Soc Open Sci 3:160347

Elliot JM (1971) Upstream movements of benthic invertebrates in a Lake District stream. J Anim Ecol 40:235–252

Epopa PS, Millogo AA, Collins CM, North A, Tripet F, Benedict MQ, Diabate A (2017) The use of sequential mark-release recapture experiments to estimate population size, survival and dispersal of male mosquitoes of the *Anopheles gambiae* complex in Bana, a west African humid savannah village. Parasit Vectors 10:376–380

Fagan WF (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243–3249

Fagan WF, Siemann E, Mitter C, Denno RF, Huberty AF, Woods HA, Elser JJ (2002) Nitrogen in insects: implications for trophic complexity and species diversification. Am Nat 160:784–802

Figuerola J, Green AJ (2002) Dispersal of aquatic organisms by water birds: a review of past research and priorities for future studies. Freshw Biol 47:483–494

Finn DS, Blouin MS, Lytle DA (2007) Population genetic structure reveals terrestrial affinities for a headwater stream insect. Freshw Biol 52:1891–1897

Fisher SG, Likens GE (1973) Energy flow in bear brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecology 43:421–439

Forbes SA (1887) The lake as a microcosm. Bull Peoria Sci Assoc:77–87

Foster WA, Treherne JE (1978) Dispersal mechanisms in an intertidal aphid. J Anim Ecol 47:205–217

Freeland JR, May M, Lodge R, Conrad KF (2003) Genetic diversity and widespread haplotypes in a migratory dragonfly, the common green darner *Anax junius*. Ecol Entomol 28:413–421

Fukui D, Murakami M, Nakano S, Aoi T (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. J Anim Ecol 75:1252–1258

Galatowitsch ML, Batzer DP (2011) Benefits and costs of Leptophlebia (Ephemeroptera) mayfly movements between river channels and floodplain wetlands. Can J Zool 89:714–723

Garcia R, Hagen KS (1987) Summer dormancy in adult *Agabus disintegratus* (Crotch) (Coleoptera: Dytiscidae) in dried ponds in California. Ann Entomol Soc Am 80:267–271

Geenen S, Jordaens K, De Block MJ (2000) Genetic differentiation and dispersal among populations of the damselfly *Lestes viridis* (Odonata). J N Am Benthol Soc 19:321–328

Giudicelli J, Botosaneanu L (1999) The remarkable case of a water striding, mainly brachypterous new species of Rhyacophila Pictet (Trichoptera) from the River Sorgue (southern France). Ann Soc Entomol France 35:265–273

Goehring L, Oberhauser KS (2002) Effects of photoperiod, temperature, and host plant age on induction of reproductive diapause and development time in *Danaus plexippus*. Ecol Entomol 27:674–685. https://doi.org/10.1046/j.1365-2311.2002.00454.x

Graham SE, Storey R, Smith B (2017) Dispersal distances of aquatic insects: upstream crawling by benthic EPT larvae and flight of adult Trichoptera along valley floors. N Z J Mar Freshwater Res 51:146–164

Grewe Y, Hof C, Dehling DM, Brandl R, Brändle M (2013) Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. Glob Ecol Biogeogr 22:403–409

Griffith MB, Barrows EM, Perry SA (1998) Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. Ann Entomol Soc Am 91:195–201

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I (2001) Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372–381

Harada T, Nishimoto T (2007) Feeding conditions modify the photoperiodically induced dispersal of the water strider, Aquarius paludum (Heteroptera: Gerridae). Eur J Entomol 104:33–37. https://doi.org/10.14411/eje.2007.005

Harrison RG (1980) Dispersal polymorphisms in insects. Annu Rev Ecol Syst 11:95–118

Hassall C, Thompson DJ (2008) The impacts of environmental warming on Odonata: a review. Int J Odonatol 11:131–153

Heino J, Mykrä H (2008) Control of stream insect assemblages: roles of spatial configuration and local environmental factors. Ecol Entomol 33:614–622

Hering D, Schmidt-Kloiber A, Murphy JF, Wolfram G (2009) Potential impact of climate change on aquatic insects: a sensitivity analysis for European caddisflies (Trichoptera) based on distribution patterns and ecological preferences. Aquat Sci 71(1):3–14

