

Mechanisms, effects, and scales of dispersal in freshwater zooplankton

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Abstract

The distribution of organisms can be regulated by local environmental factors and regional processes such as dispersal. Here, we review recent work on the role of dispersal for generating population and community structure in freshwater zooplankton. We examine evidence for different mechanisms of dispersal among lakes, for the effects of dispersal limitations on populations and communities, and for the effects of spatial scale on dispersal rates. Zooplankton move via human or animal vectors, flowing surface waters, and wind; the relative importance of the different modes of transport is poorly understood. Several lines of evidence suggest that dispersal among lakes separated over short spatial scales (<10 km) is sufficiently rapid that local interactions should limit species diversity and composition more than the supply of colonists. However, dispersal limitation over broad scales (tens to thousands of kilometers) might constrain geographic ranges and influence community structure. The current explosion in the incidence of exotic species indicates that such global- or continental-scale dispersal was limiting in the past. The spread of exotic species also provides opportunities to study the scale dependence of zooplankton dispersal. We show how patterns of range expansion can be used to estimate the change in invasion likelihood with distance to a source population. Such dispersal functions provide a crucial link between small-scale experimental studies and broad-scale geographic patterns.

Theories of geographic structure in communities and populations come from two broad schools of thought. The *regional* approach examines the importance of movement of individuals and the colonization of isolated patches of habitat separated over broad spatial scales. Parallel theories have been developed for regional control of both genetic variation in populations (Slatkin 1985) and species diversity in communities (MacArthur and Wilson 1963). The regional approach often emphasizes neutral or drift processes such as colonization and extinction and ignores differences among species or environments (Hubbell 2001). By contrast, the *local* approach examines the response of species to conditions that influence population growth rates within relatively small, homogeneous patches of habitat (MacArthur 1972). Local-scale ecology focuses on differences among organisms or habitats that allow coexistence of multiple species or genotypes. The local and regional views have both enjoyed

some success in explaining patterns in nature; however, the relative importance of the two types of processes in structuring populations or communities remains poorly understood.

Because of their isolation in an uninhabitable terrestrial matrix, we would expect dispersal to be especially limiting for organisms living in lakes. Nevertheless, studies of population and community structure in freshwater zooplankton have traditionally emphasized the role of local processes. Local factors known to influence the distribution of species include lake area (Dodson 1992), chemical composition (Tessier and Horwitz 1990), the supply of limiting nutrients (Dodson et al. 2000), competition (DeMott 1989), and predator abundance (Brooks and Dodson 1965). The importance of these local conditions can be estimated by the strength of statistical correlations of in situ measures or by manipulative experiments. Determining the role of regional processes has proven to be more challenging. Recently, a number of observational and experimental approaches have been applied to studying the role of dispersal and have yielded intriguing insights into population and community structure in lakes.

The purpose of this synthesis is to examine the role of dispersal in regulating biodiversity, species composition, and genetic structure of zooplankton in reservoirs, lakes, and ponds (hereafter called “lakes”). We review empirical evidence relating to three general questions. First, what mechanisms do zooplankton employ to move between lakes? We assess the strength of field data for various means of transport, including animal vectors, humans, wind, and surface waters. Second, what are the consequences of dispersal limitation for zooplankton genetic and community structure? Limited dispersal has the potential to constrain species and genetic diversity, community composition, and trophic structure. We examine observational and experimental evidence

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for the importance of dispersal relative to local processes, such as species interactions and abiotic constraints. Finally, we ask how dispersal in zooplankton varies across spatial scales. Because dispersal in all organisms is localized on some level, we expect short-range dispersal to occur more often than movement over longer distances. We review recent studies of the spatial spread of an invasive zooplankter, *Daphnia lumholtzi*, and the implications for scale dependence of dispersal.

Mechanisms of colonization

Zooplankton and other freshwater invertebrates have several life history characteristics that could promote rapid dispersal. First, a wide variety of invertebrates employ some mode of asexual reproduction (Bell 1982), which allows clonal propagation and also avoids the problem of mate limitation. Because most rotifers and cladocerans reproduce parthenogenetically (formation of eggs not requiring fertilization), a single individual can found a local population. Second, most zooplankton employ diapause to persist in unstable environments. Bdelloid rotifers undergo cryptobiosis, and monogononts form diapausing eggs (Wallace and Snell 2001). Diapausing eggs are also widespread in cladocerans, other branchiopods, and freshwater species of calanoid copepods and ostracods (Hairston and Cáceres 1996). Diapausing eggs are known to resist freezing, drying, and digestion by predators (Mellors 1975; Dodson and Frey 2001). These eggs provide both a long-term egg bank and a stage that can resist the harsh conditions of overland transport. Furthermore, egg cases such as *Daphnia ephippia* have spines and barbs (Hebert 1995), which enable attachment to fur and feathers, an adaptation analogous to the seed cases of many terrestrial plants. Zooplankton are linked to a wide variety of vectors enabling passive dispersal (Table 1). The importance of a particular vector depends on the rate at which eggs and free-swimming adults and juveniles are carried to a recipient waterbody (propagule load) and on survivorship during transport. Below, we consider evidence for the importance of particular vectors for transporting zooplankton to colonize new habitats.

