Annu. Rev. Ecol. Syst. 2001. 32:159–81
Copyright © 2001 by Annual Reviews. All rights reserved

DISPERSAL IN FRESHWATER INVERTEBRATES

David T. Bilton,[1] Joanna R. Freeland,[2] and
Beth Okamura[3]
[1]*Benthic Ecology Research Group, Department of Biological Sciences,*
University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom;
e-mail: dbilton@plymouth.ac.uk
[2]*Department of Biological Sciences, The Open University, Milton Keynes,*
United Kingdom MK7 6AA; e-mail: J.R.Freeland@open.ac.uk
[3]*School of Animal and Microbial Sciences, University of Reading, Whiteknights,*
P.O. Box 228, Reading RG6 6AJ, United Kingdom; e-mail: b.okamura@reading.ac.uk

Key Words gene flow, colonization, passive dispersal, active dispersal, propagule banks

■ **Abstract** Movement between discrete habitat patches can present significant challenges to organisms. Freshwater invertebrates achieve dispersal using a variety of mechanisms that can be broadly categorized as active or passive, and which have important consequences for processes of colonization, gene flow, and evolutionary divergence. Apart from flight in adult freshwater insects, active dispersal appears relatively uncommon. Passive dispersal may occur through transport by animal vectors or wind, often involving a specific desiccation-resistant stage in the life cycle. Dispersal in freshwater taxa is difficult to study directly, and rare but biologically significant dispersal events may remain undetected. Increased use of molecular markers has provided considerable insight into the frequency of dispersal in freshwater invertebrates, particularly for groups such as crustaceans and bryozoans that disperse passively through the transport of desiccation-resistant propagules. The establishment of propagule banks in sediment promotes dispersal in time and may be particularly important for passive dispersers by allowing temporal escape from unfavorable conditions. Patterns that apply to dispersal in freshwater invertebrates can be readily extended to other freshwater taxa, since common challenges arise from the colonization of isolated aquatic systems.

INTRODUCTION

Freshwater invertebrates occur in habitats that represent discrete sites surrounded by an inhospitable terrestrial landscape. Despite this lack of obvious connectivity among sites, many freshwater taxa have broad geographical ranges, as was noted by Darwin (1859). Some organisms achieve wide distributions through active

0066-4162/01/1215-0159$14.00

means such as aerial flight across the intervening landscape. Many, however, are incapable of dispersing themselves and rely on agents such as animal vectors, wind, or water flow to provide passive transport between sites. It is notable that, despite our longstanding appreciation that freshwater organisms achieve dispersal, the extent and modes of dispersal remain poorly understood. Direct study of dispersal is notoriously difficult, since it involves detection of movements by capturing, marking, and recapturing individuals (Southwood & Henderson 2000), an approach that can easily overlook infrequent but biologically significant levels of interpopulation exchange. In aquatic environments, assessment of dispersal can also pose practical problems. Methods of marking individuals may require modification for use in water, and many dispersive stages do not lend themselves to such methods.

Despite the formidable obstacles and problems associated with studying dispersal, the combination of ecological study with new molecular approaches is providing a better understanding of patterns of dispersal in freshwater invertebrates. This review synthesizes what is known of these patterns and emphasizes the ecological and evolutionary consequences of dispersal. We consider empirical studies and theoretical approaches, practical means of investigation, and the comparative biology of dispersing invertebrates that inhabit both lotic and lentic habitats. Because it is beyond the scope of this review to provide a comprehensive survey of the dispersal of invertebrates across the spectrum of freshwater habitats, we focus on systems that have received the widest investigation. In addition, we review evidence that some taxa achieve two-dimensional dispersal by exploiting both temporal and spatial scales, and we note the recent influence of humans on dispersal. Given the general nature of the issues discussed, the diversity of invertebrate life histories, and the ubiquity of invertebrates in freshwater habitats, the various patterns, processes, and predictions that arise should allow appropriate extension to other groups of organisms and to freshwater habitats not explicitly considered.

WHAT CONSTITUTES DISPERSAL?

The term dispersal has been used broadly, with the definition varying between areas of research (Dingle 1996). *The Dictionary of Ecology, Evolution and Systematics* defines dispersal as "[the] outward spreading of organisms or propagules from their point of origin or release; one-way movement of organisms from one home site to another" (Lincoln et al. 1998). As a working definition, we equate dispersal to the movement of individuals or propagules between spatially (or temporally) discrete localities or populations, and we focus mainly on evidence for the overland movement of freshwater invertebrates. Defined in this way, dispersal may or may not entail migration, colonization, or gene flow. Stenseth & Lidicker (1992) provide further discussion of the various uses and definitions of this term.

THE EVOLUTION, HERITABILITY, AND MAINTENANCE OF DISPERSAL

Why Disperse?

From an individual's point of view, there are both advantages and disadvantages to dispersing from one site to another (Stenseth & Lidicker 1992). Advantages include inbreeding avoidance, the possibility of locating a new site with low-density occupation and few resource competitors, and a potential escape from unfavorable conditions such as limited resources, predators, pathogens, and parasites. Disadvantages include an inability to locate a suitable new site, predation en route, failure to locate a mate, and outbreeding depression. The most widely perceived risk when sexually reproducing organisms fail to disperse is inbreeding, whereas overcrowding, predation, and an inability to contend with pathogens and parasites (Bell 1982) are the most obvious threats to clonally reproducing organisms.

Theoretical investigation into the evolution of dispersal has resulted in numerous mathematical models (reviewed in Johnson & Gaines 1990). Recent theoretical developments are dealt with by Clobert et al. (2001), Dieckmann et al. (1999), and Ferrière et al. (2000). Most models identify evolutionarily stable strategies based on game theory (Comins et al. 1980) and focus on variables such as risk of habitat extinction, competition among kin, temporal and spatial variability in habitat quality, costs of dispersal, and avoidance of inbreeding. Adaptive dynamics theory provides an alternative approach through assessing the potential for evolutionary invasion based on the population dynamics of mutant and resident individuals (Dieckmann et al. 1999). Although theoretical developments continue to outpace practical support (Dieckmann et al. 1999, Johnson & Gaines 1990), empirical studies are on the increase. This imbalance no doubt reflects the fact that many of the mechanisms and model parameters are exceedingly difficult to test.

Heritability and Maintenance of Dispersal

For dispersal to be selected, traits related to dispersal must be variable and heritable. Wing length is such a trait in at least two groups of freshwater insects. In the water beetle *Helophorus granularis*, the occurrence of long-winged and flightless morphs is controlled by a single locus system (Angus 1970). In a number of water skaters, the inheritance of wing-length polymorphisms appears to be polygenic (Vepsäläinen 1974, Zera et al. 1983), and in some *Gerris* species, seasonal polyphenism acts in conjunction with genetic polymorphism to determine wing length and therefore dispersal ability (Vepsäläinen 1978). In other species, environmental switches alone appear to determine wing length (Andersen 1982). Heritability of dispersal in other freshwater groups remains poorly understood.

Dispersal is likely associated with the long-term persistence of freshwater taxa, since most freshwater sites are ephemeral relative to species' lifetimes. The relationship between dispersal and persistence of freshwater species has received increasing attention (Avise 1992, Hogg et al. 1998), since dispersal may be a critical predictor of a species' ability to escape threats posed by global atmospheric change (Hogg et al. 1998, Hogg & Williams 1996).

CONSEQUENCES OF DISPERSAL

Dispersal can affect many aspects of the evolution and population genetics of a species, but only if successful colonization is followed by breeding of subsequent generations. Such colonization will result in gene flow, the transfer of genes from one population to another. The effects of dispersal and gene flow are varied and profound. For instance, dispersal can promote range expansion following colonization of new sites. Intercontinental dispersal of freshwater cladocerans (Berg & Garton 1994, Havel et al. 2000), copepods (Cordell & Morrison 1996), and snails (Zaranko et al. 1997) provides dramatic examples of such range expansions. Dispersal may also alter the probability of extinction within local populations by introducing new colonists and increasing genetic diversity, as has been demonstrated in populations of a freshwater bryozoan (Freeland et al. 2000a). In addition, dispersal can strongly reduce the amount of genetic differentiation among populations (Bohonak 1999a). Finally, in the absence of appreciable levels of gene flow, evolutionary independence of populations may result, and this may lead to reproductive isolation and speciation (see Howard & Berlocher 1998 for a recent review).