Hernandez SA, Pecarsky BL (2014) Do stream mayflies exhibit trade-offs between food acquisition and predator avoidance behaviors? Freshw Sci 33:124–133

Hershey AE, Pastor J, Peterson BJ, Kling GW (1993) Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic river. Ecology 74:2315–2325

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Glob Chang Biol 12:1–6

Hobson KA, Anderson RC, Soto DX, Wassenaar LI (2012) Isotopic evidence that dragonflies (*Pantala flavescens*) migrating through the Maldives come from the Northern Indian Subcontinent. PLoS One 7:e52594

Hof C, Brändle M, Brandl R (2008) Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. Glob Ecol Biogeogr 17:539–546

Hof C, Brändle M, Dehling DM, Mungúıa M, Brandl R, Araujo MB, Rahbek C (2012) Biol Lett 8:639–643

Horváth G (1995a) How do water insects find their aquatic habitat? Természet Világa 125:44–49

Horváth G (1995b) Reflection-polarization patterns at flat water surfaces and their relevance for insect polarization vision. J Theoret Biol 175:27–37

Horváth G, Kriska G (2008) Polarization vision in aquatic insects and ecological traps for polarotactic insects. In: Lancaster J, Briers RA (eds) Aquatic insects: challenges to populations. CABI, Wallingford, pp 204–229

Horváth G, Malik P, Kriska G, Wildermuth H (2007) Ecological traps for dragonflies in a cemetery: the attraction of Sympetrum species (Odonata: Libellulidae) by horizontally polarizing black gravestones. Freshw Biol 52:1700–1709

Hu G, Lim KS, Horvitz N, Reynolds DR CSJ, Sapir N, Chapman JW (2016) Mass seasonal bioflows of high-flying insect migrants. Science 354:1584–1587

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ

Hughes JM, Schmidt DJ, Finn DS (2009) Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. BioScience 59:573–583

Hughes JM, Huey JA, McLean AJ, Baggiano O (2011) Aquatic insects in eastern Australia: a window on ecology and evolution of dispersal in stream. Insects 2:447–461

Humphries S, Ruxton GD (2002) Is there really a drift paradox? J Anim Ecol 71:151–154

IPCC (2018) Special Report on Global Warming of 1.5°C. http://www.ipcc.ch/report/sr15/. Accessed 8 Oct 2010

Iversen LL, Rannap R, Briggs L, Sand-Jensen K (2017) Timerestricted flight ability influences dispersal and colonization rates in a group of freshwater beetles. Ecol Evol 7:824–830

Jackson JK, Fisher SG (1986) Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology 67:629–638

Jannot JE (2009) Life history plasticity and fitness in a caddisfly in response to proximate cues of pond-drying. Oecologia 161:267–277

Johansson F, Rowe L (1999) Life history and behavioral responses to time constraints in a damselfly. Ecology 80:1242–1252

Johnson CG (1969) Migration and dispersal of insects by flight. Methuen, London, 766 pp

Jones CJ, Isard SA, Cortinas MR (1999) Dispersal of synanthropic Diptera: lessons from the past and technology for the future. Ann Entomol Soc Am 92:829–839

Kennedy JS (1985) Migration: behavioral and ecological. In Rankin MA, ed., Migration: mechanisms and adaptive significance. Contrib Mar Sci 27(Suppl):5–26

Klečka J (2008) The structure and dynamics of a water beetle community in a semipermanent wetland (Vrbenské rybníky Nature Reserve, South Bohemia). BSc. Thesis, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic, p 63

Kraus JM, Vonesh JR (2010) Feedbacks between community assembly and habitat selection shape variation in local colonization. J Anim Ecol 79:795–802

Krosch MN, Baker AM, Mather PB, Cranston PS (2011) Spatial population genetic structure reveals strong natal site fidelity in Echinocladius martini (Diptera: Chironomidae) in northeast Queensland, Australia. Freshw Biol 56:1328–1341

Kukalová-Peck J (1978) Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. J Morphol 156:53–125

