

REVIEW

Ecological and evolutionary significance of dispersal by freshwater invertebrates

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Abstract

Traditional expectations for how widely and how often freshwater invertebrates disperse differ from empirical data. Freshwater invertebrates have been characterized as frequent, widespread dispersers, particularly those that are transported passively. Our review finds that this characterization may describe the *potential* for dispersal in some taxa, but it is not an accurate generalization for *actual* dispersal rates. High variance among habitats and taxonomic groups is a consistent theme. Advances in population genetics may help resolve these issues, but underlying assumptions should be carefully tested. Further, even unbiased estimates of gene flow may not equate with individual movement, because not all dispersers survive and reproduce. Some freshwater invertebrates may exist in classic Levins metapopulations. However, other species fit into a broader metapopulation definition, where temporal dispersal via diapause is functionally equivalent to spatial dispersal. In the latter case, local extinctions and rescue effects may be rare or absent. Finally, limited dispersal rates in many taxa suggest that theories of freshwater community assembly and structure can be made more robust by integrating dispersal and local processes as joint, contingent regulators. Recent research on freshwater invertebrate dispersal has substantially advanced our basic and applied understanding of freshwaters, as well as evolutionary ecology in general.

Keywords

Aquatic insects, community ecology, connectivity, diapause, gene flow, invasion, local adaptation, metacommunity, metapopulation, zooplankton.

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INTRODUCTION

‘The animals of [a lake] are, as a whole, remarkably isolated – closely related among themselves in all their interests, but so far independent of the land about them that if every terrestrial animal were suddenly annihilated it would doubtless be long before the general multitude of the inhabitants of the lake would feel the effects of this event in any important way...It forms a little world within itself – a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp’. Stephen Forbes, *The Lake as a Microcosm* (1887)

Freshwater research has traditionally (and naturally) focused on processes occurring below the waterline. This perspective dates at least to Forbes’ (1887) conception of

lakes as microcosms that represent all ecological interactions and processes of interest. The assumption that aquatic ecosystems have discrete boundaries has served population and community ecology well: much has been learned about internal factors determining productivity, diversity, and community composition (Kerfoot & Sih 1987; Carpenter & Kitchell 1993). At the same time, the bounded-ecosystem perspective has aided our understanding of ecosystem-scale processes (e.g. Odum 1957; Likens & Bormann 1995).

Nonetheless, the development of freshwater biology into a comprehensive science has placed an increasing emphasis on processes at the ‘mesoscale’ (Holt 1993) between community ecology and biogeography. This perspective is central to studies of spatial and temporal interactions in communities and ecosystems, and a more refined understanding of influential biotic interfaces between terrestrial and aquatic systems. It is the dispersal of individuals in space that links aquatic habitats, and the dispersal of genes

through time that links ecology with evolution. Therefore, a quantification of dispersal across the full range of scales provides crucial ties between these often disparate fields (e.g. Ricklefs & Schluter 1993).

For a variety of reasons, freshwater invertebrates are well suited for quantitative studies of dispersal. Freshwater habitats have relatively discrete boundaries, suggesting that populations of freshwater invertebrates should also be discrete (even streams and rivers can be considered more bounded than many terrestrial and marine systems, because of their connectivity in one dimension rather than two). The relative ease with which entire communities of zooplankton and benthic invertebrates can be sampled has led to a wealth of distributional information. In addition, individuals are typically numerous enough that population-level parameters can be estimated without severely impacting the system. Finally, human modifications of the landscape have led to the creation, elimination and alteration of countless rivers, ponds, lakes and wetlands, often permitting colonization events to be observed directly. Objectively, it would seem that the ecological and evolutionary significance of dispersal in freshwater invertebrates should have been well understood long ago. However, the challenges associated with tracking tiny, short-lived individuals or their propagules have proved formidable. Freshwater biologists have mused about numerous vectors for transporting these animals, but have rarely pursued these topics experimentally. As a result, our understanding of dispersal has been mythical, based too

often on broad generalizations, anecdotal observations and faulty taxonomic assumptions.

Our goals are to consider how current studies of freshwater invertebrate dispersal are advancing modern aquatic ecology, and to promote future research on these topics. We use the term 'dispersal' in the broadest possible sense (Box 1), to include passive (e.g. wind, phoresis) and active (e.g. winged flight) mechanisms of transport, as well as post-transport indicators of arrival and success (colonization and invasion). Our review complements recent reviews by other authors, such as Bilton *et al.* (2001), who summarized approaches to studying dispersal and relevant adaptations, Okamura & Freeland (2002), who contrasted bryozoans with zooplankton, and Malmqvist (2002), who focused on riverine ecosystems. In contrast to the long dormant stage that has characterized dispersal biology, it is now inspiring to see a rapid accumulation of studies on dispersal at multiple levels of organization (e.g. population, metapopulation, community and 'metacommunity'). This research has begun to improve our understanding of dispersal beyond the traditional anecdotes and myths, and has been integral to the maturation of aquatic ecology as an experimental, theoretically grounded science.

Overland dispersal in most freshwater taxa is often presumed to be frequent and widespread. Our review of the literature suggests that generalizations are not valid: what is needed for a more accurate ecology is specific information for each taxon, and the temporal and spatial

Box 1 Operational definitions

Population: A group of conspecific individuals that interact and mate randomly with respect to space. Most often a single pond, lake or river reach is assumed to constitute a population. However, populations are (to some degree) a theoretical construct, because interactions within a single aquatic habitat can be spatially dependent for some species (e.g. littoral vs. limnetic zones), and because population boundaries are not always clear.

Dispersal: The movement of individuals across population boundaries. Because dispersal between established populations may differ mechanistically from the colonization of uninhabited areas, the term dispersal is sometimes restricted to exchange between established populations. Here, we consider colonization to be a subset of possible dispersal events.

Colonization: The establishment of a new population by one or more dispersers.

Invasion: Colonization that impacts other species already inhabiting an area. Invasion usually is restricted to long distance dispersal events that bring non-native species into a region or continent.

Metapopulation: Levins (1969) coined this term to describe a group of populations, each subject to stochastic extinctions, and linked by dispersal. The definition has since been broadened to accommodate any group of populations that interact via dispersal (Hanski 1999). We operationally define a metapopulation as a set of populations that (1) are spatially discrete, (2) may differ in size, demography and carrying capacity, (3) may be subject to extinction and recolonization, and (4) interact via dispersal and gene flow.

Community: Populations of different species that inhabit the same habitat, often defined taxonomically (e.g. the bryozoan community) or trophically (e.g. the phytoplankton community).

Metacommunity: A community consisting of many discrete patches (Wilson 1992). The metacommunity concept acknowledges that traditional population and community concepts may be spatially and ecologically simplistic.

Gene flow: The exchange of genes between populations, or 'gene pools'. Because not all dispersers produce offspring at their destination, gene flow rates are always less than or equal to dispersal rates.

Local adaptation: The ability of individuals within a population to survive and reproduce better than immigrants from other populations. Natural selection can lead to local adaptation if selection pressures differ among populations. If local adaptation exists, immigrants can affect some, but not all ecological and evolutionary processes.

scales relevant to the process of interest (e.g. local adaptation, metapopulation dynamics, or community assembly). Admittedly, quantifying 'frequent' and 'widespread' is a difficult task, because any value will be context-dependent and perhaps arbitrary. For example, an annual immigration rate of 1–2 fairy shrimp per pond (Bohonak & Whiteman 1999) would facilitate metapopulation persistence and homogenize populations genetically, but is probably too low to be considered 'frequent' for questions regarding population density, even if the ponds are only separated by 10–100 m. In another context, that same immigration rate would constitute only 0.0001–0.0002% of a population of copepods or rotifers with 10^6 individuals. In a footnote to their seminal paper, Brooks & Dodson (1965) provide one quantitative characterization of the myth that we wish to dispel:

'The ease with which zooplankters are passively dispersed makes it probable that most species present in any continental area will be introduced into a given lake within a reasonably short time (10 to 25 years)'. John L. Brooks and Stanley I. Dodson, *Predation, Body Size, and Composition of the Plankton* (1965)

We begin with a brief review of passive dispersal in freshwater invertebrates (e.g. zooplankton), and active dispersal in insects with winged terrestrial stages. We use the major conclusions from this review to address progress that has been made in three broad areas of evolutionary ecology: Are dispersal and gene flow equivalent? Do freshwater invertebrates exist in metapopulations? Do regional processes influence freshwater invertebrate community ecology? We conclude that advances in these areas have largely occurred in the absence of actual estimates of dispersal. However, recent studies have begun to reverse this trend, and a renewed emphasis on the importance of individual movement is now discernable.