Transport by wind—Wind has long been considered a potent force for dispersing dormant stages of aquatic organisms because a substantial aerial plankton has often been observed. Viable cysts of algae and protozoa have been detected high in the atmosphere (Schlichting 1961 in Weider et al. 1996). Turbulent transport processes resulted in frequent long-distance dispersal of seeds from trees (Nathan et al. 2002). Plankton diapausing eggs, which are often much smaller than these seeds, therefore also might move considerable distances. In short-term experiments with sticky traps near dry temporary ponds, Brendonck and Riddoch (1999) found that some diapausing eggs of the fairy shrimp *Branchinecta wolfi* are carried by wind, but only over very short distances (<1 m). Recent field experiments of Cáceres and Soluk (2002) and Cohen and Shurin (2003) both suggest that wind is an important vector because colonization rates were similar in artificial pools covered with fine screens (1-mm mesh) to those in which animal vectors had free access. Fur-

thermore, Cáceres and Soluk (2002) found that colonization rates declined in the direction of the prevailing winds. Aerial movement, at least over small spatial scales, is therefore likely to be an important means of dispersal for many species. Diapausing eggs also might be carried over longer distances. Dust storms in the sub-Saharan region of Africa have created dust clouds visible from space, which are carried by trade winds across the Atlantic Ocean to South America, depositing massive quantities of soil and microbes in the Amazon basin (Griffin et al. 2002). Volcanic fragments of a size and density greater than ostracods have been collected >130 km from the site of eruptions, suggesting the potential for aerial transport of ostracods (Sohn 1996). Occasional large storms have even been shown to transport large fish long distances over land (Bajkot 1949). Wind and atmospheric transport is therefore likely to be a frequent mode of dispersal in zooplankton.

Transport by flowing water—Many lakes are connected by networks of rivers that could facilitate dispersal. River connectivity is often associated with patterns in fish community structure, indicating that movement via surface waters is important for fishes (Magnuson et al. 1998). Zooplankton likely also use stream corridors because large populations are common in rivers and floodplains (Saunders and Lewis 1989; Thorp et al. 1994). Michels et al. (2001) showed that genetic distances among *Daphnia ambigua* populations were more closely related to distance via stream corridors than geographic distance, suggesting that most movement occurs via flowing water. Drift in water flowing out of a 50-km water supply pipeline connecting two lakes revealed that *D. lumholtzi* had survived the journey and rapidly invaded the recipient lake (E. Eisenbacher and J. Havel pers. comm.). Shurin and Havel (2003) examined patterns in the spread of *D. lumholtzi* among Missouri reservoirs with respect to position within the river network. Reservoirs downstream of known populations were more likely to become invaded than those with no upstream sources, although the difference between reservoir categories could also be explained by the tendency for reservoirs with low landscape position to be larger. Nevertheless, because reservoirs lacking upstream sources were also invaded, modes of transport other than flowing water must also play a role in dispersal of *D. lumholtzi* (Shurin and Havel 2003). Thus, although rivers might provide one route for dispersal of zooplankton, other means are important as well.

Transport by animals—Numerous freshwater invertebrates also are likely transported by animals moving between lakes (Bilton et al. 2001; Table 1). *Daphnia ephippia* remain viable following gut passage in fish (Mellors 1975), which could provide a means for upstream transport. Water mites parasitize aquatic insects and are transported to new habitats with aerial adult stages of the insects (Smith et al. 2001). Water mammals, such as muskrat, have been observed to transport amphipods over short distances (Peck 1975). Fairy shrimp also are likely transported between ponds in the digestive tracts of migrating amphibians (Bohonak and White-man 1999). Because of their long-distance migrations and catholic diets, water birds have long been viewed as impor-

Table 1. Empirical data consistent with particular vectors for passive dispersal of crustacean zooplankton and other freshwater taxa.