Kukalová-Peck J (1983) Origin of the insect wing and wing articulation from the arthropodan leg. Can J Zool 61:1618–1669

Landin J (1980) Habitats, life histories, migration and dispersal by flight of two water-beetles Helophorus brevipalpis and H. strigifrons (Hydrophilidae). Ecography 3:190–201

Laurance WF, Useche DC, Shoo LP, Herzog SK, Kessler M, Escobar F, Brehm G, Axmacher JC, Chen I-C, Arellano Gamez L, Hietz P, Fiedler K, Pyrcz T, Wolf J, Merkord CL, Cardelus C, Marshall AR, Ah-Peng C, Aplet GH, del Coro Arizmendi M, Baker WJ, Barone J, Bruehl CA, Bussmann RW, Cicuzza D, Eilu G, Favila ME, Hemp A, Hemp C, Homeier J, Hurtado J, Jankowski J, Kattan G, Kluge J, Kroemer T, Lees DC, Lehner M, Longino JT, Lovett J, Martin PH, Patterson BD, Pearson RG, Peh KS-H, Richardson B, Richardson M, Samways MJ, Senbeta F, Smith TB, Utteridge TMA, Watkins JE, Wilson R, Williams SE, Thomas CD (2011) Global warming, elevational ranges and the vulnerability of tropical biota. Biol Conserv 144:548–557

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Lillehammer A (1985) Studies in short-wingedness in stoneflies (Plecoptera). Fauna Norvegica Ser B 32:58–61

Linz DM, Tomoyasu Y (2018) Dual evolutionary origin of insect wings supported by an investigation of the abdominal wing serial homologs in *Tribolium*. Proc Natl Acad Sci U S A 115:E658–E667

Lund JO, Wissinger SA, Peckarsky BL (2016) Caddisfly behavioral responses to drying cues in temporary ponds: implications for effects of climate change. Freshwater Sci 35(2):619–630

Lytle DA (1999) Use of rainfall cues by *Abedus herberti* (Hemiptera: Belostomatidae): a mechanism for avoiding flash floods. J Insect Behav 12:1–12

Lytle DA (2001) Disturbance regimes and life history evolution. Am Nat 157:525–536

Lytle DA (2002) Flash floods and aquatic insect life-history evolution: evaluation of multiple models. Ecology 83:370–385

Lytle DA (2008) Life-history and behavioural adaptations to flow regime in aquatic insects. In: Rankin J, Briers RA (eds) Aquatic insects: challenges to populations. CAB International, Wallingford, pp 122–138

Lytle DA, Smith RL (2004) Exaptation and flash flood escape in the giant water bugs. J Insect Behav 17:169–178

Lytle DA, Olden JD, McMullen LE (2008) Drought-escape behaviors of aquatic insects may be adaptations to highly variable flow regimes characteristic of desert rivers. Southwest Nat 53:399–402

MacArthur RH, Wilson EO (1967) The theory of island biogeograph*y*. Princeton University Press, Princeton, NJ

Macneale KH, Peckarsky BL, Likens GE (2004) Contradictory results from different methods for measuring direction of insect flight. Freshw Biol 49:1260–1268

Malmqvist B (2000) How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? Biol Conserv 93:271–276

Marden JH, Kramer MG (1994) Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. Science 266:427–430

Marten A, Brändle M, Brandl R (2006) Habitat type predicts genetic population differentiation in freshwater invertebrates. Mol Ecol 15:2643–2651

Matthews JH (2007a) Large-scale dragonfly migration by *Anax junius* (Odonata: Aeshnidae) results in genetic homogeneity despite temporally and spatially discrete populations. In: Research in motion: patterns of large-scale migration in dragonflies and birds. PhD Dissertation, University of Texas, pp 33–61

Matthews JH (2007b) Phenotypic plasticity determines migration strategy across large spatial scales. In Research in motion: patterns of large-scale migration in dragonflies and birds. PhD Dissertation, University of Texas, pp 62–91

May ML (2013) A critical overview of progress in studies of migration of dragonflies (Odonata: Anisoptera), with emphasis on North America. J Insect Conserv 17:1–15. https://doi.org/10.1007/s10841-012-9540-x