DO FRESHWATER INVERTEBRATES DISPERSE FREQUENTLY AND WIDELY?

'I suspended a ... duck's feet in an aquarium, where many ova of freshwater shells were hatching; and I found that numbers of extremely minute and just hatched shells crawled on the feet, and clung to them so firmly that when taken out of the water they could not be jarred off, although at a somewhat more advanced age they would voluntarily drop off. These just hatched mollusks, although aquatic in their nature, survived on the duck's feet, in damp air, from twelve to twenty hours; and in this length of time a duck or heron might fly at least six or seven hundred miles, and would be sure to alight on a pool or rivulet, if blown across the sea to an oceanic island or to any other distant point'. Charles Darwin, *On the Origin of Species* (1859)

Passively-dispersed taxa

Despite its noble pedigree, our knowledge base regarding passive dispersal in freshwater invertebrates has progressed little since Darwin's time. One might argue further that the development of ecological theory at the mesoscale has been hampered by myths surrounding the dispersal of freshwater organisms, such as an ever-present role for 'duck's feet' and 'rains of fish from the sky' (Darwin 1859; Bajkov 1949). Until 10–15 years ago, nearly all references for avian- and wind-aided transport of freshwater organisms or their propagules consisted of largely anecdotal reports (see Talling 1951; Bilton *et al.* 2001 and references therein). Apart from a handful of studies on potential dispersal via birds (see Figuerola & Green 2002) and Maguire's (1963) seminal colonization experiments, progress in the field has been incremental at best.

At first glance, Forbes' view that lakes are isolated microcosms seems at odds with Darwin's emphasis on widespread dispersal. However, Forbes (1887) discussed a terrestrial-aquatic isolation (not aquatic-to-aquatic), and he emphasized the strong interactions within the lake; an emphasis consistent with a community considered to be already saturated with potential members from the regional aquatic species pool. Therefore, Forbes (1887) does not appear to have considered lakes as being dispersal-limited, in that 'all the elemental forces are at work and the play of life goes on in full' below the waterline. In the years since Darwin and Forbes, aquatic ecology has focused almost entirely on the water-column and benthos, with the implicit presumption that biotic linkages among fresh waters are unimportant or even ubiquitous. For example, Brooks & Dodson (1965) supposed that because *Daphnia cucullata* 'can be passively disseminated, clones of large, intermediate and small forms of *D. cucullata* have almost certainly been introduced many times into each of the lakes in which *D. galeata* lives'. Some of this perception is undoubtedly a matter of scale: colonization of empty 'pools and rivulets' in evolutionary time requires rates of movement that are several orders of magnitude lower than what most ecologists would consider significant over one or a few years. Although individuals of various species certainly disperse on long time scales, we interpret the currently available evidence as *rejecting* the notion that overland dispersal in most freshwater taxa is frequent and widespread on relatively short time scales. That assumption is based in part on species distributions that have been incorrectly perceived as cosmopolitan, and the presumption that dormant stages (e.g. cysts, eggs, ephippia) are all easily transported and incredibly durable.

Cosmopolitanism (i.e. possessing a continental or global distribution) has long been assumed for a diverse set of freshwater invertebrates, most of which have small

propagules (e.g. Darwin 1859). For example, species of cladocerans, copepods, and rotifers have been considered cosmopolitan (Pennak 1989). In some cases, cosmopolitan distributions have been ascribed to entire zooplankton taxa when evidence for one or a few species is known. For protists, Finlay *et al.* (2002) went so far as to suggest that 'dispersal is rarely (if ever) restricted by geographical barriers', and that propagules up to 1 mm should disperse globally. However, the traditional taxonomy upon which these conclusions are based is wrong in many cases; taxonomic revisions have revealed numerous cryptic species with distributions more restricted than previously believed (e.g. Frey 1982; Hebert & Wilson 1994; Schwenk *et al.* 2000). In addition, sampling biases and inadequate sampling efforts have impacted perceived species richness and biogeographical distribution patterns (Dumont & Segers 1996). The general conclusion is that distributions of many zooplankton species are regional, rather than continental or global, and often the result of recent glaciation (Dumont 1983; Weider 1989; Stemberger 1995). As a result, Dodson & Frey (1991) leveled the criticism that 'cosmopolitanism reflects an unquestioning acceptance of rapid passive dispersal of these organisms via their resting eggs by wind, water, birds, insects, and mammals...' Unquestioning acceptance is a readily recognizable trademark of myths.

Many freshwater invertebrates create diapausing eggs or cysts that lie dormant in sediments for months or years at a time, until the proper hatching cue is received. These dormant life stages have been thought to disperse freely as wind-blown dust or phoretically with a variety of vertebrate and invertebrate animals (e.g. Pennak 1989; Lampert & Sommer 1997). However, this belief is based primarily on anecdotal evidence or laboratory-based experiments in which propagules were fed to waterfowl (e.g. Proctor 1964; Proctor *et al.* 1967). These studies have demonstrated the *potential* for passive dispersal to be frequent and ecologically relevant, but substantial experimental and distributional data indicate that this potential is not realized as often as one might suppose. For example, despite the fact that the bryozoan *C. mucedo* produces dormant statoblasts with apparent adaptations for dispersal, genetic data suggest that gene flow is less than one individual immigrating per population per generation. In Europe, dispersal of this species is not high enough to prevent local populations from going extinct or experiencing bottlenecks during colonization (reviewed by Okamura & Freeland 2002).

Evidence that passive dispersal is limited comes from a variety of sources, including field experiments, ecological studies of invasive and endangered species, and patterns of genetic variation. Experimental colonization studies have consistently shown that on ecologically relevant time scales, many freshwater zooplankton taxa have low dispersal rates

(e.g. Jenkins 1995). During a colonization study of 12 identical experimental ponds, Jenkins & Buikema (1998) found that only 14 of 61 species colonized all the ponds over the course of 1 year. More than 50% of those that colonized were found in fewer than half of the ponds, and only eight species colonized in the first 3 months. Among-replicate variation in Cáceres & Soluk's (2002) colonization experiments led them to conclude that dispersal was not widespread, and that traits such as dormant eggs or parthenogenesis correlate poorly with colonization success. Very few propagules have been intercepted in experiments specifically focused on transport in wind and/or rain (Jenkins & Underwood 1998; Brendonck & Riddoch 1999). Like Bilton *et al.* (2001) and Cáceres & Soluk (2002), we doubt that dispersal in these media is widespread or frequent; a far greater role may be ascribed to phoretic transport in natural populations. Although difficult to study experimentally, a handful of studies to date support this conclusion (e.g. Bohonak & Whiteman 1999). Similarly, several recent reviews recognize the potential for dispersal of freshwater invertebrates by waterfowl (e.g. Figuerola & Green 2002), although they call for more studies to explicitly address the *realization* of that potential. If waterfowl are the primary vectors of passively dispersed freshwater invertebrates (other than unionid mussels), then even more emphasis should be placed on waterfowl conservation with regards to the preservation of wetland biodiversity. More replicated and long-term studies are needed to resolve the relative roles that wind, rain and vertebrate vectors play.