Vector	Taxa transported	Evidence	Reference
Natural mechanisms			
Birds	<i>Alona</i> , <i>Macrothrix</i> , <i>Cypridopsis</i> , <i>Physocypria</i> ; <i>Daphnia laevis</i>	Eggs hatched from feces of gadwall and green-wing teal shot in the field; genetic differentiation between flyways greater than along flyways	Proctor (1964) Taylor et al. (1998)
Insects	Copepod nauplii; water mites	External washings off <i>Notonecta</i> ; parasitic larvae on eight orders of amphibiotic insects	Schlichting and Sides (1969); Smith et al. (2001)
Floating in sea ice	Arctic <i>Daphnia pulex</i>	Widespread circum-Arctic clones with diapausing eggs tolerant of seawater	Weider et al. (1996)
Flooding	Numerous cladoceran and copepod species	New floodplain lakes quickly colonized following flooding	Havel et al. (2000b)
Mammals	Amphipods	Isolation from fur of beaver and muskrat	Peck (1975)
Salamanders	Fairy shrimp	Distribution, diapausing egg survivorship, and salamander movement patterns	Bohonak and Whiteman (1999)
Wind	<i>Mesocyclops</i> (2 spp.)	Biogeography in Africa and South America; storms known to transmit large quantities of soil across the Atlantic Ocean	Reid and Pinto-Coelho (1994); Griffin et al. (2002)
Human-mediated mechanisms			
Aquarium trade	Walking catfish	Fish escaped from transport truck traveling from airport to aquarium farm	Carlton (1992)
Bait buckets	Rusty crayfish	Fishers release bait into new range of lakes	Lodge et al. (1998)
Canals and pipelines	Amphipods	Several species of <i>Gammarus</i> crossed from one drainage to another after construction of canals	Jazdzewski (1980)
Construction equipment	<i>Daphnia lumholtzi</i> ; <i>Daphnia exilis</i> , <i>Daphnia curvirostris</i> ; rotifers and cladocerans	Sampled end of 50-km water supply pipeline; link between introductions and industry in Onondaga Lake (USA); link between imported equipment and fauna of Eildon Dam (Australia)	E. Eisenbacher (pers. comm.); Hairston et al. (1999); Duffy et al. (2000); Koste and Shiel (1989)
Fish stocking	<i>Daphnia lumholtzi</i>	First U.S. population appeared in lake stocked with Nile Perch from Lake Victoria	Sorensen and Sterner (1992)
Recreational boats	Cladocera and copepods; <i>Dreissena veligers</i>	Present in 19 of 47 boats; present in 138 of 835 boats	Havel and Stelzleni-Schwent (2000); Johnson et al. (2001)
Ship ballast tanks	Calanoids and cyclopoids (25 spp.) and numerous other pelagic species	Present in 157 of 159 ships	Carlton and Geller (1993)
Shipping, tires	Asian tiger mosquito larvae	Larvae in tires from 17 states. International and interstate commerce	Lyon and Berry (2000)

tant vectors of aquatic plants and animals (Darwin 1878; Proctor 1964; Figuerola and Green 2002). material isolated from bird feathers (Croll and Holmes 1982) and excrement (Proctor and Malone 1965) reveals viable algae, zooplankton eggs, and plant seeds. Feeding experiments demonstrated that zooplankton eggs can survive gut passage in birds (Proctor and Malone 1965). Zooplankton and other invertebrates thus appear adapted to use birds as vectors for dispersal. Indeed, genetic studies reveal a concordance between clonal distributions and direction of bird migration (Taylor et al. 1998; Freeland et al. 2000). However, the relative importance of animals promoting colonization is still unclear. Two recent colonization experiments failed to detect higher colonization rates in pools open to animal vectors than in pools from which vectors were excluded (Cáceres and Soluk

2002; Cohen and Shurin 2003). Thus, as with flowing surface water, animal vectors appear to be used by zooplankton to disperse into new habitats, although they might not be the most important vector for many species.

Human effects—Humans have greatly increased the rate of introduction of aquatic species into lakes. Human effects include habitat modification, deliberate introductions, and accidental releases (Carlton 1992; Lodge 1993). The construction of canals for shipping has allowed movement through water between formerly discontinuous drainages (Jazdzewski 1980). Large ships transport numerous exotic species between the continents in their ballast water (Ricciardi and MacIssac 2000). Collection of plankton from ship ballast tanks revealed 367 species, with some, such as co-

pepods, at densities over 1.5 individuals/liter, indicating that large ships can carry enormous numbers of species and individuals (Carlton and Geller 1993). Even the residual sediments carry viable eggs, suggesting that ballast water exchange might not always be effective in removing exotic invertebrates (H. MacIsaac pers. comm.). Recreational boaters are likely important for transporting zooplankton and other species, such as macrophytes, among smaller inland lakes. Patterns in range expansion by zebra mussels have been associated with boater movements (Buchan and Padilla 1999), most likely through adults attached to macrophytes (Johnson and Padilla 1996). Recreational boats can individually carry only small volumes of water in live wells (residual volume ~0.1 liter), but the large number of boats and their "promiscuous" use of different lakes could carry a regular stream of zooplankton and other invertebrates among lakes (Johnson et al. 2001). Indeed, a wide variety of living zooplankton can be collected in the residual water in live wells, and in experiments, adult *Daphnia* can survive up to 3 d, a period during which many boaters move to new lakes (Havel and Stelzleni-Schwent 2000).