May ML, Matthews JH (2008) Migration in Odonata: an overview with special focus on Anax junius. In: Córdoba-Aguilar A (ed) Dragonflies, Model organisms for ecological and evolutionary research. Oxford University Press, Oxford, pp 63–77

May ML, Gregoire JS, Gregoire SM, Aliberti Lubertazzi M, Matthews JH (2017) Emergence phenology, uncertainty, and the evolution of migratory behavior in *Anax junius* (Odonata: Aeshnidae). PLoS One 12:e0183508. https://doi.org/10.1371/journal.pone.0183508

Mazzucco R, Nguyen TV, Kim D-H, Chon T-S , Dieckmann (2015) Adaptation of aquatic insects to the current flow in streams. Ecol Model 309–310:143–152

McCauley SJ (2005) Differential dispersal propensities between individualsin male *Leucorrhinia intacta* (Odonata: Libellulidae). Int J Odonatology 8:223–232

McCauley SJ (2006) The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. Ecography 29:585–595

McCauley SJ (2007) The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients. Oikos 116:121–133

McCauley SJ (2010) Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). Ecol Entomol 35:377–385

McCauley SJ (2013) Relationship between morphology, dispersal, and habitat distribution in threes species of Libellula (Odonata, Anisoptera). Aquat Insects 35:195–204

McCauley SJ, Davis J, Werner EE, Robeson MS (2014) Dispersal, niche breadth and population extinction colonization ratios predict range size in North American dragonflies. J Anim Ecol 83: 858–865

McCauley SJ, Rowe L (2010) *Notonecta* exhibit threat-sensitive, predator-induced dispersal. Biol Lett 6:449–452

McLachlan A (1985) The relationship between habitat predictability and wing length in midges (Chironomidae). Oikos 44:391–397

McPeek MA (1989) Differential dispersal tendencies among *Enallagm*a damselflies (Odonata) inhabiting different habitats. Oikos 56:187–195

Medeiros MCI, Boothe EC, Roarke EB, Hamer GL (2017) Dispersal of male and female *Culex quinquefasciatus* and *Aedes albopictus* mosquitoes using stable isotope enrichment. PLoS Negl Trop Dis 11:e0005347

Michiels NK, Dhondt AA (1991) Characteristics of dispersal in sexually mature dragonflies. Ecol Entomol 16:449–459

Miller MP, Blinn DW, Keim P (2002) Correlations between observed dispersal capabilities and patterns of genetic differentiation in populations of four aquatic insect species from the Arizona White Mountains, USA. Freshw Biol 47:1660–1673

Mokany A, Mokany K (2006) Effects of habitat permanence cues on larval abundance of two mosquito species. Hydrobiologia 563:269–276

Mugnai R, Filho AS, Nessimian JL, Kury AB (2014) Spatial distribution of hyporheic chironomid larvae in a neotropical stream, Atlantic forest, Rio de Janeiro, Brazil. J Insect Sci Photon 115:195–206

Müller K (1954) Investigations on the organic drift in North Swedish streams. Inst Freshwater Res Drottningholm Rep 52:133–148

Müller K (1982) The colonization cycle of freshwater insects. Oecologia 52:202–207

Nicoletti FJ (1997) American Kestrel and Merlin migration correlated with Green Darner movements at Hawk Ridge. Loon 68:216–221

Ohba S, Takagi H (2005) Food shortage affects flight migration of the giant water bug *Lethocerus deyrollei* in the prewintering season. Limnology 6:85–90

Pachepsky E, Lutscher F, Nisbet RM, Lewis MA (2005) Persistence, spread and the drift paradox. Theor Pop Biol 67:61–73

Paetzold A, Bernet JF, Tockner K (2006) Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage. Freshw Biol 51:1103–1115

Paulson DR (2011) Dragonflies of the East. Princeton University Press. 544 pp

Peckarsky BL, McIntosh AR (1998) Fitness and community consequences of avoiding multiple predators. Oecologia 113:565–576

Peckarsky BL, Kerans BL, Taylor BW, McIntosh AR (2008) Predator effects on prey population dynamics in open systems. Oecologia 156:431–440