Dispersal rates have been estimated in some invasive species, because of their potential economic and ecological impacts. For example, potential rates of spread have been estimated for a number of species based on experimental ecology and historical reconstructions (e.g. Allen & Ramcharan 2001; Havel *et al.* 2002). In most of these species, it is obvious that recreational boating and intercontinental commerce disperse more individuals than 'natural' passive processes (e.g. Johnson *et al.* 2001; Havel *et al.* 2002). These generalizations are supported by Hebert & Cristescu's (2002) estimation that invasions may now be occurring at rates 50 000 times greater than have occurred in the past. If true, the continued escalation of international trade and human-aided transport is more likely to become an increasingly important determinant of biogeographical patterns for many aquatic organisms, as well as ecosystem integrity. It is obvious that successful management and eradication of exotics such as the zebra mussel *Dreissena polymorpha* requires a precise understanding of current dispersal rates and agents. However, the full significance of increased dispersal in an invasive species can only be appreciated with a greater understanding of how historical rates of dispersal have shaped its ecology and life history in its native range.

However, relatively few species are invasive, and for each invasive species, many more are threatened or endangered. The limited distribution characteristic of endangered or threatened species is usually exacerbated by their limited means for extending that distribution (e.g. four fairy shrimp listed in California). Low rates of dispersal, together with habitat destruction and the loss of necessary prey or host species (such as fishes for bivalve glochidia) can limit the ability of such species to persist. Habitat destruction can further reduce effective dispersal rates as stepping-stones for dispersal between distant populations are eliminated (Jenkins *et al.* 2003). Clearly, movement among habitats is neither widespread nor frequent in most species of concern for conservation.

The categorical assertion that most dormant propagules remain viable after dispersal and for long periods of time seems premature. Admittedly, egg banks play an important role in determining annual population dynamics in the water column of lakes (Cáceres & Hairston 1998; Cáceres 1998), and some extreme cases of propagule longevity exist. The most well-known example is Hairston *et al.*'s (1995) recovery of viable, 300 year old copepod eggs from anoxic pond sediments (although mortality rates suggest that less than half survive longer than 65 years). However, these studies have been concentrated in temperate, glaciated regions. The age distribution of diapausing eggs in temporary ponds and wetlands that lack cool, anaerobic sediments to facilitate long-term storage is unknown. It is possible that the dry phase of temporary wetlands increases diapausing egg mortality when compared with lakes. However, sediment disturbance and mixing is also higher in temporary wetlands than lakes, which increases the number of eggs with access to hatching cues. Age structure in the egg bank will reflect these processes, and the average egg age will be less in a temporary pond than in a lake with stratified sediments. Because the relative importance of these and other factors is unknown, we believe that studies of egg banks in permanent lakes with layered, anaerobic sediments should not be extrapolated to all taxa and all habitats. The viability of diverse dormant life stages should be investigated under a variety of natural conditions.

Finally, studies employing molecular techniques often find that local populations of freshwater invertebrates are genetically divergent. This implies that (1) rates of movement are actually low, even on small spatial scales, or (2) the dispersal of genes (gene flow) is not strong enough to counteract other contemporary or historical evolutionary factors. While the relative roles of these factors are debatable (Boileau *et al.* 1992; Bohonak & Roderick 2001; De Meester *et al.* 2002), it is clear that genetic patterns characterized as 'microgeographical heterogeneity', 'persistent founder effects', 'regional fragmentation', 'endemism' and 'deep phylogeographical structuring' are the norm in

freshwater invertebrates (Weider & Hebert 1987; Boileau *et al.* 1992; Hebert & Wilson 1994; Gómez *et al.* 2000). We should not assume that taxa with diapausing eggs are genetically homogeneous among populations; they rarely are. In addition to the possibilities that dispersal is low or that gene flow estimates are biased, local adaptation may play a supplementary role in preventing immigrating propagules from hatching, surviving and then integrating genetically into the new population (see below).

In summary, the *potential* for frequent and widespread dispersal of passively dispersed invertebrates should be considered distinct from the actual estimation of dispersal rates. Studies from many subdisciplines of freshwater biology have revealed more geographically complex patterns than one would expect based on frequent continental, regional or even local dispersal. Further experimental studies of passive dispersal are needed across a range of habitats and taxa.

Actively dispersed taxa

Active overland dispersal by freshwater invertebrates is most obvious and best documented in the winged insects, although crayfish have also been observed dispersing terrestrially (Cooper & Braswell 1995). (Categorization of dispersal in water mites as active or passive is somewhat arbitrary, because larvae parasitize insect adults, dispersing only if their host does). However, the dispersal of aquatic insect adults has been enigmatic and difficult to quantify. Few mark and recapture studies have been conducted on a large enough scale to accurately quantify dispersal in most aquatic insect taxa. Studies of Culicidae provide a notable exception, in part because of their applied relevance. For mosquitoes, available data suggest that adult dispersal in most species may be limited to < 5 km, and < 1 km in some cases (see Service 1997).

Even dragonflies and damselflies (Odonata) resist generalization, despite the fact that they are easier than most taxa to mark, release and recapture. Although large-scale migrations are known in some odonate adults (Williams 1958), high territoriality and very low dispersal has been found in others (e.g. McPeck 1989). Interpretation of mark and recapture studies in most odonates is difficult because males may forage away from their territory, and both sexes disperse during the teneral (initial terrestrial) phase prior to territory acquisition (Corbet 1980). Thus, behavioural studies focused on territoriality may miss important dispersal events. Recent studies have noted low genetic population differentiation in odonates that are known to disperse poorly as adults (e.g. Geenen *et al.* 2000), lending support to the hypothesis that dispersal may be widespread, but concentrated in the teneral stage. However, very few ecological or behavioural studies have been conducted on this portion of the life cycle.

Enough studies of dispersal in stream-dwelling insect taxa have been conducted to warrant general consideration. Many of these have focused on the hypothesis that downstream larval drift needs to be balanced by significant upstream dispersal in the adult stage (Müller 1954). This 'colonization cycle hypothesis' has been tested using direct and indirect estimates of movement with varying conclusions (Allan 1995). Some authors have concluded that small-scale movement of juveniles or adults is sufficient to resolve the 'drift paradox', and that large scale dispersal in adults may not be necessary (e.g. Humphries & Ruxton 2002). Further, direct studies have found surprisingly limited dispersal rates in some species (Collier & Smith 1997; Griffith *et al.* 1998). Indirect (genetic) methods of estimating movement have shown a wide variety of patterns, including evidence for limited adult movement, the lingering effects of postglacial recolonization, and in general, high variation among taxa (Wilcock *et al.* 2001; Monaghan *et al.* 2002; Schultheis *et al.* 2002). The numerous genetic studies by Hughes and colleagues on stream-dwelling insects in Australia illustrate particularly well that even qualitative conclusions about aquatic insect dispersal vary widely among species (e.g. Hughes *et al.* 1999; Wishart & Hughes 2003).

On balance, the only clear generalizations for actively-dispersed taxa are that (1) there is high variance among species in the direction and magnitude of dispersal as adults, (2) local landscape features and environmental gradients play a central role in dispersal behaviour, and (3) although not reviewed here, taxonomic concerns over presumed cosmopolitanism should be exercised in aquatic insects as well as zooplankton (e.g. Jackson & Resh 1998). Over-simplifications regarding widespread, frequent dispersal by winged adults should be supplanted by conclusions specific to each taxon, and the varied environmental conditions surrounding its habitat.

Based on our brief review, our answer to the question 'Do freshwater invertebrates disperse frequently and widely?' is that many taxa do not demonstrably do so. We must also conclude that little progress has been made toward a comprehensive answer to this question, partly because the answer has long been presumed to be affirmative. We expect that this question will be explicitly addressed more frequently in the future with experimental studies and molecular techniques, and that the results of these studies will be important to the ecology and management of freshwater ecosystems.

ARE DISPERSAL AND GENE FLOW EQUIVALENT?

For practical purposes, gene frequency distributions reflect a dynamic interaction of founder number with dispersal rate, population sizes and age. Information on all of these parameters is necessary in order to understand

the genetic structure of populations ...[B]ecause of the substantial half-life periods required to decay differences [the] age must not be ignored when interpreting data from North American taxa because glaciers only recently receded permitting organisms to expand their ranges'. Marc G. Boileau, *Non-Equilibrium Frequency Divergence: Persistent Founder Effects in Natural Populations* (1992)

Molecular markers have played a central role in our current understanding of dispersal, and will increase in importance because of technological advances. Genetic similarities among populations provide a 'long-term' average of gene flow that is less limited in space or time than a traditional mark and recapture study. Thus, rare dispersal events that would be missed in an ecological study are implicitly averaged into gene flow estimates. Genetic assays can also be applied to nearly all life history stages, including dormant eggs or embryos (e.g. Gómez *et al.* 2000).