METHODS OF ASSESSING DISPERSAL

Feasibility studies

The difficulties in quantifying dispersal mean that much of the evidence remains anecdotal, including collections of aquatic insects in traps (Zalom et al. 1980); observations of aquatic insects in flight (Freeman 1945); observations of adults and propagules attached externally to vertebrates and invertebrates (see Figure 1) and in vertebrate digestive tracts (see Table 1); demonstration that propagules remain viable after passing through vertebrate digestive tracts (see Table 1); and colonization of new sites (Jenkins 1995, Maguire 1963). With the exception of colonization events, this body of evidence confirms the feasibility of dispersal but provides little information on its extent or frequency.

Mark-Recapture Techniques

Mark-recapture techniques were developed in ecology principally for estimates of population size (Southwood & Henderson 2000) but can also be applied to assessments of dispersal (Service 1993). Physical marking methods for invertebrates include the use of dyes, stains, and fluorescent or colored powders and pigments (Conrad et al. 1999, Nürnberger & Harrison 1995, Service 1993) applied either to the entire organism or as discrete spots, letters, and numbers (see Figure 2, color

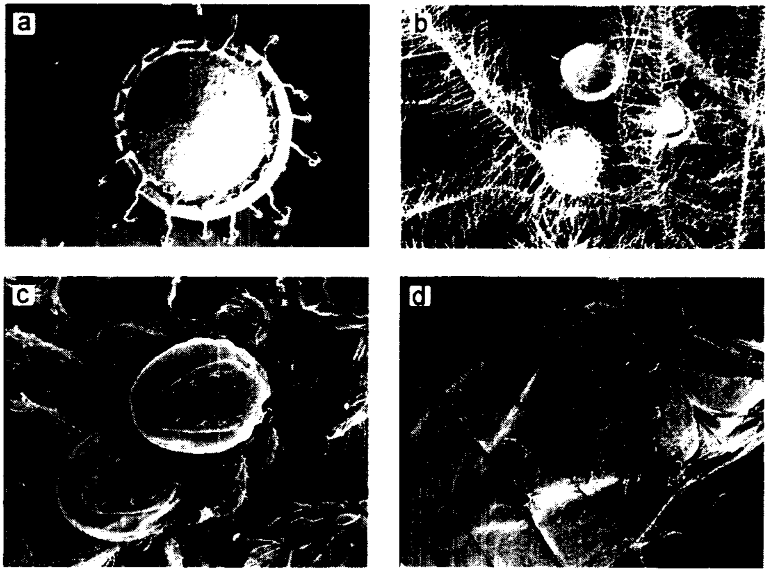

Figure 1 Examples of phoretic dispersal in freshwater invertebrates. (*a*) Statoblast of the bryozoan *Cristatella mucedo*. Gas-filled cells confer buoyancy, making floating statoblasts available for entanglement in, e.g., fur and feathers. Note marginal hooks and spines that are suitable for such attachment. (*b*) Statoblasts of *Cristatella mucedo* entangled in a moulted feather. (*c*, *d*) Larvae of the water mite, *Eylais* sp., attached to the water boatman *Sigara falleni*. Larvae are parasitic, but this relationship also allows phoretic transport of mites between waterbodies.

insert). Such methods are particularly suited to terrestrial adults of aquatic insects. Methods suitable for fully aquatic organisms with hardened external surfaces include the use of a modified dentist's drill or a fine abrasive needle to produce a permanent mark (Svensson 1998). Such marks will not be lost if organisms reenter the water, are unlikely to disappear due to abrasion, and do not introduce toxic organic solvents (present in many waterproof pigments). The incorporation of colored beads in caddisfly larval cases provides a special means of following movements of marked individuals (Erman 1986, Jackson et al. 1999). One potential problem with direct marking is that it may change the behavior of marked individuals, a possibility that is seldom explored. More fundamental problems include the practicalities of marking sufficient numbers of individuals to be able to detect relatively infrequent dispersal events.

Radioactive and stable isotopes have been used to investigate dispersal distances of freshwater insects (Service 1993). Discharge of ^{65}Zn from atomic reactor cooling water demonstrated upstream dispersal in caddisflies (Coutant 1982), and stable isotopes (^{15}N) revealed upstream flight in *Baetis* mayflies (Hershey et al. 1993). In recent years, miniaturized transponder tags have been exploited to track

TABLE 1 Some observations and experiments providing evidence that animal vectors conceivably disperse freshwater invertebrates among sites

Invertebrate	Animal Association	References
Larval and juvenile stages of zebra mussel (*Dreissena polymorpha*)	Zebra mussel stages found on mallard ducks (*Anas platyrhynchos*)	Johnson & Carlton 1996
Adults and juveniles of sphaeriid bivalves (*Pisidium* & *Sphaerium* spp.)	Mussels found attached to the limbs of a range of freshwater insects and amphibians	Kew 1893, Rees 1952, Lansbury 1955
Juvenile mussel (*Anodonta cygnea*)	Individual attached to plover's foot	Adams 1905
Eggs and adults of the river limpet (*Ancylus fluviatilis*)	Limpet eggs and adults found attached to the wing cases of a water beetle (*Acilius sulcatus*)	Kew 1893
Juvenile pond snails (*Lymnaea stagnalis*, *Stagnicola elodes*, *Helisoma triviolis*)	Adherence to whistling swan (*Olor colombianus*) feathers and survival in air	Boag 1986
Adult Ostracoda	Viable adults recovered from the gut of the least sandpiper (*Erolia minutilla*) and found attached to the abdominal hair fringe of water boatmen (*Notonecta glauca* & *N. obliqua*)	Proctor et al. 1967, Lansbury 1955
Adult Amphipoda (*Hyallela azteca* & *Gammarus lacustris*)	Living amphipods collected from the fur of beavers and muskrats	Peck 1975
Adult and cocoon stages of ectoparasitic leeches, *Theromyzon rude* & *Placobdella papillifera*	Attachment of nonfeeding adult leeches to domestic ducks (*Anas platyrhynchos*); viability of some cocoons fed to ducks	Davies et al. 1982
Larval water mites (Hydracarina)	Attachment of parasitic larval stages to winged adult freshwater insects	Bohonak 1999b
Various crustacean eggs	Viability of eggs recovered from digestive tract and feces of domesticated and wild ducks	Proctor & Malone 1965, Proctor et al. 1967
Eggs of brine shrimp (*Artemia salina*)	Exposure of eggs to digestive enzymes has no effect on hatching	Horne 1966
Statoblasts of freshwater bryozoans	Some statoblasts remain viable after passing through digestive tracts of ducks, amphibians, and reptiles	Brown 1933

insects moving close to the ground. These tags capture and reradiate some of the energy emitted from hand-held radar, producing a characteristic signal (Riley et al. 1996). Such methods have obvious potential for studying short-distance movement and dispersal in adult aquatic insects and will no doubt see increased use in the future.

Population Genetic Approaches

Population genetic studies provide indirect methods for studying dispersal. Levels of gene flow among populations can be inferred from the genetic characterization of individuals using molecular markers such as allozymes (Crease et al. 1997, Hughes et al. 1999), mitochondrial DNA (Crease et al. 1997, Taylor et al. 1998), randomly amplified polymorphic DNA (RAPD) (Thomas et al. 1998), and microsatellite loci (Freeland et al. 2000a,b). Indirect assessment of gene flow from genetic data is based on the spatial distributions of alleles or chromosomal segments (reviewed in Slatkin 1985). High levels of dispersal will result in shared alleles and little genetic subdivision between populations, whereas low levels of dispersal will result in genetic divergence among populations as a result of drift and/or selection (but see Nürnberger & Harrison 1995). An important caveat is that the apparent genetic similarity of populations will depend to some extent on the relative mutation rate and the mode of inheritance (e.g., nuclear versus mitochondrial) of the molecular markers that are employed. Different regions of the genome evolve at different rates, which can influence, sometimes profoundly, our interpretation of dispersal patterns (Avise 1994).