Peckarsky BL, Encalada AC, AR MI (2011) Why do vulnerable mayflies thrive in trout streams? Am Entomol 57:152–164

Peters RH (1986) The ecological implications of body size. Cambridge University Press, Cambridge, p 329

Petersen I, Winterbottom JH, Orton S, Friberg N, Hildrew AG, Spiers DC, Gurney WSC (1999) Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, UK. Freshw Biol 42:401–416

Pfeiler E, Markow TA (2017) Population connectivity and genetic diversity in long distance migrating insects: divergent patterns in representative butterflies and dragonflies. Biol J Linnean Soc 20:1–8

Phillipsen IC, Kirk EH, Bogan MT, Mims MC, Olden JD, Lytle DA (2015) Dispersal ability and habitat requirements determine landscape-level genetic patterns in desert aquatic insects. Mol Ecol 24:54–69

Pintar MR, Resetarits WJ (2017a) Context-dependent colonization dynamics: regional reward contagion drives local compression in aquatic beetles. J Anim Ecol 86:1124–1135

Pintar MR, Resetarits WJ (2017b) Prey-driven control of predator assemblages: zooplankton abundance drives aquatic beetle colonization. Ecology 98:2201–2215

Pintar MR, Resetarits WJ (2017c) Tree leaf litter composition drives temporal variation in aquatic beetle colonization and assemblage structure in lentic systems. Oecologia 183:797–807

Pintar MR, Bohenek JR, Eveland LL, Resetarits WJ (2018) Colonization across gradients of risk and reward: nutrients and predators generate species specific responses among aquatic insects. Funct Ecol 32(6):1589–1598. https://www.matthewpintar.net/publications.html. Accessed 22 May 2018. https://doi.org/10.1111/1365-2435.13086

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape ecology and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

Rainey RC (1951) Weather and the movement of locust swarms: a new hypothesis. Nature 168:1057–1060

Rainey RC (1976) Flight behaviour and aspects of the atmospheric environment. In: Rainey RC (ed) Insect flight. Blackwell Scientific Publishers, Oxford, pp 75–112

Rankin MA (1978) Hormonal control of insect migratory behavior. In: Dingle H (ed) Evolution of insect migration and diapause, Proceedings in life sciences. Springer, New York, NY, pp 5–32

Reppert SM, Guerra PA, Merlin C (2016) Neurobiology of monarch butterfly migration. Annu Rev Entomol 61:25–42

Resetarits WJ, Binkley CA (2009) Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. Ecology 90: 869–876

Resetarits WJ, Binckley CA (2013) Patch quality and context, but not patch number, drive multiscale colonization dynamics in experimental aquatic landscapes. Oecologia 173:933–946

Resetarits WJ, Binckley CA, Chalcraft DR (2005) Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, IL, pp 374–398

Resetarits WJ, Pintar MR (2016) Functional diversity of non-lethal effects, chemical camouflage, and variation in fish avoidance in colonizing beetles. Ecology 97:3517–3529

Resetarits WJ, Silberbush A (2016) Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. Ecol Lett 19:191–200

Reynolds AM, Reynolds AR, Chapman JR (2014) Non-volant modes of migration in terrestrial arthropods. Anim Migr 2:8–28

Ribera I, Foster GN, Vogler AP (2003) Does habitat use explain large scale species richness patterns of aquatic beetles in Europe? Ecography 26:145–152

Ribera I, Vogler AP (2000) Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. Biol J Linn Soc 71:33–52

Roff DA (1990) The evolution of flightlessness in insects. Ecol Monogr 60:389–421

Roff DA (1991) Life history consequences of bioenergetic and biomechanical constraints on migration. Am Zool 31:243–251

Rowe RJ (1978) *Ischnura aurora* (Brauer), a dragonfly with unusual mating behaviour (Zygoptera: Coenagrionidae). Odonatologica 7:375–383

Ruffieux L, Elouard J-L, Sartori M (1998) Flightlessness in mayflies and its relevance to hypotheses on the origin of insect flight. Proc R Acad Lond B 265:2135–2140