The central tenet of population genetics is that patterns of genetic variation are the result of five main processes: non-random mating, natural selection, mutation, random drift (a function of effective population size) and gene flow (often called 'migration' by geneticists). In both theoretical and empirical studies, the role of one or several of these processes are inferred by making simplifying assumptions about the others. For example, temporal changes in gene frequencies can be used to estimate effective population size under the assumption that the other four processes are unimportant (e.g. Lehmann *et al.* 1998). Similarly, if one assumes that natural selection and mutation are unimportant, the genetic distance among populations should reach an equilibrium state where divergence (promoted by drift) is balanced by gene flow (which maintains some degree of cohesion). Analytic models that make these assumptions can be used to estimate gene flow in natural populations.

It is generally appreciated that caution should accompany the use of gene flow estimates for making inferences about dispersal (Whitlock & McCauley 1999; Bohonak & Roderick 2001). These concerns can be divided conceptually into two categories: (1) Gene flow estimates are either implicitly or explicitly derived from models with underlying assumptions that may not be met. (2) Even if gene flow estimates are accurate, the movement of individuals is not always equivalent to the movement of genes.

With regards to the first concern, Bohonak & Roderick (2001) discussed various approaches for critically assessing the models that underlie traditional gene flow estimates in freshwater invertebrates (see also Boileau *et al.* 1992). No one has yet conducted a single, comparative review of the assumptions that underlie a growing list of newer analytic approaches (e.g. coalescent-based techniques, nested clade analysis). However, many of the principles reviewed by Bohonak & Roderick (2001) are widely applicable. For

example, any gene flow estimate that is based on allele frequencies or coalescence times assumes that populations are in a long-term equilibrium between drift and gene flow. Violation of any scientific model's underlying assumptions can lead to faulty inferences. Gene flow estimates are of special concern because in many cases the magnitude and direction of potential biases are unknown. Some of these biases will diminish as newer laboratory and analytic methods are developed. However, ecological studies of individual movement will always provide an important benchmark for comparison with gene flow estimates.

Does local adaptation uncouple dispersal from gene flow?

A related topic is whether gene flow is *mechanistically* uncoupled from dispersal, regardless of estimation error or bias. Is the transfer of genes among breeding pools equivalent to the movement of individuals? An obvious discrepancy occurs when immigrants to a population do not successfully mate. For processes such as competition and predation, it may be important to estimate the total number of immigrants into a population, including those that fail to eventually reproduce.

Some studies have directly estimated the survival or mating success of freshwater invertebrates in immigrants vs. residents under field conditions. For example, Shurin (2000) conducted experimental invasions in field enclosures, and found that most inoculated species did not succeed, apparently because of the effects of residents. Studies of local adaptation in *Daphnia* often suggest that immigrants may experience a reduction in survivorship and reproduction (e.g. Cousyn *et al.* 2001). Weider & Hebert (1987) found that clonal lines of *D. pulex* were adapted to the water chemistry of their pond of origin. Even within the same pond, Lynch (1987) documented temporal fluctuations in allozyme frequencies that seemed to reflect fluctuating selection on the underlying clones. De Meester (1996) and

De Meester *et al.* (2002) emphasized that local adaptation can occur rapidly in zooplankton, and may be widespread.

It should be possible to experimentally quantify each of the factors collectively called 'local adaptation' in freshwater invertebrates, although to our knowledge this has not been carried out under natural conditions. We outline an example in Fig. 1, with the passive dispersal of diapausing crustacean eggs into a temporary pond. Depending on the degree of local adaptation, a diapausing egg may experience lower hatching success than residents (because hatching cues in the pond of origin differ), lowered survivorship as a juvenile (because of nutritional requirements or predation regime) and lowered fecundity (considered here to be production of resting eggs before the pond dries). Gene flow has only occurred after all phases of the life cycle are complete. DeClerck *et al.* (2001) conducted a reciprocal transplant experiment in the laboratory with *D. galeata* from two permanent ponds that had been connected by an open ditch only a year earlier. All individuals in four clonal lines from one of the ponds survived for 15 days when cultured in water from the same pond. However, when raised in water from the neighbouring pond, survivorship dropped to 0–75% (depending on the clone). Clearly dispersal and gene flow will be uncoupled in these ponds despite their close proximity.

Similarly, Hairston & Walton (1986) documented strong, natural selection on the timing of diapause induction in the copepod *Diaptomus sanguineus*. In a pond with predatory fish, copepods switch from making immediately hatching eggs to diapausing eggs annually on 24 March. In a nearby pond without fish, diapause induction begins 1 month later. Dispersal probably occurs, as the ponds are only 200 m apart. But dispersers are likely to have reduced fitness, as they are producing diapausing eggs at a suboptimal time of the year for the pond in which they arrive (for example, if an immigrating copepod is genetically programmed to produce diapausing eggs in late April, that individual and its offspring

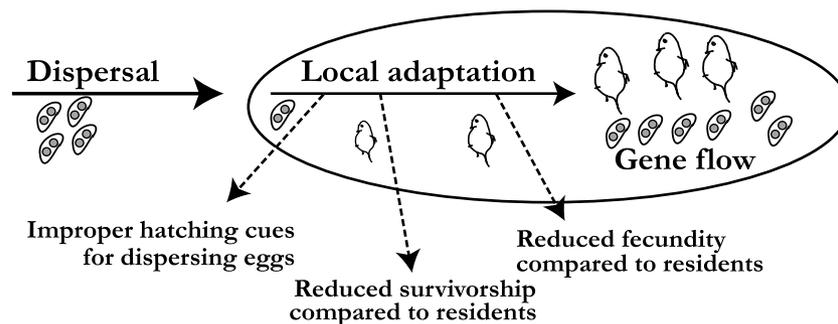


Figure 1 Role of local adaptation in uncoupling dispersal (the movement of propagules among populations) from gene flow (transfer between gene pools). Local adaptation collectively describes processes that can lead to lowered survivorship or reproduction in immigrants vs. residents. Natural selection can lead to differences among ponds in hatching cues, growth rates, adaptations to predation and timing of reproduction.

are unlikely to persist more than 1 year in the pond with fish). Thus, gene flow and the dispersal of individuals will also be uncoupled in this system.

A dispersal – gene flow paradox?

De Meester *et al.* (2002) identified a dispersal – gene flow paradox for freshwater invertebrates: despite evidence for a ‘high dispersal capacity’, restricted gene flow is observed among multiple taxa. They proposed a ‘Monopolization Hypothesis’ to explain this paradox, in which early colonists develop such large populations that genetic contributions from later colonists are mathematically minor. Boileau *et al.* (1992) asserted that genetic ‘founder effects’ are mathematically reasonable in light of likely colonization scenarios, population carrying capacities and rates of dispersal. De Meester *et al.* (2002) updated this hypothesis to emphasize the role of local adaptation, highlight recent studies in zooplankton evolutionary ecology, and discuss how essential features of this process depend on life history. For example, bryozoans have only limited sexual reproduction, and European populations seem to exist in metapopulations dominated by extinction/recolonization dynamics (Okamura & Freeland 2002). This suggests less potential for local adaptation than more permanent populations of cyclical parthenogens that undergo sexual reproduction annually (De Meester *et al.* 2002).

De Meester *et al.* (2002) cite evidence for high dispersal and low gene flow largely from the same types of studies that we review here, yet our interpretation is quite different for several reasons. First, as discussed above, we interpret the literature as failing to support the hypothesis that freshwater invertebrates disperse frequently and widely. The possession of diapausing eggs does not necessarily indicate high rates of movement among ponds or lakes, and not all species rapidly colonize new habitats when they become available. More broadly, high dispersal *capacity* does not translate cleanly into high dispersal rates for the reasons discussed above.