Humans have likely introduced zooplankton and related species by a variety of other methods as well (Table 1). For instance, numerous species have been introduced as hitchhikers with aquaculture and fisheries activities (Carlton 1992). Similarly, anecdotal evidence from the distribution of an exotic clam shrimp suggested that they were imported from abroad with cattle stocked in Texas game ranches (Sisom 1980). Some invasions from overseas also have been linked to the importation of industrial and earth-moving equipment, which had presumably been contaminated with diapausing eggs (Koste and Shiel 1989; Duffy et al. 2000). Many lines of evidence thus indicate that humans have greatly altered natural dispersal rates and patterns for zooplankton and other aquatic organisms.

Effects of dispersal

Dispersal can have diverse effects at different spatial and temporal scales and at different levels of biological organization. In terms of biogeography, extensive dispersal on a global scale could lead to cosmopolitanism of species. However, most zooplankton are restricted to single continents (Frey 1982; P. Hebert pers. comm.), and a number of species are now known to be narrowly endemic (Hebert 1995). A similar pattern has also been reported for lotic meiofauna, such as harpacticoid copepods (Rundle et al. 2000). Biogeographic patterns of calanoid copepods in deglaciated regions suggest restricted dispersal. Those species that used glacial refugia have not expanded their range very far since the last glaciation (Hebert and Hann 1986) and have generally followed historical hydrologic pathways (Stemberger 1995). Other species, such as the tropical cladoceran *D. lumholtzi* (discussed in detail below) and Arctic populations of *Daphnia pulex* are broadly distributed across several continents (Benzie 1988; Weider et al. 1996). It is unclear to what extent biogeographic patterns in species ranges reflect recent, human-mediated range expansions or taxonomic reassignments (Frey 1982; Dumont 1997). For instance, Polynesians

are suspected of transporting a small zooplankton fauna to Easter Island (Dumont and Martens 1996). Therefore, it is quite possible that the "natural ranges" of many species are in fact a result of human migration.

Genetic structure of populations—Dispersal promotes gene flow and homogeneity of genes among populations, whereas limited dispersal leads to divergence of populations by genetic drift and natural selection (Slatkin 1985). Although some zooplankton clones have intercontinental distributions (Weider et al. 1996), most are more restricted in distribution. Indeed, strong divergence among local populations is evident in a variety of microcrustaceans, including anostracans (Brendonck et al. 2000), cladocerans (Hebert and Moran 1980), copepods (Boileau and Hebert 1988), and ostracods (Havel et al. 1990). High degrees of differentiation in allozyme gene frequencies are evident even over small spatial scales (<10 m) (Hebert and Moran 1980; Havel et al. 1990). Multiple polymorphic marker loci that show the same patterns imply that selection does not create the spatial structure. Instead, low rates of gene flow might result from low dispersal rates. However, an alternative explanation is that the pattern is a result of founder and priority effects (Hebert 1974), an idea expanded recently into the "monopolization hypothesis" (De Meester et al. 2002). This hypothesis states that early-arriving clones quickly develop a numerical advantage through rapid population growth rates, development of an egg bank, and local adaptation, and this advantage leads to competitive exclusion of later invaders.

Genetic data also have been useful for examining the history of past invasions and for determining the sources of colonists. Comparisons of genetic identity at 11 allozyme loci showed that populations of the cladoceran *Bythotrephes cederstroemi*, which invaded the Laurentian Great Lakes, were most similar to populations found in Finland, consistent with the hypothesis that the Baltic Sea served as the source of the North American invasion (Berg and Garton 1994). A similar approach using both allozyme and mitochondrial DNA data from *D. lumholtzi* established that North American populations were likely derived from populations in Africa or Asia, but not Australia (Havel et al. 2000a), a result consistent with the hypothesis that *D. lumholtzi* were introduced with stocked fish from Africa (Sorensen and Sterner 1992). Phylogenetic analysis of mitochondrial data from the estuarine copepod *Eurytemora affinis* revealed at least eight independent invasions of freshwater reservoirs along well-defined corridors (Lee 1999). A similar approach allowed Cristescu et al. (2001) to establish that the recent Ponto-Caspian invader, *Cercopagis pengoi*, likely first invaded from the Black Sea into the Baltic Sea and then was transported to the Laurentian Great Lakes. Combining genetic data from unknown *Daphnia* ephippia with a gene library from known species has been used to confirm the identity of species in the egg bank. Over the past 80 yr, two *Daphnia* species (*D. exilis* and *D. curvirostris*) invaded Lake Onondaga, New York, became abundant enough to lay down detectable numbers of diapausing eggs, and later became extinct (Hairston et al. 1999; Duffy et al. 2000). Genetic data thus allow us to examine dispersal over much longer time scales than contemporary studies.