The most common approach for inferring gene flow (N*m*) from genetic data is based on the variance in allele frequencies among populations, e.g., Wright's F_{ST} (Wright 1951), Nei's G_{ST} (Nei 1972), and Weir's θ (Weir & Cockerham 1984). Although widely used, such derivations of N*m* should be interpreted with caution, since numerous assumptions such as constant population size, an infinite number of populations, and a constant rate of migration are frequently violated, particularly in nonequilibrium populations (Whitlock & McCauley 1999). Furthermore, F-statistics and their analogs can yield varying estimates of population differentiation and gene flow (Freeland et al. 2000c, Raybould et al. 1998), and there is no consensus on which method is most appropriate. Despite these drawbacks, estimates of N*m* can often provide a useful indication of the relative amount of gene flow between pairs of populations (Slatkin 1993). They should ideally be supplemented by alternate methods for calculating gene flow, however. These include assignment tests, in which multilocus genotypes are assigned to populations based on frequency (Paetkau et al. 1995), Bayesian (Rannala & Mountain 1997) or genetic distance methods (Cornuet et al. 1999), and discriminant function analyses (Freeland et al. 2000a,b). None of these methods is infallible. For example, assignment tests assume Hardy-Weinberg proportions and a complete lack of linkage disequilibrium and can yield different results depending on the molecular marker(s) that is employed and the mutation pattern that is assumed

(Cornuet et al. 1999). Another drawback common to these methods is that all individuals are assigned to a population regardless of whether their population of origin was sampled.

Alternative approaches to N*m* for inferring gene flow from mitochondrial data include nested clade analysis, which can offer greater power than traditional F_{ST} approaches in detecting geographical associations and hence estimating gene flow (Templeton 1998). This technique may also differentiate between ongoing and historical gene flow and can provide a means of detecting range expansions. However, as with any mitochondrial-based inference of gene flow, the influences of stochastic change and/or selection on a single genetic locus may provide misleading results. Furthermore, since mitochondrial DNA is uniparentally inherited, the dispersal patterns of one gender in gonochoristic taxa will be largely ignored. It is therefore advisable to use data from multiple genetic loci and to subject these data to several analytical methods in order to maximize the accuracy of gene flow estimates.

MODES AND MECHANISMS OF DISPERSAL

The many different mechanisms of dispersal can be broadly classified into two modes: active and passive. Active dispersal entails self-generated movements of individual organisms, while passive dispersal entails movements achieved by use of an external agent. Consideration of dispersal as a result of human activities is deferred to a later section.

Passive Dispersal

In lotic habitats, passive dispersal of invertebrates by water currents or downstream drift can displace from 1% to 2% of benthic stream organisms (Waters 1972) and can result in movement of individuals between spatially discrete populations. Drift is the most common means of transport for many stream invertebrates, such as baetid mayflies and amphipod crustaceans. Passive transport of freshwater invertebrates to new water bodies may be achieved using both animal vectors and wind (Maguire 1963). Passive transport via hitchhiking or phoresy is achieved by the movement of resistant resting stages or of individuals that become attached to mobile animal vectors such as waterfowl or other aquatic vertebrates (see Figure 1). Such vector-mediated dispersal may also occur through transport of adults or resting stages in the guts of animal vectors followed by defecation of viable stages. Examples of such dispersal are reviewed in Table 1.

Wind dispersal may result in short-distance transport of anostrocan eggs (Brendonck & Riddoch 1999) and, by extension, may disperse other small desiccation-resistant stages. Longer-distance dispersal such as aerial plankton is likely in small weakly flying insects, such as stoneflies, mayflies, caddisflies, and some members of Diptera (Kelly et al. 2001). However, for many organisms we question the reliability of dispersing by wind to suitable freshwater habitats owing to the high likelihood of terrestrial deposition.

Active Dispersal

In freshwater invertebrates, active dispersal results predominantly from flight in adult insects that show varying degrees of dispersal according to taxonomic group, situation, and prevailing environmental conditions. An additional means of active dispersal is seen in some molluscs (Kerney 1999) and flightless beetles (Balfour-Browne 1958) that can move between sites via intervening areas of wet habitat.

APPARENT ADAPTATIONS FOR DISPERSAL

Active dispersal may be triggered by environmental conditions that are changing or may be predicted to change in the near future. For example, both increasing temperature and decreasing water depth play a role in triggering the dispersal of aquatic members of Heteroptera and Coleoptera (Velasco et al. 1998). In general, however, the cues that trigger aquatic insects to disperse are poorly understood. Achieving passive transport is likely to be a relatively rare event, and many taxa display features that appear to increase its likelihood. These include hooks on bryozoan statoblasts (Wood 1991) (see Figure 1); sticky envelopes, knobs, and spines on branchiopod crustacean eggs (Fryer 1996) and cladoceran ephippia (Dole-Olivier et al. 2000); and release of large numbers of small dispersing stages to coincide with the timing of peak waterfowl migrations (Okamura & Hatton-Ellis 1995).

Active and passive dispersal stages must be equipped for at least brief exposure to terrestrial/aerial conditions, apart from the special case of internal transport in digestive tracts. For passive dispersers this is accomplished with small dormant stages with reduced metabolic rates and resistance to desiccation and extremes of temperature (Williams 1987). Such stages occur in a wide range of taxa, including sponges (Simpson & Fell 1974), monogonont rotifers (Gilbert 1974), bryozoans (Bushnell & Rao 1974), tardigrades (Nelson & Marley 2000), cladocerans (Dodson & Frey 1991), copepods (Dahms 1995), and branchiopods (Korovchinsky & Boikova 1996). Although suited for overland dispersal, some of the characteristics of these propagules may have evolved under a variety of selection regimes, for example following the drying of temporary ponds or a seasonal reduction in food and temperature.

The exploitation of aquatic habitats is a derived condition in insects and most commonly occurs in pterygote larvae, which often represent the main feeding stage in the life cycle. The adult insect is typically winged, and selection for dispersal between habitats is often used to explain the retention of the terrestrial adult phase. With the exception of the Coleoptera and Heteroptera, an alternative explanation is that wings would be unable to function after periods of inundation. Fully aquatic adult beetles and bugs are able to protect their functional hindwings by sclerotized forewings, the elytra and hemielytra, respectively.

VARIATION IN DISPERSAL ABILITY

Intraspecific differences in dispersal abilities are found in some passively dispersing species. For example, *Branchipodopsis wolfi*, the southern African fairy shrimp, produces both sticky and smooth eggs, with the latter showing a higher likelihood of dispersal among sites (Brendonck & Riddoch 1999). The freshwater bryozoan *Plumatella repens* produces two types of statoblasts: stationary sessoblasts and dispersing floatoblasts. The higher proportion of floatoblasts produced by larger colonies suggests that dispersal provides an escape from local resource depletion zones (Karlson 1992).

Variation in dispersal ability is also found within some actively dispersing insect species that contain both winged and wingless forms (Harrison 1980, Roff & Fairbairn 1991). Presumably such wing dimorphism evolved as a result of the differing relative fitness of dispersing offspring under different environmental scenarios. A relatively high frequency of flightless insect morphs is associated with stable habitats (Roff 1990, Vepsäläinen 1974). Short-wingedness is the optimal within-site strategy in a range of water striders of the genus *Gerris*, owing to the greater local reproductive efficiency of this morph (Vepsäläinen 1974, 1978). Long-wingedness is the optimal between-sites strategy, since dispersing individuals can establish new populations when sites temporarily dry out. The persistence of wing dimorphism within populations may occur as a result of dispersal within the metapopulation even though dimorphism is not a locally optimal strategy.

The evolutionary maintenance of flight ability in insects, and the trade-offs between dispersal and other life-history parameters, have been reviewed by Roff (1990, 1994). Since flight in insects is energetically expensive (Chapman 1999) and reduces egg production in some taxa (Roff 1977), it can be expected that aquatic insects will show variation in apparent trade-offs between flight ability and other life-history parameters related to fitness. Some aquatic taxa appear to conform to the oogenesis-flight syndrome (Johnson 1969), in which dispersal occurs early in adult life, and energy for reproduction is then obtained through the autolysis of flight musculature (Hocking 1952). Examples of trade-offs between dispersal and fitness parameters in aquatic insects are reviewed in Table 2.