Rundle SD, Bilton DT, Abbott JC, Foggo A (2007) Range size in North American Enallagma damselflies correlates with wing size. Freshw Biol 52:471–477

Russell RW, May ML, Soltesz KL, Fitzpatrick JW (1998) Massive swarm migrations of dragonflies (Odonata) in eastern North America. Am Midl Nat 140:325–342

Saijo H (2001) Seasonal prevalence and migration of aquatic insects in paddies and an irrigation pond in Shimane Prefecture. Jpn J Ecol 51:1–11

Samraoui B, Bouzid S, Boulahbal R, Corbet PS (1998) Postponed reproductive maturation in upland refuges maintains life-cycle continuity during the hot, dry season in Algerian dragonflies (Anisoptera). Int J Odonatol 1(2):119–135

Saunders DS (2010) Photoperiodism in insects: migration and diapause responses. In: Nelson RJ et al (eds) Photoperiodism: the biological calendar. Oxford University Press, Oxford, pp 218–258

Schäfer ML, Lundström JO (2006) Different responses of two floodwater mosquito species, Aedes vexans and Ochlerotatus sticticus (Diptera: Culicidae), to larval habitat drying. J Vector Ecol 31:123–128

Schindler DE, Smits AP (2016) Subsidies of aquatic resources in terrestrial ecosystems. Ecosystems 20:78–93

Schmidt SK, Hughes JM, Bunn SE (1995) Gene flow among conspecific populations of *Baetis* sp. (Ephemeroptera): adult flight and larval drift. J N Am Benthol Soc 14:147–157

Service MW (1980) Effects of wind on the behaviour and distribution of mosquitoes and blackflies. Int J Biometeorol 24:347–353

Service MW (1993) Mosquito ecology field sampling methods. Elsevier, London, p 988

Shah RDT, Shah DN, Domisch S (2012) Range shifts of a relict Himalayan dragonfly in the Hindu Kush Himalayan region under climate change scenarios. Int J Odonatol 15:209–222

Shlizerman E, Phillips-Portillo J, Forger DB, Reppert SM (2016) Neural integration underlying a time-compensated sun compass in the migratory monarch butterfly. Cell Rep 15:683–69

Short AEZ, Caterino MS (2009) On the validity of habitat as a predictor of genetic structure in aquatic systems: a comparative study using California water beetles. Mol Ecol 18:403–414

Short AEZ, Liebherr JK (2007) Systematics and biology of the endemic water scavenger beetles of Hawaii (Coleoptera, Hydrophilidae, Hydrophilini). Syst Entomol 32:601–624

Siepielski AM, Hung K-L, Bein EEB, McPeek MA (2010) Experimental evidence for neutral community dynamics governing an insect assemblage. Ecology 91:847–857

Smith RL (1973) Aspects of the biology of three species of the genus *Rhantus* (Coleoptera: Dytiscidae) with special reference to the acoustical behavior of two. Can Entomol 105:909–919

Snodgrass RE (1935) Principles of insect morphology. McGraw-Hill, New York, p 667

Southwood TRE (1962) Migration of terrestrial arthropods in relation to habitat. Biol Rev 37:171–214

Stav G, Blaustein L, Margalit J (1999) Experimental evidence for predation sensitive oviposition by a mosquito, *Culiseta longiareolata*. Ecol Entomol 24:202–207

Stefanescu C, Páramo F, Åkesson S et al (2012) Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palaearctic. Ecography 35:1–14

Stevens LE, Polhemus JT, Durfee RS, Olson CA (2007) Large mixed-species dispersal flights of predatory and scavenging aquatic Heteroptera and Coleoptera, northern Arizona, USA. West North Am Nat 67:587–592

Stubbington R (2012) The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. Mar Freshw Res 63:293–311

Suarez-Tovar CM, Sarmiento CE (2016) Beyond the wing planform: morphological differentiation between migratory and nonmigratory dragonfly species. J Evol Biol 29:690–703

Svensson, BW (1974) Population movements of adult Trichoptera in a south Swedish stream. Oikos 25:175–175

Taylor LR (1958) Aphid dispersal and diurnal periodicity. Proc Linn Soc Lond 169:67–73