Community structure—Comparative studies of species diversity and composition suggest a role for dispersal in structuring communities. Incorporating spatial effects of potential dispersal in statistical models is less straightforward than local factors that are measured in situ. One approach is to ignore local environmental features and examine associations between communities and geographic patterns. For example, dispersal routes have been inferred from the biogeography of freshwater copepods and patterns of deglaciation (Stemberger 1995). As the Wisconsinian ice sheet retreated, several species of *Skistodiaptomus* living in glacial refugia took advantage of new river drainages to invade new lake habitats. Pinel-Alloul et al. (1995) and Cottenie et al. (2003) illustrate an alternative approach for assessing the importance of dispersal. By including spatial coordinates of lakes in univariate and multivariate statistical models, they partitioned the variance into portions explained by local conditions, spatial location, and interactions between the two, representing geographic gradients in local environmental factors. Most of the variation in zooplankton community composition among Quebec lakes was explained by local water chemistry features and relatively little (usually < 10%) by spatial location, suggesting a minor role for spatially contagious dispersal in structuring these communities (Pinel-Alloul et al. 1995). However, Pinel-Alloul (1995) used geographic position as their measure of spatial position. Euclidian distances might not reflect the effective distance among lakes if zooplankton move largely via surface waters. When Cottenie et al. (2003) performed a similar analysis for a set of Belgian ponds connected by stream corridors, they found that distance via streams explained more variation in community structure than did geographic distance.

Another widely used approach for estimating the role of regional processes in survey data is to examine the shape of the relationship between local and regional species richness (Cornell and Lawton 1992). Linear, positive correlations would suggest that the supply of colonists from the region limits local species diversity, whereas saturated or curvilinear patterns would suggest strong local control. However, spatial scale can influence the shape of the relationship between local and regional richness and the inferences drawn from such studies (Srivastava 1999). Hillebrand and Blenckner (2002) showed that the shape of this function is most strongly regulated by the extent of the local and regional scales. For example, after controlling for scale, freshwater zooplankton show linear, positive correlations between local and regional richness (Shurin et al. 2000). This result suggests a dominant role for dispersal relative to local interactions in structuring lake plankton communities (i.e., strong dispersal limitation). However, this interpretation contrasts with a variety of experimental evidence for strong local interactions (see “Experimental studies of dispersal” below). Two possible resolutions to this conflict have been considered. One is that the importance of colonization limitation is dependent on scale, with dispersal being more limiting over long distances than short distances (Havel et al. 2002; see “Synthesis: Effects of scale on dispersal” below). The second explanation is that positive correlations between local and regional diversity are consistent with strong local interactions. One way this might occur is if local processes pro-

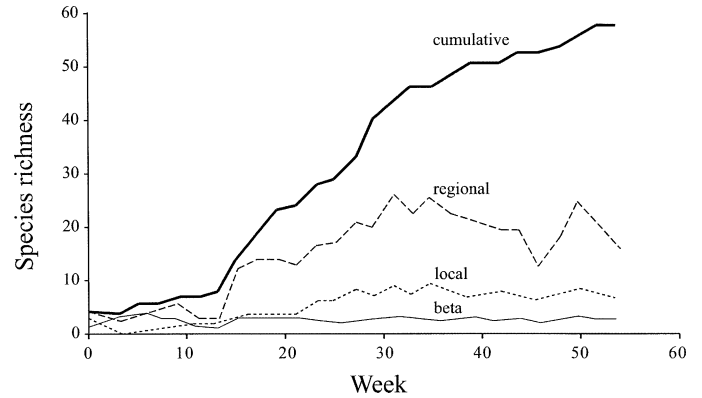


Fig. 1. Changes in zooplankton species richness over time in Jenkins and Buikema's (1998) experimental ponds. The lines show changes in local, regional, beta, and cumulative diversity over time. Beta diversity is the ratio of regional to local diversity and represents differentiation among ponds.

moted both local and regional richness. Shurin and Allen (2001) showed with metacommunity models that predators that facilitate local coexistence between competing prey can give rise to positive correlations between local and regional species richness. Thus, if interspecific facilitation plays a major role in structuring communities, patterns of local and regional species richness could be uninformative as to the roles of local and regional processes.

Experimental studies of dispersal—Another approach to studying the effects of dispersal is to use manipulative experiments. Two general experimental designs have been employed: *colonization* and *invasibility*. The first design examines natural colonization of artificial habitats by new species through time. Jenkins and Buikema (1998) first employed this approach in an elegant experiment on the succession of zooplankton in 12 newly created ponds in Virginia with intensive sampling over 1 yr. They sampled fortnightly to record the succession of zooplankton colonizing the ponds. By the end of the experiment, 57 species of crustaceans and rotifers had established, with 60% of them in half or more of the ponds. Both local (within-pond) and regional (among-pond) species richness increased over the first 6 months and then remained relatively constant, indicating that the ponds rapidly reached species saturation at both the local and regional scales (Fig. 1). Because local and regional diversity showed similar patterns over time, beta diversity (regional divided by local) remained constant over the entire experiment. This constancy indicates that differentiation among ponds did not change through succession. Cumulative richness increased monotonically, although at an apparently decreasing rate (Fig. 1), showing that novel species continued to invade the array throughout the entire year. The communities coexisting in the water column of these ponds reached colonization–extinction balance after ~6 months, although new species were still being added to the dormant pool as the cumulative number of invasions continued to rise (Fig. 1). Thus, species turnover and invasions continued after local and regional diversity in the ponds became saturated halfway through the experiment. Over this

time period, most apparent extinctions probably represent species entering dormancy, whereas colonization events indicate dispersal from outside the pond. Such processes are even more important over longer time periods because species turnover has been shown to be substantial among years (Arnott et al. 1999). In such cases, colonization of the pelagic community includes hatching of dormant eggs (Cáceres 1998).