Second, there is an important distinction between low *estimates* of gene flow that are frequently found in zooplankton, and low gene flow itself. If founder effects (a central part of the Monopolization Hypothesis) are taxonomically widespread and persist for long periods of time, then gene flow estimates will be inaccurate. There is no way to know the actual amount of gene flow that is occurring without a detailed model that makes assumptions about the demography of colonization events, how long ago they occurred, and the size of each population (Bohonak & Roderick 2001). We suspect that future studies of dispersal and gene flow will support some form of the Monopolization Hypothesis in some species, but we are pessimistic that the majority of freshwater invertebrates possess the unique

combination of dispersal rate, population size, life history and mode of colonization that it requires (see De Meester *et al.* 2002 for a more detailed comparison of different freshwater taxa).

In summary, dispersal and gene flow *may* be equivalent, but a definitive answer to the question asked at the start of this section requires a continuing evaluation of analytic methods, and a mechanistic understanding of dispersal and local adaptation. The ultimate goal is to determine how widely (in terms of taxonomy and habitat) we can apply generalizations regarding dispersal and gene flow, based on this synergism between organismal and molecular ecology.

DO FRESHWATER INVERTEBRATES EXIST IN METAPOPOPULATIONS?

‘It is the heterogeneity of nature, of the areas that populations may inhabit, of the places where animals may live and the consequent colonial or “spotty” distribution of the populations of the animals themselves that makes dispersal so important. Heterogeneity in space may, on occasion, be studied and explained in terms of geology, pedology, topography, climatology, or mathematical probability; for example, in a tropical forest with its enormous diversity of species, chance must play a large part in determining the pattern of distribution of the plants and hence of the food and places where animals may live. Heterogeneity in time may be related to weather, the ordinary processes of growth, senescence, and decay, and ecological succession. Temporal changes bring spatial changes in their wake, and the species which is not adapted to provide for the future may be expected not to persist’. Herbert George Andrewartha and L. Charles Birch, *The Distribution and Abundance of Animals* (1954)

The recognition that most habitats are not stable over evolutionary or ecological time scales has prompted theoretical considerations of how species persist despite this variability. Cases of complete recruitment failure in freshwater invertebrates provide the most striking examples: for example, how can fairy shrimp persist in a pond with repeated reproductive failures when the pond dries prematurely (Simovich & Hathaway 1997)? Numerous authors have pointed out that the long-term persistence of species in variable environments can be accomplished in three ways. First, a species can possess or evolve the physiological and ecological tolerance necessary for survival and reproduction across a broad set of environmental conditions. Examples of generalist species that are phenotypically ‘plastic’ can be found in both aquatic and terrestrial communities (e.g. Cousyn *et al.* 2001). However, physical, developmental and genetic constraints place limits on the ability of a single phenotype to survive and reproduce everywhere. As a result,

the adaptive utility of phenotypic plasticity is limited to particular environmental attributes and particular species.

Second, a species can rapidly adapt to environmental change as it occurs. Population genetic theory suggests a number of characteristics necessary for the success of this strategy. Most notably, characteristics that maintain ample genetic variation should be present, because the rate of adaptive change is proportional to the amount of genetic variation (Fisher 1958). These characteristics would include a short generation time, high intrinsic rate of growth (r) and large effective population size (N_e). Although adaptation can require a relatively slow rate of environmental change (compared with generation time), several examples exist of adaptation in freshwater zooplankton on the order of generations (Hairston & Walton 1986; Hairston *et al.* 1999; Cousyn *et al.* 2001).

Third, organisms can succeed in unstable environments by dispersing to favourable habitats randomly, or in a directed fashion. As has been long recognized, dispersal may be either 'temporal' or spatial; therefore, diapause and migration can be thought of as alternative strategies for spreading risk through time and space. (As an alternative to diapause, a long-lived adult stage can also spread reproductive risk across multiple generations: Hairston & Cáceres 1996; Tuljapurkar & Wiener 2000. However, this strategy is uncommon in freshwater invertebrates). Both empirical data and theoretical models have shown that the temporal and spatial variability typical of many freshwater habitats selects for dispersal and/or diapause (e.g. McPeck & Holt 1992; Philippi *et al.* 2001). The evolutionary and ecological advantages of spatial dispersal motivate traditional metapopulation theory, as well as related phenomena such as source-sink dynamics and the 'rescue effect' (Pulliam 1988). These concepts focus on the effects of immigration on extinction probability and population size. Researchers are now expanding these approaches to determine how dispersal and diapause might jointly affect stability in the same community or even the same species (e.g. Brendonck & Riddoch 1999).

Metapopulation theory provides the most common theoretical construct for considering the long-term impacts of dispersal. In its original formulation, a metapopulation contains a group of demographically identical patches, each of which is subject to stochastic extinctions (Levins 1969). The concept was gradually broadened to represent any set of local populations linked by dispersal (Hanski 1999; see Box 1). Metapopulation theory can make novel contributions to population biology if the dynamics of individual populations (including likelihood of long-term persistence and population size) depend at least partially on interactions among populations, and cannot be predicted from single-population parameters alone. Many freshwater invertebrates satisfy these criteria: populations vary in time and space in

terms of size or recruitment to a diapausing egg bank, and may be subject to local extinctions (e.g. Cáceres 1997; Berendonk & Bonsall 2002). Metacommunity concepts that extend and build upon metapopulation foundations may also apply to many freshwater habitats (Wilson 1992). If dispersal in space or recruitment from a long-lived egg bank appreciably influences community dynamics (Cáceres & Hairston 1998), freshwater invertebrates can be considered metapopulations and metacommunities under the broadest definition. Hence, the broad appreciation for heterogeneity in space and time that is central to metapopulation ecology helps unite population, community and landscape ecology in a single theoretical framework (e.g. Freeland *et al.* 2000; Shurin & Allen 2001).

Beyond simply determining *if* freshwater invertebrate populations exist in a metapopulation or metacommunity, dispersal studies play a critical role in *quantifying* how immigrants impact population and community processes. Dispersal can prevent extinction, maintain species diversity and contribute novel genetic variation. For example, Cáceres (1997) showed that over a 30-year period, *Daphnia* species diversity in a large lake was maintained only because of a reservoir of diapausing eggs. Freeland *et al.* (2001) hypothesized that increases in bryozoan clonal diversity over time were because of contributions from the statoblast bank. Berendonk & Bonsall (2002) quantified extinction risk and dispersal ability in multiple populations of two *Chaoborus* species, showing how divergent metapopulation processes determine the distribution of each. Similarly, the many studies of Hanski and colleagues (e.g. Hanski & Ranta 1983) have shown how metapopulation theory can successfully explain local and regional co-existence of species in terms of extinction, colonization and competition. Multispecies studies are particularly exciting because they typically address dispersal at different scales (e.g. population, community, region), and provide a spatial and temporal perspective on species coexistence. As freshwater invertebrate ecology contributes to these rapidly developing fields, more metapopulation and metacommunity studies will need to be conducted, and accurate estimates of movement incorporated in the models.

If spatial dispersal is frequent, widespread, and relevant to metapopulation ecology of freshwater invertebrates, then rescue effects for struggling populations should be easily demonstrated. Consistent source-sink dynamics should also be established among habitats. However, if spatial dispersal in most species is limited, these concepts may not widely apply. Because our central premise is that dispersal in most freshwater invertebrates is not widespread or frequent, we propose the following hypotheses: (1) Local metapopulations of aquatic insects with terrestrial adults are often maintained by dispersal (e.g. Berendonk & Bonsall 2002), but the scale of local metapopulation structure is taxon- and

habitat-dependent. (2) Passive, overland dispersal of other taxa (including zooplankton) becomes relevant over time scales longer than those of population dynamics. Thus, spatial metapopulation dynamics will be difficult to observe. It follows logically that metapopulations of these species will be maintained by diapause (the 'temporal rescue effect') much more often than spatial dispersal (e.g. Cáceres 1997; Freeland *et al.* 2001). (3) In some systems, passive, hydrologically-driven dispersal can lead to observable spatial metapopulation dynamics (Havel *et al.* 2000; Michels *et al.* 2001). The roles played by spatial dispersal in balancing extinction on longer evolutionary time scales are largely unknown, beyond the trivial observation that all occupied habitats have been colonized at least once from an outside source.