THE COMPARATIVE BIOLOGY OF DISPERSAL

In order to attain a broad overview of dispersal in freshwater invertebrates, we now focus on several relatively well-studied systems. In particular, we compare passive dispersers that have contrasting life histories in standing waters with actively dispersing taxa that inhabit continuous and discontinuous riverine habitats.

TABLE 2 Trade-offs between dispersal and fitness parameters in aquatic insects and apparent cases of oogenesis-flight syndrome

Invertebrate	Observation	References
Pondskaters (*Limnoporus canaliculatus*, *Gerris* spp.)	Brachypterous females have higher egg output than their macropterous conspecifics	Vespäläinen 1978, Zera 1984
Water boatmen (*Sigara* spp.)	Individuals lacking functional flight musculature have higher fecundity than those capable of flight	Young 1965
Whirligig beetles (*Gyrinus opacus*)	Lifetime reproductive success maximized by remaining resident in first year, then dispersing to other pools	Svensson 1998
Aquatic Heteroptera (*Mesovelia*, *Gerris*), water beetle (*Helophorus strigifrons*)	Autolysis of flight musculature on commencement of reproductive activity (oogenesis-flight syndrome)	Galbreath 1975, Vespäläinen 1978, Landin 1980
Diving beetles (Dytiscidae)	Variable flight muscle development; developed musculature present only in tenerals; suggests oogenesis-flight syndrome	Jackson 1956, Bilton 1994

It will become apparent that even in fully winged invertebrates, dispersal between sites may be rather limited. Darwin's observation of the widespread distribution of freshwater species is tempered by the recognition of cryptic allopatric taxa in some groups.

Dispersal of Zooplankton and Bryozoans from Ponds and Lakes

Studies of zooplankton and bryozoans do not reveal any consistent patterns of either historical or ongoing dispersal. Cladoceran populations, for example, commonly show high levels of genetic differentiation across short geographical distances (Boileau et al. 1992, Crease et al. 1990), and there have been several discoveries of species complexes and cryptic endemics (Hebert & Finston 1997, Weider et al. 1999). Rotifers also show strong phylogeographical structuring over several hundred kilometers (Gómez et al. 2000). However, genetic lineages in zooplankton may also show little divergence over several thousand kilometers (Hann 1995, Hebert & Finston 1996), a discrepancy that suggests very different levels of connection across varying spatial scales, or varying mutation rates. Similarly contradictory patterns were found in the freshwater bryozoan *Cristatella mucedo*. A study of *C. mucedo* in Europe revealed evidence for gene flow among populations over broad spatial scales (Freeland et al. 2000a), whereas conspecific populations in North America remained genetically isolated from one another (Freeland et al. 2000b).

Connection among populations of freshwater species that rely on passive dispersal is influenced by the vectors that transport their propagules. For example, the *C. mucedo* populations studied in Europe were located along a transect that roughly corresponds to a commonly used waterfowl migration route, and therefore waterfowl may act as vectors that link subpopulations within a large metapopulation in northwest Europe (Freeland et al. 2000a). Conversely, the North American *C. mucedo* populations were located along multiple and divergent waterfowl migratory routes, and connection among these sites should be less predictable (Freeland et al. 2000b). Waterfowl have also been implicated in the dispersal of zooplankton propagules. The distribution of genetic lineages within North American populations of the cladoceran *Daphnia laevis* is roughly concordant with three major waterfowl flyways (Taylor et al. 1998). Similar agreement between mitochondrial haplotype distribution and waterfowl migratory routes suggests that waterfowl have played an important role in the postglacial expansion of *Daphnia pulex* in Greenland and Iceland (Weider et al. 1996), and Beringia (Weider & Hobæk 1997).

Although waterfowl migrations apparently play at least an occasional role in the dispersal of freshwater zooplankton and bryozoans, there are several reasons why it will be difficult to fully determine the extent that waterfowl link sites through genetic studies. First, there are likely to be additional vectors of dispersal, e.g., animals, boats, and lotic channels. Second, it is logistically impossible to sample an appreciable proportion of zooplankton or bryozoan populations from most sites, and therefore the genetic identity assigned to a population may depend on which individuals are sampled. In a similar vein, many species can be found in a large number of sites, and those sites that share relatively high levels of gene flow may not have been sampled. Third, it is worth reiterating here that data from different molecular markers will influence conclusions. It was not until both microsatellite and mitochondrial data were obtained from North American *C. mucedo* that a pattern suggesting two cryptic species emerged (Freeland et al. 2000c). Estimates of gene flow will be artificially reduced when data from two species are combined, and this may at least partially explain the apparent lack of gene flow among North American *Cristatella* populations. Similar situations may at times influence gene flow estimates among zooplankton, as, for example, molecular data have suggested that some morphologically similar cladoceran populations are actually distinct species or subspecies (Crease et al. 1997, Taylor et al. 1998). Studies of dispersal have only recently been enhanced by molecular data, and these have targeted a small proportion of taxa. Therefore, some element of caution should be retained when generalizations based on inferences of gene flow are proposed.

Active Dispersal in Riverine Taxa

Running waters are comprised of drainage networks (Banarescu 1990), with the extent and position in the landscape dependent on local topography. Individual watersheds may be viewed as discrete freshwater systems that are only occasionally interconnected by processes such as river capture (Bishop 1995). Given the often highly disturbed nature of stream environments, the populations and assemblages present within local reaches may be strongly determined by dispersal movements of individuals, both in stream and overland (Palmer et al. 1996). In stream-dwelling insects with flying adults, the possibility of lateral dispersal between streams and catchments may lead to gene flow between populations in different watercourses. To date, however, direct studies of dispersal in adult aquatic insects have largely focused on testing Müller's (1954) colonization cycle, whereby upstream adult dispersal compensates for the downstream losses of individuals due to drift (Hershey et al. 1993, Williams & Williams 1993). Significantly higher rates of upstream dispersal have been reported in a range of Plecoptera, Ephemeroptera, and Trichoptera, although the generality of these results has recently been questioned (Petersen et al. 1999). Upstream distances traveled by individual insects have rarely been estimated, but mark-recapture using stable isotopes has revealed them to be on the order of 1 km in *Baetis* mayflies (Hershey et al. 1993). For insects in short headwater streams, such dispersal may allow individuals to move from one headwater to another without lateral dispersal. This can happen if larvae drift downstream to a position below the confluence of two first-order streams, and then adults move upstream into an adjacent headwater (Griffith et al. 1998).

Direct estimates of lateral dispersal away from streams have relied on malaise traps (Griffith et al. 1998), sticky traps (Jackson & Resh 1989), light traps (Kovats et al. 1996), or a combination of approaches (Collier & Smith 1998). These studies suggest limited lateral dispersal in the majority of stream-dwelling insects, particularly weakly flying species of Trichoptera and Plecoptera. Population structure at the drainage level would therefore be expected to follow a stepping-stone model with isolation by distance (Kimura & Weiss 1964). However, the potentially homogenizing effects of upstream dispersal and downstream drift will likely result in less isolation by distance within streams than between streams. Unfortunately, genetic studies of stream insects have rarely involved a sampling design that would allow testing of the above hypothesis through hierarchical analysis of the spatial distribution of genetic diversity. To date, most genetic studies of stream insect populations have relied on allozyme data, and most have found that populations in different stream systems show moderate to high levels of genetic differentiation, including evidence of cryptic speciation (Hughes et al. 1999, Jackson & Resh 1992, Preziosi & Fairbairn 1992).