Jenkins and Buikema (1998) concluded from their experiments that either many species were unable to reach all of the ponds or else the local communities set up barriers to further invasion early in the assembly process. If the first explanation is correct, then their results imply a strong role for dispersal in constraining zooplankton diversity and composition, at least in the early stages of pond succession. An experiment in artificial wading pools supported this interpretation, in that relatively few species were able to colonize the pools (Jenkins and Underwood 1998). If the second interpretation is correct, then local biotic resistance and exclusion become important quite early and should be of primary importance in natural waters that have undergone longer periods of succession. In this case, the supply of colonists via dispersal from neighboring habitats limits diversity and composition only in very young communities. If priority effects or persistent founder effects are important, then early colonization events could continue to influence community composition even as assembly proceeds through time.

These experiments provide valuable estimates of dispersal rates for many species, which is an important step toward understanding the roles of local and regional processes. However, they leave several important questions unanswered. First, it is unclear whether the number of species that colonize the ponds is a large or small portion of the regional species pool. Second, we do not know whether distance from source populations influences the rate of colonization. To address these two issues, Cohen and Shurin (2003) placed replicate artificial pools at each of four distances (5, 10, 30, and 60 m) from two naturally fishless ponds in Michigan. They also employed a positive control, where zooplankton from the two source ponds were introduced into the pools, to determine which species were able to survive in the experimental conditions. Seventy-eight percent of the species that established in the control also colonized the treatment pools, indicating that most species that were able to live in the pools could also disperse over land. Cohen and Shurin (2003) also found that a new species colonized each pool on average once every 4 d and that the rate of arrival was only weakly related to distance from a source. These results are in agreement with those of Cáceres and Soluk (2002), who also found a rapid accumulation of species over the first year of their study. Thus, isolation at the scale of <60 m might place few limits to zooplankton dispersal, whereas dispersal could vary substantially over scales of 1–100 km (see “Synthesis: Effects of scale on dispersal” below).

Although dispersal experiments can help us estimate zooplankton dispersal rates and their dependence on spatial scale over short distances, they cannot directly address the roles of local and regional processes because the importance of colonization limitation depends not on the absolute rate of

dispersal, but on the relationship between colonization and extinction probabilities. In a metapopulation, a species' equilibrium habitat occupancy is $1 - e/c$, where e is the extinction rate of local populations and c is the per-population colonization rate (Levins 1969). For example, a species for which dispersal events occur, on average, only once every 100 yr might appear to be a poor colonizer. However, if local populations only go extinct every 1,000 years, the species will eventually occupy 90% of the suitable habitat. If zooplankton extinction rates are low because of storage effects (egg banks, Hairston 1996) or large local population size, then apparently slow colonization could in fact be sufficient to nearly saturate the environment. Thus, the second class of experiments (invasibility experiments) is essential for estimating local and regional control of zooplankton communities.

Shurin (2000) performed an invasibility experiment in which the bulk of species from the regional pool were introduced as rare invaders into the zooplankton communities of 11 fishless Michigan ponds in large field enclosures. Over 90% of the species introduced failed to establish when the native community was intact. Those species that did colonize the ponds remained rare over many generations, comprising only ~1% of total zooplankton community biomass and having no detectable effect on zooplankton biomass or diversity. A second treatment found that severely reducing the density of the resident community allowed 4-fold more novel species to invade and achieve 16-fold higher biomass. The contrast between the treatments with intact versus disturbed local communities indicates that biotic resistance repelled many potential invaders. A second experiment (Shurin 2001) found that introducing fish and insect predators also made communities much more susceptible to invasion, much in the same way as artificially reducing the density of resident species. Taken together, these experiments indicate a major role for local processes, in general, and interspecific interactions, in particular, in generating variation in zooplankton composition and diversity. These results are in good agreement with the conclusions of Cáceres and Soluk (2002) and Cohen and Shurin (2003), in that they suggest that colonization rates for many species are high relative to local extinction rates. Dispersal therefore appears to place fewer constraints on zooplankton diversity, composition, and biomass than local interactions, at least over relatively small regional scales.