The metapopulation ecology of freshwater invertebrates is also shaped by the hierarchical structure that is characteristic of many aquatic habitats. Lotic systems are arranged as reaches nested within streams, streams nested within catchments, and catchments within watersheds. Lentic systems (e.g. ponds and lakes) may also be spatially distributed in a hierarchical, disjunct manner. For example, wetlands are often clustered where geologic or land-use conditions are favourable, with large distances separating those clusters. The recognition of these hierarchies is a standard part of most population genetic studies but its significance for freshwater metapopulation ecology has not been determined. We think that the formal incorporation of these discontinuities in metapopulation models will profoundly affect our understanding of population connectivity for two reasons. First, the size and arrangement of populations can dramatically impact landscape-level processes and the likelihood of species persistence (Hanski 1999). Groups of populations that interact according to a hierarchical scheme will possess different dynamics than those with simpler rules for dispersal. Second, the degree of spatial autocorrelation in habitat quality is also an important determinant of metapopulation dynamics. In freshwater habitats, environmental fluctuations are more likely to be highly correlated on small spatial scales (because of hydrological linkages and local climatic effects), and decrease as analyses are scaled up to the entire landscape. The efforts of Michels *et al.* (2001) to assess potential complexities in habitat linkages using genetic data can serve as a model for initial efforts in metapopulation and metacommunity ecology.

In summary, freshwater invertebrates seem to be strong candidates for metapopulations and metacommunities. However, 'metapopulation' is broadly defined, and certain metapopulation concepts are only applicable in specific taxa. We suggest that freshwater invertebrate ecologists be explicit in the metapopulation concept that they are using, its assumptions, and how it directly relates to the ecology of

the organisms under study. With this attention to detail, freshwater invertebrates offer a valuable system to test these important concepts in evolutionary ecology.

HOW IMPORTANT ARE REGIONAL PROCESSES FOR FRESHWATER INVERTEBRATE COMMUNITY ECOLOGY?

'A deep understanding of the local consequences of regional processes will require a melding of experimental, theoretical, and comparative techniques. I believe that an important item on the agenda for community ecology will be to grapple with the messy reality that local communities contain species that experience the world at vastly different spatial scales. The structure of a community will surely reflect the interplay of disparate regional processes'. Robert D. Holt, *Ecology at the Mesoscale: The Influence of Regional Processes on Local Communities* (1993)

Community ecology has traditionally focused on local processes (e.g. predation, competition, abiotic tolerance limits) as primary regulators of community structure. For example, Jenkins & Buikema (1998) presented the apparent working hypothesis in zooplankton ecology as follows: communities are assembled quickly (given rapid dispersal), and thereafter local processes are most important as regulators of community structure and function. They made the analogy of a quorum at a meeting: if a quorum is promptly reached, decisions are made locally, without constraint by the arrival process. In Fig. 2, we divide the factors that influence community structure and function into three categories: local processes, regional processes, and processes that involve particular local and regional effects in a specific combination. Prompt quorum assembly is equated with the assumption that the regional logic path in Fig. 2 is less important than the local logic path. However, if dispersal is slow (and a quorum is delayed), then the ascendancy of local processes as primary regulators of community structure and function is delayed, because the arrival sequence and rates can strongly influence the resulting community (Robinson & Dickerson 1987).

A major question in community assembly is then 'How long does it take a community to assemble?' The answer obviously depends on dispersal rates. To address the uncertainty of local vs. regional regulators of community structure and function, experiments like those of Shurin (2000) are required in systems that range in age and isolation. Shurin found communities regulated by local interactions, rather than the regional process of dispersal. Similar experimental approaches across other regions and types of freshwater habitats may lead to generalizations regarding local and regional regulation of communities, and steer further studies in complementary directions (Fig. 2). For

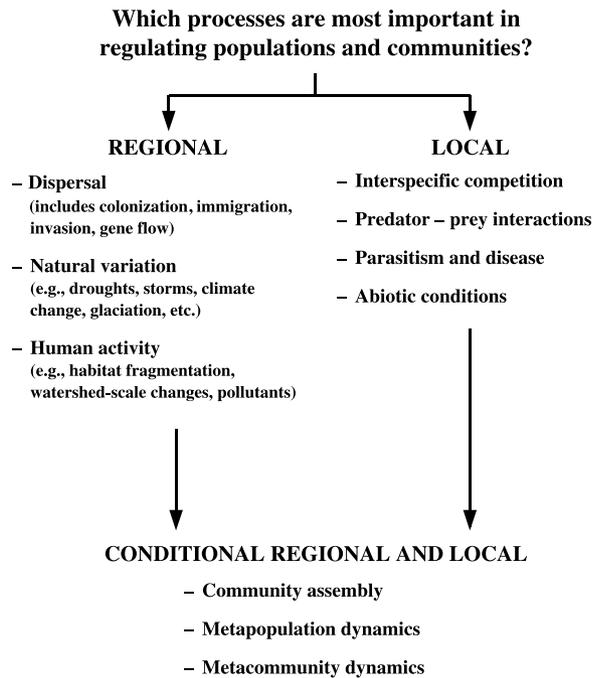


Figure 2 Conceptual framework for studies of community assembly and regulation. Processes can be divided into those that are strictly regional, those that are strictly local, and those which involve conditional combinations of regional and local factors.

example, if a community is readily invaded by new species (i.e. the community is unsaturated), then studies of competition or predation as major regulatory processes may be irrelevant. On the other hand, invasion resistance suggests that studies of local processes are warranted. Continued studies on the conditions and interactions of local vs. regional regulatory processes could then be more clearly interpreted than if we continue to proceed otherwise.

Platt (1964) argued that progress is most rapid in fields that most actively employ ‘strong inference’. In this framework, alternative hypotheses are tested in a logical progression. If the potential roles of dispersal are considered within a strong-inference framework (Fig. 2), freshwater invertebrate ecology might be accused of putting the cart before the horse. Parallel studies of strictly regional and strictly local processes should precede conditional hypotheses that combine local and regional elements. Yet, as broad combinatorial theories (e.g. community assembly, metapopulation and metacommunity processes) have been developed for freshwater invertebrates, the fact that dispersal is poorly understood has largely been ignored. Community ecology may be considered more robust by some critics (e.g. Peters 1990) if the field had applied a strong inference approach.

It is, of course, unfair to suggest that a large affiliation of scientists independently pursuing diverse interests for decades should have adhered to this or any other research

framework. However, the recent increase in studies investigating dispersal in freshwater invertebrates indicates that others have already recognized the argument above. We present this framework to help focus future research on modern ecological and evolutionary concepts that require quantitative dispersal information. Studies of dispersal are often difficult in freshwater invertebrates. However, if we continue to treat these systems as if dispersal is irrelevant, we exclude them from a major portion of ecology’s future.

PATHOLOGIES IN DISPERSAL ECOLOGY?

‘If we want to build a predictive, informative science we must begin with enough samples to describe the state variables, we must use theories that contain a small enough number of variables that we can hope to make the measurements necessary for prediction; we must build calculating systems which do not so proliferate error that any measurement will confirm the prediction, but none will falsify it’. Robert Peters, *Pathologies in Limnology* (1990)

Until relatively recently, the precise estimation of freshwater invertebrate dispersal as an important state variable has been considered impossible, impractical or irrelevant. As a result, freshwater population and community ecology have, until recently, developed under the assumption that invertebrates disperse widely and rapidly. Yet, many current ecological and evolutionary paradigms contradict long-standing presumptions about the magnitude and importance of dispersal. Although impossible to assess retrospectively, development of these fields may have been hampered by the pervasiveness of these myths. As a practical example, most freshwater biologists know the feelings of amusement and embarrassment that accompany an answer to the question ‘How often do they disperse?’ at the end of a seminar. Our answers are typically vague, and frankly, we do not even know if it matters that we are vague. Methodological problems estimating dispersal have been circumvented in creative ways: biogeographical distributions, colonization studies, gene flow estimates and diapausing egg production have all been used as surrogates for dispersal. Scientific progress seems to have occurred despite the available information on how often and how far individuals disperse, not because of it. Fortunately, studies of connectivity in freshwater ecosystems are increasingly hypothesis-driven, integrative across multiple scales, and aimed at actually estimating the movement of individuals in space and time (Cáceres 1997; Brendonck & Riddoch 1999; Shurin 2000; Berendonck & Bonsall 2002).