The only direct attempts to compare population differentiation within and among individual streams and drainages have been undertaken by Bunn and colleagues (Bunn & Hughes 1997, Schmidt et al. 1995), mostly in small rainforest streams in northern Australia. Population genetic data for a mayfly (*Baetis* sp.), a water strider (*Rheumatometra* sp.), and a caddisfly (*Tasiagma ciliata*) all reveal a striking and rather unexpected relationship between levels of genetic differentiation and spatial scale. In all three taxa, genetic differentiation (F_{ST}) decreases with level in the stream hierarchy, being highest between populations in different reaches of the same stream and lowest between separate catchments. Such a pattern is counterintuitive, as relatively low genetic differentiation between catchments points to regular adult dispersal, a scenario that must be reconciled with high differentiation within streams. Schmidt et al. (1995) suggest that unexpectedly high F_{ST} values at smaller spatial scales may be explained if instream movement is restricted, and if individuals within a reach are the offspring of a limited number of females. In these Australian systems, unpredictable climatic conditions lead to asynchronous adult emergence, and therefore relatively few breeding adult insects are present at any given time. These patterns appear to be mirrored in the subtropical Canary Islands (Kelly et al. 2001) but may not hold for stream insects with synchronized emergences. This hypothesis is supported by a study of the synchronously emerging stonefly *Yoraperla brevis* (see Hughes et al. 1999), in which among-stream differentiation (F_{ST}) was an order of magnitude higher than that within streams. Such findings are in keeping with our understanding of adult movement in most stream insect taxa in the northern hemisphere, where, in general, dispersal rates within a drainage network appear to be higher than those between separate catchments, even in organisms capable of active flight.

DISPERSAL IN TIME

Recent evidence indicates that some invertebrate taxa may achieve temporal dispersal through the accumulation and subsequent release of dormant propagules that create a reservoir of genetic material analogous to seed banks in plants. Such dispersal in time will be a function of the dormant period of viable propagules and therefore could vary considerably between taxa. Here we must distinguish between the routine year-to-year continuity of populations maintained via dormant overwintering stages produced in the preceding year, and the recruitment of stages that have remained dormant over longer periods. The latter can result in temporal dispersal that may promote the long-term persistence of both genotypes and local populations during extended adverse conditions (Gómez & Carvalho 2000, Freeland et al. 2001).

The dormancy period of resting stages has been studied in a number of species. In copepods, there is evidence that recruitment of genotypes from sediments occurs when favorable conditions return (Hairston & Caceres 1996). Recent studies provide evidence that egg banks of rotifers and cladocerans contribute to population genetic structure following the hatching of dormant eggs throughout the growing season, a process that contributes to the maintenance of genetic diversity in these populations (Caceres 1998, Gómez & Carvalho 2000). Temporal dispersal has also been inferred from the differential hatching regime of stonefly eggs (Zwick 1996) and from genetic analyses of bryozoan populations sampled over several different timescales (Freeland et al. 2001).

The importance of temporal dispersal via propagule banks is suggested by the fact that some diapausing zooplankton eggs can remain viable in sediment for 200 years or more (Hairston et al. 1995, Caceres 1998). Such an extension of generation time may profoundly influence genetic structure, for example by influencing the rate and direction of microevolution following directional and temporally fluctuating selection (Hairston et al. 1996). Temporal dispersal may particularly benefit predominantly clonal or inbred organisms that have a limited ability to produce novel genotypes and therefore would otherwise remain at a disadvantage in the Red Queen race (Tooby 1982). Furthermore, temporal gene flow may be important to taxa that are incapable of actively dispersing among sites. Notably, many zooplankton and benthic taxa are both clonal and incapable of active dispersal, and these taxa present most of the evidence for temporal gene flow via propagule banks.

HUMAN-MEDIATED DISPERSAL

Dispersal of freshwater organisms through human activities has recently been the focus of considerable investigation (reviewed by Claudi & Leach 2000). Introductions of nonindigenous invertebrates have been achieved through intentional stocking programs for fisheries and for biocontrol, release of organisms from the aquarium or horticultural trade, release of organisms along with bait fish by fishermen, release of ballast water, deliberate establishment of exotic food sources for human consumption, and the creation of humanmade water channels. Clearly, some of these mechanisms of dispersal will have resulted in the dispersal of indigenous species as well. In many cases, patterns of occurrence strongly implicate human-mediated dispersal but, because many invasions occurred before biological surveys, the number of species involved is not known.

Introduction of a number of nonindigenous species has resulted in dramatic postinvasion spread and severe economic and ecological impacts. For instance, release of larvae in ballast water into Lake St. Clair in 1985 or 1986 was the original mechanism by which the zebra mussel, *Dreissena polymorpha*, was introduced to North America (Hebert et al. 1989). Since then *D. polymorpha* has invaded most of the major North American river systems (Mackie 2000) through a combination of further release of larvae in ballast, bilge, and engine cooling water, transport of adults and juveniles on boats and macrophytes entangled on boat trailers, and downstream dispersal of planktonic larval stages. Severe ecological and socioeconomic impacts have resulted (Kinzelbach 1992, Mackie 2000).

Human activities may also impede dispersal among freshwaters. The disruption and fragmentation of rivers by a series of impoundments (Englund & Malmqvist 1996) may diminish dispersal, as is suggested by the relative development of riparian floras and patterns of movement of fish and plant diaspores (Jansson et al. 2000).

KEY DIRECTIONS FOR FUTURE RESEARCH

Integrative Approaches

Few studies combine direct and indirect approaches to estimate levels of dispersal in freshwater invertebrates (but see Nürnberger & Harrison 1995). Consequently, our understanding of local dispersal rates within metapopulations, and the influence of landscape features, is severely limited. Such integrated studies should be conducted across a range of phylogenetically independent taxa, with the simultaneous application of several molecular markers targeting regions of nuclear and mitochondrial DNA that have inherently variable mutation rates. Key areas for such study include lateral dispersal of stream insects, particularly those with aquatic adult stages, and short-range dispersal of pond insects with differing mobilities.

Temporal Dispersal and Propagule Survival in Passive Dispersers

Recent developments indicate that temporal gene flow via propagule banks plays an important role in the metapopulation biology of many freshwater invertebrates. Understanding the extent to which dispersal in both space and time allows the long-term persistence of metapopulations will provide important insights into the maintenance of biodiversity in freshwater systems and may be of particular relevance to conservation issues. Newly created sites, or sites with histories of disturbance, may not be the best habitats for protection if temporal gene flow is important. An awareness of dispersal through time and space highlights the fallacy of viewing populations as discrete units and should serve as a warning that the effects of restricting or otherwise altering patterns of dispersal may have unforeseen and potentially far-reaching consequences.

While passive dispersal via animal vectors has been inferred from both direct and indirect observations, the survival of passive dispersers under different regimes is poorly understood. More systematic study is required before we can determine whether particular vector species and habitat types favor passive transport.

Historical Versus Ongoing Gene Flow

Molecular markers have contributed enormously to our understanding of the movements of many freshwater taxa. However, such approaches can lead to new sets of problems. For example, range extensions of freshwater taxa at the end of the last ice age may have introduced multiple genetic lineages into individual lakes and ponds (Stemberger 1995), and such historical events may not be readily distinguishable from ongoing gene flow without the use of rapidly evolving molecular markers (Freeland et al. 2000c). Notably few studies have used mitochondrial DNA data to infer historical patterns of range expansion and dispersal in freshwater invertebrates (Avise 2000; but see Bilton 1994, Nürnberger & Harrison 1995, Meyran et al. 1997, Weider & Hobæk 1997, Gómez et al. 2000). Disentangling the extent to which population structure results from recurrent forces, such as gene flow, versus historical events, such as fragmentation and range expansion, will be crucial to understanding the frequency of dispersal in freshwater taxa. With the further development of molecular and analytical approaches and the streamlining of laboratory practices, it will become easier to genetically characterize individuals at multiple loci and to conduct more suitable analyses of the data through adoption of increasingly refined models.

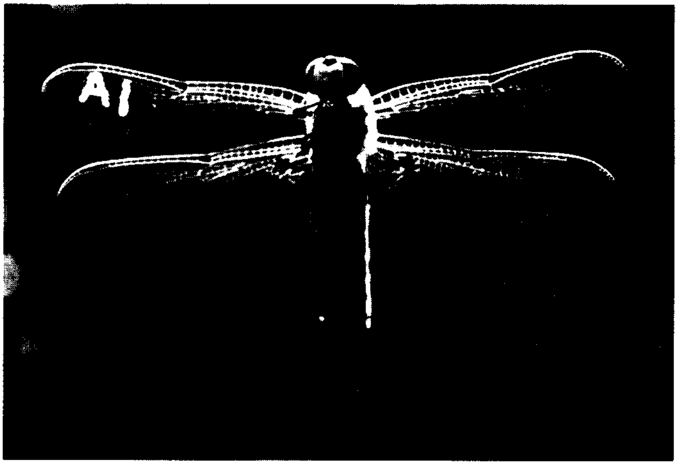

Figure 2 Mark-recapture in action. Adult *Libellula quadrimaculata* showing individual paint-marking.