Synthesis: Effects of scale on dispersal

One important distinction between the observational and experimental studies of dispersal discussed above is that the two approaches examine processes operating over very different spatial and temporal scales. Dispersal and invasibility experiments generally measure processes over small scales (meters to kilometers and weeks to years), whereas surveys compare lakes separated over tens to thousands of kilometers (e.g., Shurin et al. 2000) that have diverged over geologic time scales. Broad-scale dispersal experiments would entail placing target habitats long distances from source lakes, a logistical impossibility in regions with many lakes. Broad-

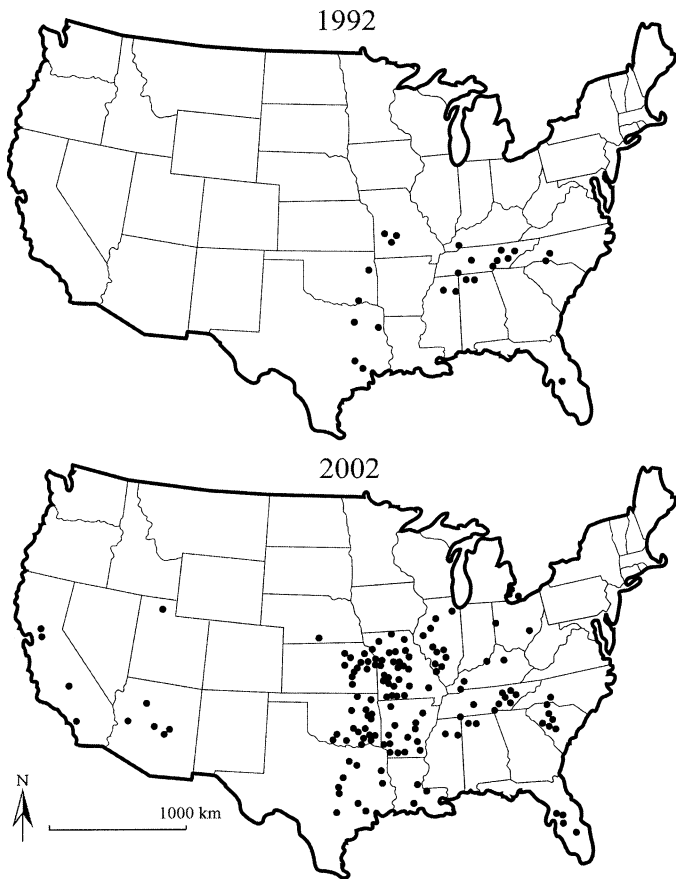


Fig. 2. Invasion of *Daphnia lumholtzi* into North America. Data points compiled from various studies by the authors and other sources (list of sites and references available in Web Appendix 1: http://www.aslo.org/lo/toc/vol_49/issue_4_part2/1229a1.pdf).

scale invasibility experiments, by transporting nonnative zooplankton between continents or biogeographic regions, are possible but have major ethical implications. Because the studies discussed above drew contrasting conclusions regarding the importance of dispersal limitation for zooplankton, it is important to integrate studies of zooplankton dispersal across spatial scales.

Studies of range expansion by exotic zooplankton provide an opportunity to achieve such a synthesis. Invasive species can serve as biological “tracers” because patterns of geographic spread can be measured over time. By contrast, patterns of apparent colonization of native species could represent either movement among lakes or resurrection of populations via dormant stages (Cáceres 1998). Below, we discuss range expansion in an exotic cladoceran and its implications for zooplankton dispersal in general.

The exotic cladoceran *D. lumholtzi* Sars is a distinctive species that was first discovered in North America in a small Texas lake in 1990 (Sorensen and Sterner 1992). *D. lumholtzi* is native to tropical and subtropical regions in Africa, Asia, and Australia, where it inhabits reservoirs, river oxbows (“billibongs”), and deep tectonic lakes (Swar and Fernando 1979; Benzie 1988). Discovery of this species early in its invasion history allowed us to use a time series ap-

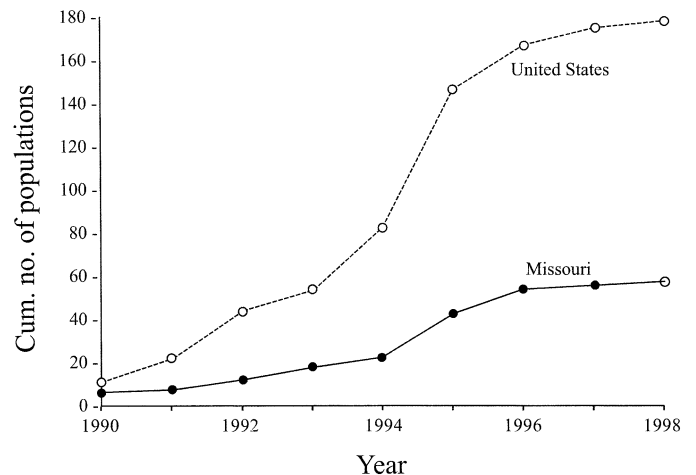


Fig. 3. Cumulative number of *Daphnia lumholtzi* populations for Missouri and the United States, 1990–2001.

proach for studying its dispersal. By 1992, *D. lumholtzi* had already spread across the southeastern United States (Havel and Hebert 1993) and, over an 11-yr period, has become widespread across the country, with over 180 invasions reported to date (Fig. 2). This rapid invasion was likely facilitated by its occurrence in river floodplains (Havel et al. 2000b), formation of viable diapausing eggs (Havel unpubl. data), and survival in live wells of recreational boats (Havel and Stelzleni-Schwent 2000). Annual surveys over a 7-yr period (1992–1998) in a large group of Missouri reservoirs found that the prevalence of *D. lumholtzi* increased from 6% to 34% (Havel et al. 2002; Fig. 3).