Thompson DJ (1991) Size-biased dispersal prior to breeding in a damselfly: conflicting evidence from a natural population. Oecologia 87:600–601

Troast D, Suhling F, Jinguji H, Sahlén G, Ware J (2016) A global population genetic study of *Pantala flavescens*. PLoS One 11:e0148949. https://doi.org/10.1371/journal.pone.0148949

Trottier R (1971) Effect of temperature on the life-cycle of *Anax junius* (Odonata: Aeshnidae) in Canada. Can Entomol 103:1671–1683

Trueman JWH (1990) Evolution of insect wings a leg exite plus endite model. Can J Zool 68:1333–1335

Ueda T (1988) Diversity in the life history of the dragonfly Sympetrum frequens (Odonata: Insecta). Bull Ishikawa Agric Coll 18:98–110

Velasco J, Millan A (1998) Insect dispersal in a drying desert stream: effects of temperature and water loss. Southwest Nat 43:80–87

Vepsäläinen K (1978) Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In: Dingle H (ed) Evolution of insect migration and diapause, Proceedings in Life Sciences. Springer, New York, NY, pp 218–253

Vonesh JR, Kraus JM, Rosenberg JS, Chase JM (2009) Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. Oikos 118:1219–1229

Washburn JO, Washburn L (1984) Active aerial dispersal of minute wingless arthropods: exploitation of boundary-layer velocity gradients. Science 223:1088–1089

Waters TF (1972) The drift of stream insects. Annu Rev Entomol 17:253–272

Wikelski M, Moskowitz D, Adelman J, Cochran J, Wilcove DS, May ML (2006) Simple rules guide dragonfly migration. Biol Lett 2:325–329

Wikipedia (2018a) Lake Baikal. https://en.wikipedia.org/wiki/Lake_Baikal. Accessed 6 June 2018

Wikipedia (2018b) List of rivers by age. https://en.wikipedia.org/wiki/List_of_rivers_by_age. Accessed 6 June 2018

Wilcock HR, Bruford MW, Nichols RA., Hildrew AG (2007) Landscape, habitat characteristics and the genetic population structure of two caddisflies. Freshw Biol 52:1907–1929

Wilcock HR., Nichols RA, Hildrew AG (2003) Genetic population structure and neighbourhood population size estimates of the caddisfly Plectrocnemia conspersa. 48: 1813–1824

Wildermuth H, Horváth G (2005) Visual deception of a male *Libellula depressa* by the shiny surface of a parked car (Odonata: Libellulidae). Int J Odonatol 8:97–105

Williams DD (1981) Migrations and distribution of stream benthos. In: Lock MA, Williams DD (eds) Perspectives in running water ecology. Plenum, New York, pp 155–207

Williams DD (1996) Environmental constraints in temporary fresh waters and their consequences for the insect fauna. J N Am Benthol Soc 15:634–650

Williams DD, Williams NE (1993) The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream Freshw Biol 30:199–218

Wilson DS (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73:1984–2000

Winterbourn MJ, Chadderton WL, Entrekin SA, Tank JL, Harding JS (2007) Distribution and dispersal of adult stream insects in a heterogeneous montane environment. Archiv für Hydrobiologie 168: 127–135

Wooster D, Sih A (1995) A review of the drift and activity responses of stream prey to predator presence. Oikos 73:3–8

Wright S (1951) The genetical structure of populations. Ann Eugen 15:323–354

Yee DA, Taylor S, Vamosi SM (2009) Beetle and plant density as cues initiating dispersal in two species of adult predaceous diving beetles. Oecologia 160:25–36

Young EC (1965) Flight muscle polymorphism in British Corixidae: ecological observations. J Anim Ecol 34:353–390

Zera AJ (1984) Differences in survivorship, development rate and fertility between long-winged and wingless morphs of the water strider, *Limnoporus canaliculatus*. Evolution 38:1023–1032

Zera AJ, Denno RF (1997) Physiology and ecology of dispersal polymorphism in insects. Annu Rev Entomol 42:207–230

Zwick P (2000) Phylogenetic system and zoogeography of the Plecoptera. Annu Rev Entomol 45:709–746