Understanding Anthropogenic Influences

While a large proportion of original wetlands have been lost (Carp 1980, Rackham 1986), humans have created new water bodies through damming of rivers (Moss 1998), creation of small farm ponds (Gerking 1966) and ornamental lakes (Bennion et al. 1997), and digging of gravel pits. The distribution of freshwater invertebrates in many, if not most, places on earth is now a result of contraction from natural habitats and expansion into humanmade environments. It is unclear how this changing array of habitats will influence dispersal patterns of freshwater invertebrates. Global climate change and habitat degradation may mean that the persistence of populations and species will rely on increasingly frequent dispersal events. At the same time, human-mediated dispersal often provides a new degree of connectivity between populations. Many predictions regarding the fate of freshwater taxa under rapidly changing environmental conditions remain speculative. In order to refine these predictions, we must improve our understanding of dispersal patterns and processes among freshwater populations.

ACKNOWLEDGMENTS

We are grateful to Gary Carvalho, Dagmar Frisch, Peter Hammond, Lucy Kelly, Björn Malmqvist, Simon Rundle, and Steve Threlkeld for editing and commenting on the manuscript. Roy Moate and Paul Taylor kindly produced the SEM photographs used in Figure 1, and Antonio Di Sabatino identified the mite larvae. Kelvin Conrad provided the photo of the marked dragonfly for Figure 2 (see color insert). Thanks also to Lucy Kelly, Ron Carr, and David Sims for providing references. BO and JRF wish to thank the Natural Environment Research Council Work for funding to study dispersal in *Cristatella mucedo* (grants GR3/11068, GR3/8961).

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

Adams LE. 1905. A plover with *Anodonta cygnea* attached to its foot. *J. Conchol.* 11: 175

Andersen NM. 1982. *The Semiaquatic Bugs.* Klampenborg, Denmark: Scandinavian Sci. 455 pp.

Angus RB. 1970. Genetic experiments on *Helophorus* F. (Coleoptera: Hydrophilidae). *Trans. R. Entomol. Soc. London* 122:257–76

Avise JC. 1992. Molecular population structure and the biogeographic history of a regional fauna—a case history with lessons for conservation biology. *Oikos* 63:62–76

Avise JC. 1994. *Molecular Markers, Natural History and Evolution.* New York: Chapman & Hall. 511 pp.

Avise JC. 2000. *Phylogeography. The History and Formation of Species.* Cambridge, MA: Harvard Univ. Press. 384 pp.

Balfour-Browne WAF. 1958. *British Water Beetles.* London: Ray Soc. 210 pp.

Banarescu P. 1990. *Zoogeography of Fresh Waters. General Distribution and Dispersal* *of Freshwater Animals*. Wiesbaden: Aula–Verlag

Bell G. 1982. *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*. Berkeley: Univ. Calif. Press

Bennion HR, Harriman R, Battarbee R. 1997. A chemical survey of standing waters in south-east England, with reference to acidification and eutrophication. *Freshwater Forum* 8:28–44

Berg DJ, Garton DW. 1994. Genetic differentiation in North American and European populations of the cladoceran *Bythotrephes*. *Limnol. Oceanogr.* 39:1503–16

Bilton DT. 1994. Phylogeography and recent historical biogeography of *Hydroporus glabriusculus* Aubé (Coleoptera: Dytiscidae) in the British Isles and Scandinavia. *Biol. J. Linn. Soc.* 51:293–307

Bishop P. 1995. Drainage rearrangement by river capture, beheading and diversion. *Prog. Phys. Geogr.* 19:449–73

Boag DA. 1986. Dispersal in pond snails: potential role of waterfowl. *Can. J. Zool.* 64:904–9

Bohonak AJ. 1999a. Dispersal, gene flow, and population structure. *Q. Rev. Biol.* 74:21–45

Bohonak AJ. 1999b. Effect of insect-mediated dispersal on the genetic structure of postglacial water mite populations. *Heredity* 82:451–61

Boileau MG, Hebert PDN, Schwartz SS. 1992. Nonequilibrium gene frequency divergence: persistent founder effects in natural populations. *J. Evol. Biol.* 5:25–39

Brendonck L, Riddoch BJ. 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biol. J. Linn. Soc.* 67:87–95

Brown CJD. 1933. A limnological study of certain fresh-water Polyzoa with special reference to their statoblasts. *Trans. Am. Microsc. Soc.* 52:271–314

Bunn SE, Hughes JM. 1997. Dispersal and recruitment in streams: evidence from genetic studies. *J. N. Am. Benth. Soc.* 16:338–46

Bushnell JH, Rao KS. 1974. Dormancy or quiescent stages and structures among the Ectoprocta: physical and chemical factors affecting viability and germination of statoblasts. *Trans. Am. Microsc. Soc.* 93:524–43

Caceres CE. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79:1699–710

Carp E. 1980. *A Directory of Western Palaearctic Wetlands*. Gland: IUCN

Chapman RF. 1999. *The Insects: Structure and Function*. London: Chapman & Hall

Claudi R, Leach JR, eds. 2000. *Nonindigenous Freshwater Organisms. Vectors, Biology, and Impacts*. Boca Raton, FL.: Lewis. 464 pp.

Clobert J, Danchin E, Dhont AA, Nichols JD. 2001. *Dispersal*. Oxford: Oxford Univ. Press

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

Comins HM, Hamilton WD, May RM. 1980. Evolutionary stable dispersal strategies. *J. Theor. Biol.* 82:205–30

Conrad KF, Wilson KH, Harvey IF, Thomas CJ, Sherratt TN. 1999. Dispersal characteristics of seven odonate species in an agricultural landscape. *Ecography* 22:524–31

Cordell JR, Morrison SM. 1996. The invasive Asian copepod *Pseudodiaptomus inopinus* in Oregon, Washington, and British Columbia estuaries. *Estuaries* 19:629–38

Cornuet JM, Piry S, Luikart G, Estoup A, Solignac M. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics* 153:1989–2000

Coutant CC. 1982. Evidence for upstream dispersal of adult caddisflies (Trichoptera: Hydropsychidae) in the Colombia River. *Aquat. Insects* 4:61–66

Crease TJ, Lee SK, Yu SI, Spitze K, Lehman N, Lynch M. 1997. Allozyme and mtDNA variation in populations of the *Daphnia pulex* complex from both sides of the Rocky mountains. *Heredity* 79:242–51

Crease TJ, Lynch M, Spitze K. 1990. Hierarchical analysis of population genetic variation in mitochondrial and nuclear genes of *Daphnia pulex*. *Mol. Biol. Evol.* 7:444–58

Dahms H-U. 1995. Dormancy in the Copepoda—an overview. *Hydrobiologia* 306:199–211

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection*. London: John Murray

Davies RW, Linton LR, Wrona FJ. 1982. Passive dispersal of four species of freshwater leeches (Hirudinoidea) by ducks. *Fresh. Invert. Biol.* 1:40–44

Dieckmann U, O'Hara B, Weisser W. 1999. The evolutionary ecology of dispersal. *TREE* 14:88–90

Dingle H. 1996. *Migration. The Biology of Life on the Move*. Oxford, UK: Oxford Univ. Press. 480 pp.