We used patterns in the invasion of the Missouri lakes over time to estimate the importance of distance to source populations and local limnological features for predicting *D. lumholtzi* invasion (Havel et al. 2002). We modeled invasion probability as a function of local site characteristics and distance to source populations using multiple logistic regression. Potential dispersal was included through a variable describing the dispersal “load” experienced by each target lake on the basis of its position relative to all known potential source populations. The dispersal term represents the total number of propagules received from all sources. The shape of the decline in propagule pressure with increasing distance to a source (the “dispersal kernel”) is unknown and is, in fact, the critical insight we hoped to obtain from the study. To estimate the shape of the dispersal kernel, we assumed exponential decline and varied the value of the parameter describing the shape of the kernel over a wide range. We compared models with different values of the dispersal parameter by maximum likelihood techniques to determine which parameter provided the best agreement between the model and the data (Akaike Information Criterion, Hilborn and Mangel 1997). To estimate the importance of dispersal relative to the constraints of water chemistry, temperature, and lake morphometry, we compared models containing local variables, the dispersal term, or both together (Havel et al. 2002).

The results showed that physicochemical factors (particularly area and temperature) were more important than dis-

tance for predicting invasion. Nevertheless, including the dispersal term along with the local terms improved the fit of the model in half of the years studied, and the estimated shape of the dispersal kernel was highly consistent among years. The number of propagules declined sharply by 20–30 km from a source and remained relatively constant at greater distances. Depending on the year studied, lakes within 1 km of an infected lake received 3–10 times more propagules than those 100 km from a source (Havel et al. 2002). The analysis thus indicated weak but detectable effects of dispersal in constraining the spread of *D. lumholtzi*.

The decline in dispersal of *D. lumholtzi* with distance to a source offers an interesting contrast with Cohen and Shurin's (2003) experimental results that found only weak effects of distance on colonization between 5 and 60 m from source ponds. Assuming that *D. lumholtzi* have a similar propensity to disperse as other lake zooplankton, these studies suggest that zooplankton dispersal becomes most limiting >20 km from a source. Estimating long-distance dispersal is difficult in many organisms (Nathan et al. 2002), and prospective studies of invasions offer a promising approach when direct empirical observation is infeasible. Another statistical method is to use mechanistic models of dispersal, such as gravity models, with data on vector movement (Buchan and Padilla 1999; Bossenbroek et al. 2001). This method is quite powerful when our knowledge of dispersal vectors for the invader of interest is well known. For instance, it may be reasonable to assume that zebra mussels or macrophytes are transported primarily by boaters. For organisms such as zooplankton, this approach could be premature until more is known about the mechanisms of their dispersal.

Perspectives and directions for future research

The extent of our knowledge on the role of dispersal in zooplankton communities is still much less developed than our understanding of local biotic and abiotic processes. Several questions stand out as demanding further attention. (1) What life history or ecological traits are related to dispersal ability in zooplankton? Asexual species or those that frequently produce dormant stages might be expected to be more effective dispersers because they are less susceptible to Allee effects or stochastic extinction. If dormant stages are costly for animals to produce, then there could be trade-offs between dispersal ability and other ecological functions, such as competitive ability or population growth rates. Such trade-offs have the potential to greatly promote species diversity (Chesson 2000), and other trade-offs are known to be important in zooplankton (e.g., Tessier et al. 2000). (2) What is the relationship between zooplankton dispersal ability and dormancy? If dormant stages are critical to both processes, then there might be interspecific relationships or evolutionary constraints that influence dispersal and diapause. (3) How important is dispersal through space versus time for maintaining zooplankton diversity? If most colonists come from the sediment egg bank rather than neighboring lakes, then the definition of regional diversity should be expanded to include the dormant community. (4) What is the relative

importance of different transport vectors, and are they similar across taxonomic groups? Developing mechanistic models of dispersal demands further elaboration of these roles and will also benefit efforts to predict which species are risks for becoming invasive. (5) What are the roles of local adaptation, dispersal limitation, and priority effects for regulating gene flow and maintaining regional genetic diversity? Evidence for local adaptation has been shown (Tessier et al. 1992; DeClerck et al. 2001), although its contribution to population structure relative to dispersal is unclear. Integrating our understanding of local and regional processes in zooplankton should be a high priority for future research.

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