Studies in evolutionary ecology assess the power of natural selection to optimize fitness criteria within bounds imposed by historical and contemporary constraints. This provides a possible metaphor for the development of

freshwater invertebrate ecology. Logistic constraints have hampered aquatic ecologists' ability to accurately estimate rates of dispersal, and historical presumptions regarding these rates have in turn constrained advances in ecological theory. We have reviewed here three areas of ecology and evolution that are likely to advance as more accurate and precise estimates of dispersal become available. Our treatment of only three topics is itself constrained, in light of other recent advances in speciation theory, landscape ecology, reserve design, and the evolution of dispersal (and dormancy) itself. In many taxa, technological challenges in tracking the movement of individuals remain a limiting factor. Nonetheless, it is unlikely that persistent historical constraints imposed by antiquated myths will continue to thwart meaningful developments in freshwater invertebrate ecology.

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REFERENCES

- Allan, J.D. (1995). *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, New York.
- Allen, Y.C. & Ramcharan, C.W. (2001). *Dreissena* distribution in commercial waterways of the U.S.: using failed invasions to identify limiting factors. *Can. J. Fish. Aquat. Sci.*, 58, 898–907.
- Andrewartha, H.G. & Birch, L.C. (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, IL.
- Bajkov, A.D. (1949). Do fish fall from the sky? *Science*, 109, 402.
- Berendonk, T.U. & Bonsall, M.B. (2002). The phantom midge and a comparison of metapopulation structures. *Ecology*, 83, 116–128.
- Bilton, D.T., Freeland, J.R. & Okamura, B. (2001). Dispersal in freshwater invertebrates. *Ann. Rev. Ecol. Syst.*, 32, 159–181.
- Bohonak, A.J. & Roderick, G.K. (2001). Dispersal of invertebrates among temporary ponds: are genetic estimates accurate? *Isr. J. Zool.*, 47, 367–386.
- Bohonak, A.J. & Whiteman, H.H. (1999). Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydro-period and salamanders. *Limnol. Oceanogr.*, 44, 487–493.
- Boileau, M.G., Hebert, P.D.N. & Schwartz, S.S. (1992). Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *J. Evol. Biol.*, 5, 25–39.
- Brendonck, L. & Riddoch, B.J. (1999). Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biol. J. Linn. Soc.*, 67, 87–95.
- Brooks, J.L. & Dodson, S.I. (1965). Predation, body size, and composition of the plankton. *Science*, 150, 28–35.
- Cáceres, C.E. (1997). Temporal variation, dormancy and coexistence: a field test of the storage effect. *Proc. Natl. Acad. Sci. USA*, 94, 9171–9175.
- Cáceres, C.E. (1998). Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology*, 79, 1699–1710.
- Cáceres, C.E. & Hairston, N.G. Jr (1998). Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. *Ergebnisse der Limnologie*, 52, 163–174.
- Cáceres, C.E. & Soluk, D.A. (2002). Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia*, 131, 402–408.
- Carpenter, S.R. & Kitchell, J.F. (1993). *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.
- Collier, K.J. & Smith, B.J. (1997). Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. *Hydrobiologia*, 361, 53–65.
- Cooper, J.E. & Braswell, A.L. (1995). Observations on North Carolina crayfishes (Decapoda: Cambaridae). *Brimleyana*, 22, 87–132.
- Corbet, P.S. (1980). Biology of Odonata. *Ann. Rev. Ent.*, 25, 189–217.
- Cousyn, C., De Meester, L., Colbourne, J.K., Brendonck, L., Verschuren, D. & Volckaert, F. (2001). Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. *Proc. Natl. Acad. Sci. USA*, 98, 6256–6260.
- Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 6th edn. John Murray, London.
- De Meester, L. (1996). Local genetic differentiation and adaptation in freshwater zooplankton populations; patterns and processes. *Ecoscience*, 3, 385–389.
- De Meester, L., Gómez, A., Okamura, B. & Schwenk, K. (2002). The Monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica*, 23, 121–135.
- Declerck, S., Cousyn, C. & De Meester, L. (2001). Evidence for local adaptation in neighbouring *Daphnia* populations: a laboratory transplant experiment. *Freshwater Biol.*, 46, 187–198.
- Dodson, S.I. & Frey, D.G. (1991). Cladocera and other Branchiopoda. In: *Ecology and Classification of North American Freshwater Invertebrates* (eds Thorp, J.H. & Covich, A.P.), Academic, New York, pp. 723–786.
- Dumont, H.J. (1983). Biogeography of rotifers. *Hydrobiologia*, 104, 19–30.
- Dumont, H.J. & Segers, H. (1996). Estimating lacustrine zooplankton species richness and complementarity. *Hydrobiologia*, 341, 125–132.
- Figuerola, J. & Green, A.J. (2002). Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biol.*, 47, 483–494.
- Finlay, B.J., Monaghan, E.B. & Maberly, S.C. (2002). Hypothesis: the rate and scale of dispersal of freshwater diatom species is a function of their global abundance. *Protist*, 153, 261–273.
- Fisher, R.A. (1958). *The Genetical Theory of Natural Selection*, 2nd edn. Dover, New York.
- Forbes, S.A. (1887). The lake as a microcosm. *Bull. Peoria Sci. Assoc.*, 77–87.
- Freeland, J.R., Noble, L.R. & Okamura, B. (2000). Genetic consequences of the metapopulation biology of a facultatively sexual freshwater invertebrate. *J. Evol. Biol.*, 13, 383–395.
- Freeland, J.R., Rimmer, V.K. & Okamura, B. (2001). Genetic changes within freshwater bryozoan populations suggest temporal gene flow from statoblast banks. *Limnol. Oceanogr.*, 46, 1121–1129.