Dodson SI, Frey DG. 1991. Cladocera and other Branchiopoda. See Thorp & Covich 1991, pp. 723–86

Dole-Olivier M-J, Galassi DMP, Marmonier P, Creuzé des Châtelliers M. 2000. The biology and ecology of lotic microcrustaceans. *Freshwater Biol.* 44:63–91

Englund G, Malmqvist B. 1996. Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regul. Rivers Res. Manage.* 12:433–45

Erman NA. 1986. Movements of self-marked caddisfly larvae, *Chyranda centralis* (Trichoptera: Limnephilidae), in a Sierran spring stream, California, U.S.A. *Freshwater Biol.* 16:455–64

Ferriere R, Belthoff JR, Olivieri I, Krackow S. 2000. Evolving dispersal: where to go next? *TREE* 15:5–7

Freeland JR, Noble LR, Okamura B. 2000a. Genetic consequences of the metapopulation biology of a facultatively sexual freshwater invertebrate. *J. Evol. Biol.* 13:383–95

Freeland JR, Noble LR, Okamura B. 2000b. Genetic diversity of North American populations of *Cristatella mucedo*, inferred from microsatellite and mitochondrial DNA. *Mol. Ecol.* 9:1375–89

Freeland JR, Romualdi C, Okamura B. 2000c. Gene flow and genetic diversity: a comparison of freshwater bryozoan populations in Europe and North America. *Heredity* 85:498–508

Freeland JR, Rimmer VK, Okamura B. 2001. Genetic changes within freshwater bryozoan populations suggest temporal gene flow from statoblast banks. *Limnol. Oceanogr.* 46:1121–29

Freeman JA. 1945. Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. *J. Anim. Ecol.* 14:128–54

Fryer G. 1996. Diapause, a potent force in the evolution of freshwater crustaceans. *Hydrobiologia* 320:1–14

Galbreath JE. 1975. Thoracic polymorphism in *Mesovelia mulsanti* (Hemiptera, Mesoveliidae). Kansas Univ. *Sci. Bull.* 50:457–82

Gerking SD. 1966. Central states. In *Limnology in North America*, ed. DG Frey, pp. 239–68. Madison: Univ. Wisc. Press. 752 pp.

Gilbert JJ. 1974. Dormancy in rotifers. *Trans. Am. Microsc. Soc.* 93:490–513

Gómez A, Carvalho GR. 2000. Sex, parthenogenesis and genetic structure of rotifers: microsatellite analysis of contemporary and resting egg bank populations. *Mol. Ecol.* 9:203–14

Gómez A, Carvalho GR, Lunt DH. 2000. Phylogeography and regional endemism of a passively dispersing zooplankter: mitochondrial DNA variation in rotifer resting egg banks. *Proc. R. Soc. London Ser. B* 267:2189–97

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

Hairston NGJ, Van Brunt RA, Kearns CM, Engstrom DR. 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76:1706–11

Hairston NGJ, Caceres CE. 1996. Distribution of crustacean diapause: micro- and macroevolutionary pattern and process. *Hydrobiologia* 320:27–44

Hairston NGJ, Kearns CM, Ellner SP. 1996. Phenotypic variation in a zooplankton egg bank. *Ecology* 77:2382–92

Hann BJ. 1995. Genetic variation in *Simocephalus* (Anomopoda, Daphniidae) in North America: patterns and consequences. *Hydrobiologia* 307:9–14

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

Havel JE, Colbourne JK, Hebert PDN. 2000. Reconstructing the history of intercontinental dispersal of *Daphnia lumholtzi* by use of genetic markers. *Limnol. Oceangr.* 45:1414–19

Hebert PDN, Finston TL. 1996. Genetic differentiation in *Daphnia obtusa*: a continental perspective. *Freshwater Biol.* 35:311–21

Hebert PDN, Finston TL. 1997. A taxonomic reevaluation of North American Daphnia (Crustacea: Cladocera). 3. The *D. catawba* complex. *Can. J. Zool.* 75:1254–61

Hebert PDN, Wilson CC, Murdoch MH, Lazar R. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Can. J. Zool.* 59:405–9

Hershey AE, Pastor J, Peterson BJ, Kling GJ. 1993. Stable isotopes resolve the drift paradox for *Baetis* mayflies in an arctic river. *Ecology* 74:2415–25

Hocking B. 1952. Autolysis of flight muscle in a mosquito. *Nature* 169:1101

Hogg ID, Eadie JM, De Lafontaine Y. 1998. Atmospheric change and the diversity of aquatic invertebrates: Are we missing the boat? *Environ. Mon. Assess.* 49:291–301

Hogg ID, Williams DD. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* 77:395–407

Horne FR. 1966. The effect of digestive enzymes on the hatchability of *Artemia salina* eggs. *Trans. Am. Microsc. Soc.* 85:271–74

Howard DJ, Berlocher S. 1998. *Endless Forms: Species and Speciation*. Oxford, UK: Oxford Univ. Press

Hughes JM, Mather PB, Sheldon AL, Allendorf FW. 1999. Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. *Freshwater Biol.* 41:63–72

Jackson DJ. 1956. Observations on flying and flightless water beetles. *J. Linn. Soc. London* 43:18–43

Jackson JK, McElravy EP, Resh VH. 1999. Long-term movements of self-marked caddisfly larvae (Trichoptera: Sericostomatidae) in a California coastal mountain stream. *Freshwater Biol.* 42:525–36

Jackson JK, Resh VH. 1989. Distribution and abundance of adult aquatic insects in the forest adjacent to a northern Californian stream. *Environ. Entomol.* 18:278–83

Jackson JK, Resh VH. 1992. Variation in genetic structure among populations of the caddisfly *Helicopsyche borealis* from three streams in northern California, U.S.A. *Freshwater Biol.* 27:29–42

Jansson R, Nilson C, Renofalt B. 2000. Fragmentation of riparian floras in rivers with multiple dams. *Ecology* 81:899–903

Jenkins DG. 1995. Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiologia* 313:15–20

Johnson CG. 1969. *Migration and Dispersal of Insects by Flight*. London: Methuen. 763 pp.

Johnson LE, Carlton JT. 1996. Post-establishment spread in large-scale invasions: dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. *Ecology* 77:1686–90

Johnson ML, Gaines MS. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu. Rev. Ecol. Syst.* 21:449–80

Karlson RH. 1992. Divergent dispersal strategies in the freshwater bryozoan *Plumatella repens*—ramet size effects on statoblast numbers. *Oecologia* 89:407–11

Kelly LC, Bilton DT, Rundle SD. 2001. Genetic differentiation and dispersal in the Canary Island caddisfly *Mesophylax aspersus* (Trichoptera: Limnephilidae). *Heredity* 86:370–77

Kerney MP. 1999. *Atlas of the Land and Freshwater Molluscs of Britain and Ireland.* Colchester: Harley. 264 pp.

Kew HW. 1893. *The Dispersal of Shells.* London: Kegan Paul, Trench, Trübner

Kimura M, Weiss GH. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* 49:561–76

Kinzelbach R. 1992. The main features of the phylogeny and dispersal of the zebra mussel *Dreissena polymorpha.* In *The Zebra Mussel* Dreissena polymorpha. *Ecology, Biological Monitoring and First Applications in the Water Quality Management,* ed. D Neumann, HA Jenner, pp. 5–17. Stuttgart: Gustav Fischer. 280 pp.

Korovchinsky NM, Boikova OS. 1996. The resting eggs of Ctenopoda (Crustacea: Branchiopoda): a review. *Hydrobiologia* 320: 131–40

Kovats ZE, Ciborowski JJH, Corkum LD. 1996. Inland dispersal of adult aquatic insects. *Freshwater Biol.* 36:265–76

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

Lansbury I. 1955. Some notes on invertebrates other than Insecta found attached to water bugs (Hemipt.-Heteroptera). *Entomologist* 88:139–40

Lincoln R, Boxshall G, Clark P. 1998. *A Dictionary of Ecology, Evolution and Systematics.* Cambridge, UK: Cambridge Univ. Press. 350 pp.

Mackie GL. 2000. Ballast water introductions of Mollusca. See Claudi & Leach 2000, pp. 219–54

Maguire BJ. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecol. Monogr.* 33:161–85

Meyran JC, Monnerot M, Taberlet P. 1997. Taxonomic status and phylogenetic relationships of some species of the genus *Gammarus* (Crustacea, Amphipoda) deduced from mitochondrial DNA sequences. *Mol. Phyl. Evol.* 8:1–10

Moss B. 1998. *Ecology of Fresh Waters. Man and Medium.* Oxford, UK: Blackwell Sci.