- Frey, D.G. (1982). Questions concerning cosmopolitanism in Cladocera. *Arch. Hydrobiol.*, 93, 484–502.
- Geenen, S., Jordaens, K., De Block, M., Stoks, R. & DE Bruyn, L. (2000). Genetic differentiation and dispersal among populations of the damselfly *Lestes viridis* (Odonata). *J. North. Am. Benthol. Soc.*, 19, 321–328.
- Gómez, A., Carvalho, G.R. & Lunt, D.H. (2000). Phylogeography and regional endemism of a passively dispersing zooplankton: mitochondrial DNA variation in rotifer resting egg banks. *Proc. R. Soc. Lond. B*, 267, 2189–2197.
- Griffith, M.B., Barrows, E.M. & Perry, S.A. (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.
- Hairston, N.G. Jr & Cáceres, C.E. (1996). Distribution of crustacean diapause: micro- and macroevolutionary pattern and process. *Hydrobiology*, 320, 27–44.
- Hairston, N.G. Jr & Walton, W.E. (1986). Rapid evolution of a life history trait. *Proc. Natl. Acad. Sci. USA*, 83, 4831–4833.
- Hairston, N.G. Jr, Van Brunt, R.A., Kearns, C.M. & Engstrom, D.R. (1995). Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology*, 76, 1706–1711.
- Hairston, N.G. Jr, Lampert, W., Cáceres, C.E., Holtmeier, C.L., Weider, L.J., Gaedke, U. *et al.* (1999). Rapid evolution revealed by dormant eggs. *Nature*, 401, 446.
- Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press, Oxford, UK.
- Hanski, I. & Ranta, E. (1983). Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *J. Anim. Ecol.*, 52, 263–279.
- Havel, J.E., Eisenbacher, E.M. & Black, A.A. (2000). Diversity of crustacean zooplankton in riparian wetlands: colonization and egg banks. *Aquat. Ecol.*, 34, 63–76.
- Havel, J.E., Shurin, J.B. & Jones, J.R. (2002). Estimating dispersal from patterns of spread: spatial and local control of lake invasions. *Ecology*, 83, 3306–3318.
- Hebert, P.D.N. & Cristescu, M.E.A. (2002). Genetic perspectives on invasions: the case of the Cladocera. *Can. J. Fish. Aquat. Sci.*, 59, 1229–1234.
- Hebert, P.D.N. & Wilson, C.C. (1994). Provincialism in plankton: endemism and allopatric speciation in Australian *Daphnia*. *Evolution*, 48, 1333–1349.
- Holt, R.D. (1993). Ecology at the mesoscale: the influence of regional processes on local communities. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 77–88.
- Hughes, J.M., Mather, P.B., Sheldon, A.L. & Allendorf, F.W. (1999). Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. *Freshwater Biol.*, 41, 63–72.
- Humphries, S. & Ruxton, G.D. (2002). Is there really a drift paradox? *J. Anim. Ecol.*, 71, 151–154.
- Jackson, J.K. & Resh, V.H. (1998). Morphologically cryptic species confound ecological studies of the caddisfly genus *Gumaga* (Trichoptera: Sericostomatidae) in Northern California. *Aquat. Insects*, 20, 69–84.
- Jenkins, D.G. (1995). Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiology*, 313 & 314, 15–20.
- Jenkins, D.G. & Buikema, A.L. Jr (1998). Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol. Monogr.*, 68, 421–443.
- Jenkins, D.G. & Underwood, M.O. (1998). Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiology*, 387 & 388, 15–21.
- Jenkins, D.G., Grissom, S. & Miller, K. (2003). Drainage of the tallgrass prairie and the consequences for microcrustacean biodiversity and metapopulations. *Conserv. Biol.*, 17, 158–167.
- Johnson, L.E., Ricciardi, A. & Carlton, J.T. (2001). Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecol. Appl.*, 11, 1789–1799.
- Kerfoot, W.C. & Sih, A. (1987). *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, NH.
- Lampert, W. & Sommer, U. (1997). *Limnology: The Ecology of Lakes and Streams*. Oxford University Press, New York.
- Lehmann, T., Hawley, W.A., Grebert, H. & Collins, F.H. (1998). The effective population size of *Anopheles gambiae* in Kenya: implications for population structure. *Mol. Biol. Evol.*, 15, 264–276.
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Ent. Soc. Am.*, 15, 237–240.
- Likens, G.E. & Bormann, F.H. (1995). *Biogeochemistry of a Forested Ecosystem*, 2nd edn. Springer-Verlag, New York.
- Lynch, M. (1987). The consequences of fluctuating selection for isozyme polymorphisms in *Daphnia*. *Genetics*, 115, 657–670.
- McPeck, M.A. (1989). Differential dispersal tendencies among *Enallagma* damselflies (Odonata) inhabiting different habitats. *Oikos*, 56, 187–195.
- McPeck, M.A. & Holt, R.D. (1992). The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.*, 140, 1010–1027.
- Maguire, B. Jr (1963). The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecol. Monogr.*, 33, 161–185.
- Malmqvist, B. (2002). Aquatic invertebrates in riverine landscapes. *Freshwater Biol.*, 47, 679–694.
- Michels, E., Cottenie, K., Neys, L., De Gelas, K., Coppin, P. & De Meester, L. (2001). Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Mol. Ecol.*, 10, 1929–1938.
- Monaghan, M.T., Spaak, P., Robinson, C.T. & Ward, J.V. (2002). Population genetic structure of three alpine stream insects: Influences of gene flow, demographics, and habitat fragmentation. *J. North. Am. Benthol. Soc.*, 21, 114–131.
- Müller, K. (1954). Investigations on the organic drift in north Swedish streams. *Report of the Institute of Freshwater Research of Drottningholm*, 35, 133–148.
- Odum, H.T. (1957). Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.*, 27, 55–112.
- Okamura, B. & Freeland, J.R. (2002). Gene flow and the evolutionary ecology of passively dispersing aquatic invertebrates. In: *Dispersal Ecology* (eds Bullock, J.M., Kenward, R.E. & Hails, R.S.). Blackwell Science, Malden, MA, pp. 194–216.
- Pennak, R.W. (1989). *Fresh-Water Invertebrates of the United States*, 3rd edn. John Wiley and Sons, New York.

- Peters, R.H. (1990). Pathologies in limnology. In: *Scientific Perspectives in Theoretical and Applied Limnology. Mem. Ist. Ital. Idrobiol.* (eds de Bernardi, R., Giussani, G. & Barbanti, L.), 47, 181–217.
- Philippi, T.E., Simovich, M.A., Bauder, E.T. & Moorad, J.A. (2001). Habitat ephemerality and hatching fractions of a diapausing anostracan (Crustacea: Branchiopoda). *Isr. J. Zool.*, 47, 387–395.
- Platt, J.R. (1964). Strong inference. *Science*, 146, 347–353.
- Proctor, V.W. (1964). Viability of crustacean eggs removed from ducks. *Ecology*, 45, 656–658.
- Proctor, V.W., Malone, C.R. & DeVlaming, V.L. (1967). Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive killdeer. *Ecology*, 48, 672–676.
- Pulliam, H.R. (1988). Sources, sinks, and population regulation. *Am. Nat.*, 132, 652–661.
- Ricklefs, R.E. & Schluter, D. (1993). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, IL.
- Robinson, J.V. & Dickerson, J.E. Jr (1987). Does invasion sequence affect community structure? *Ecology*, 68, 587–595.
- Schultheis, A.S., Weigt, L.A. & Hendricks, A.C. (2002). Gene flow, dispersal, and nested clade analysis among populations of the stonefly *Peltoperla tarteri* in the Southern Appalachians. *Mol. Ecol.*, 11, 317–327.
- Schwenk, K., Posada, D. & Hebert, P.D.N. (2000). Molecular systematics of European Hyalodaphnia: the role of contemporary hybridization in ancient species. *Proc. R. Soc. Lond. B*, 267, 1833–1842.
- Service, M.W. (1997). Mosquito (Diptera: Culicidae) dispersal: the long and short of it. *J. Med. Entomol.*, 34, 579–588.
- Shurin, J.B. (2000). Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology*, 81, 3074–3086.
- Shurin, J.B. & Allen, E.G. (2001). Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.*, 158, 624–637.
- Simovich, M.A. & Hathaway, S.A. (1997). Diversified bet-hedging as a reproductive strategy of some ephemeral pool anostracans (Branchiopoda). *J. Crustacean Biol.*, 17, 38–44.
- Stemberger, R.S. (1995). Pleistocene refuge areas and postglacial dispersal of copepods of the northeastern United States. *Can. J. Fish. Aquat. Sci.*, 52, 2197–2210.
- Talling, J.F. (1951). The element of chance in pond populations. *Naturalist*, 1951, 157–170.
- Tuljapurkar, S. & Wiener, P. (2000). Escape in time: stay young or age gracefully? *Ecol. Modell.*, 133, 143–159.
- Weider, L.J. (1989). Spatial heterogeneity and clonal structure in arctic populations of apomictic *Daphnia*. *Ecology*, 70, 1405–1413.
- Weider, L.J. & Hebert, P.D.N. (1987). Ecological and physiological differentiation among low-arctic clones of *Daphnia pulex*. *Ecology*, 68, 188–198.
- Whitlock, M.C. & McCauley, D.E. (1999). Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity*, 82, 117–125.
- Wilcock, H.R., Hildrew, A.G. & Nichols, R.A. (2001). Genetic differentiation of a European caddisfly: past and present gene flow among fragmented larval habitats. *Mol. Ecol.*, 10, 1821–1834.
- Williams, C.B. (1958). *Insect Migration*. Collins, London.
- Wilson, D.S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, 73, 1984–2000.
- Wishart, M.J. & Hughes, J.M. (2003). Genetic population structure of the net-winged midge, *Elporia barnardi* (Diptera: Blephariceridae) in streams of the south-western Cape, South Africa: implications for dispersal. *Freshwater Biol.*, 48, 28–38.

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