Müller K. 1954. Investigations on the organic drift in North Swedish streams. *Rep. Inst. Freshwater Res. Drottingholm* 34:133–48

Nei M. 1972. Genetic distance between populations. *Am. Nat.* 106:283–92

Nelson DR, Marley NJ. 2000. The biology and ecology of lotic Tardigrada. *Freshwater Biol.* 44:93–108

Nürnberger B, Harrison RG. 1995. Spatial population structure in the whirligig beetle *Dineutus assimilis*: evolutionary influences based on mitochondrial DNA and field data. *Evolution* 49:266–75

Okamura B, Hatton-Ellis T. 1995. Population biology of bryozoans—correlates of sessile, colonial life-histories in fresh-water habitats. *Experientia* 51:510–25

Paetkau D, Calvert W, Stirling I, Strobeck C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Mol. Ecol.* 4:347–54

Palmer MA, Allan JD, Butman CA. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *TREE* 11:322–26

Peck SB. 1975. Amphipod dispersal in the fur of aquatic mammals. *Can. Field Nat.* 89:181–82

Petersen I, Winterbottom JH, Orton S, Hildrew AG. 1999. Does the colonization cycle exist? In *Biodiversity in Benthic Ecology. Proc. Nordic Benthol. Meet.*, ed. N Friberg, JD Carl, pp. 59–62. Silkeborg, Denmark: NERI Tech. Rep. No. 226

Preziosi RF, Fairbairn DJ. 1992. Genetic population structure and levels of gene flow in the stream dwelling waterstrider. *Aquarius* (=*Gerris*) *remigis* (Hemiptera, Gerridae). *Evolution* 46:430–44

Proctor VW, Malone C. 1965. Further evidence of the passive dispersal of small aquatic organisms via the intestinal tract of birds. *Ecology* 46:728–29

Proctor VW, Malone CR, DeVlaming VL.

1967. Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive killdeer. *Ecology* 48:672–76

Rackham O. 1986. *The History of the Countryside*. London: Dent. 464 pp.

Rannala B, Mountain JL. 1997. Detecting immigration by using multilocus genotypes. *Proc. Natl. Acad. Sci. USA* 94:9197–201

Raybould AF, Mogg RJ, Aldam C, Gliddon CJ, Thorpe RS, Clarke RT. 1998. The genetic structure of sea beet (*Beta vulgaris* ssp. *maritima*) populations. III. Detection of isolation by distance at microsatellite loci. *Heredity* 80:127–32

Rees WJ. 1952. The role of amphibia in the dispersal of bivalve molluscs. *Br. J. Herpetol.* 1:125–29

Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL, et al. 1996. Tracking bees with harmonic radar. *Nature* 379:29–30

Roff DA. 1977. Dispersal in dipterans: its costs and consequences. *J. Anim. Ecol.* 46:443–56

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

Roff DA. 1994. The evolution of flightlessness: Is history important? *Evol. Ecol.* 8:639–57

Roff DA, Fairbairn DJ. 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the insects. *Am. Zool.* 31:251

Schmidt SF, Hughes JM, Bunn SE. 1995. Gene flow among conspecific populations of *Baetis* (Ephemeroptera): adult flight and larval drift. *J. N. Am. Benth. Soc.* 14:47–57

Service MW. 1993. *Mosquito Ecology Field Sampling Methods*. London: Elsevier. 988 pp.

Simpson TL, Fell PE. 1974. Dormancy among the Porifera: gemmule formation and germination in fresh-water and marine sponges. *Trans. Am. Microsc. Soc.* 93:544–77

Slatkin M. 1985. Gene flow in natural populations. *Annu. Rev. Ecol. Syst.* 16:393–430

Slatkin M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* 47:264–79

Southwood TRE, Henderson PA. 2000. *Ecological Methods*. Oxford, UK: Blackwell Sci.

Stemberger RS. 1995. Pleistocene refuge areas and postglacial dispersal of copepods of the northeastern United States. *Can. J. Fish. Aquat. Sci.* 52:2197–210

Stenseth NC, Lidicker WC Jr. 1992. The study of dispersal: a conceptual guide. In *Animal Dispersal: Small Mammals as a Model*, ed. NC Stenseth, WC Lidicker Jr, pp. 5–20. New York/London: Chapman & Hall

Svensson BW. 1998. Local dispersal and its life-history consequences in a rock-pool population of a gyrinid beetle. *Oikos* 82:111–22

Taylor DJ, Finston TL, Hebert PDN. 1998. Biogeography of a widespread freshwater crustacean: pseudocongruence and cryptic endemism in the North American *Daphnia laevis* complex. *Evolution* 52:1648–70

Templeton A. 1998. Nested clade analyses of phylogeographic data: testing hypotheses about gene flow and population history. *Mol. Ecol.* 7:381–97

Thomas EP, Blinn DW, Keim P. 1998. Do xeric landscapes increase genetic divergence in aquatic landscapes? *Freshwater Biol.* 40:587–93

Thorp JH, Covich AP, eds. 1991. *Ecology and Classification of North American Freshwater Invertebrates*. New York: Academic

Tooby J. 1982. Pathogens, polymorphism, and the evolution of sex. *J. Theor. Biol.* 97:557–76

Velasco J, Suarez ML, Vidal-Abarca MR. 1998. Factores que determinan la colonizacion de insectos acuaticos en pequenos estanques. *Oecol. Aquat.* 11:87–99

Vepsäläinen K. 1974. Determination of wing length and diapause in water striders (*Gerris* Fabr., Heteroptera). *Hereditas* 77:163–76

Vepsäläinen K. 1978. Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In *Evolution of Insect Migration and Diapause*, ed. H Dingle, pp. 218–53. New York: Springer-Verlag. 284 pp.

Waters TF. 1972. The drift of stream insects. *Annu. Rev. Entomol.* 17:253–72

Weider LJ, Hobæk A. 1997. Postglacial dispersal, glacial refugia, and clonal structure in Russian/Siberian populations of the arctic *Daphnia pulex* complex. *Heredity* 78:363–72

Weider LJ, Hobæk A, Crease TJ, Stibor H. 1996. Molecular characterization of clonal population structure and biogeography of arctic apomictic *Daphnia* from Greenland and Iceland. *Mol. Ecol.* 5:107–18

Weider LJ, Hobæk A, Colbourne JK, Crease TJ, Dufresne F, Hebert PDN. 1999. Holarctic phylogeography of an asexual species complex. I. Mitochondrial DNA variation in Arctic *Daphnia*. *Evolution* 53:777–92

Weir BS, Cockerham CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–70

Whitlock MC, McCauley DE. 1999. Indirect measures of gene flow and migration: Fst $\neq$ 1/(4Nm+1). *Heredity* 82:117–25

Williams DD. 1987. *The Ecology of Temporary Waters*. London: Croom Helm. 205 pp.

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

Wood TS. 1991. Bryozoans. See Thorp & Covich 1991, pp. 481–99

Wright S. 1951. The genetical structure of populations. *Eugenics* 15:323–54

Young EC. 1965. Flight muscle polymorphism in British Corixidae: ecological observations. *J. Anim. Ecol.* 34:353–90

Zalom FG, Grigarick AA, Way MO, Grigarick AA, Way MO. 1980. Diel flight periodicities of some Dytiscidae (Coleoptera) associated with California rice paddies. *Ecol. Entomol.* 5:183–87

Zaranko DT, Farara DG, Thompson FG. 1997. Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). *Can. J. Fish. Aquat. Sci.* 54:809–14

Zera AJ. 1984. Differences in survivorship, developmental rate and fertility between the long-winged and wingless morphs of the water strider *Limnoporus canaliculatus*. *Evolution* 38:1023–32

Zera AJ, Innes DT, Saks ME. 1983. Genetic and environmental determinants of wing polymorphism in the water strider *Limnoporus canaliculatus*. *Evolution* 37:513–22

Zwick P. 1996. Variable egg development of *Dinocras* spp. (*Plecoptera, Perlidae*) and the stonefly seed bank theory. *Freshwater Biol.* 35:81–100