

Biological invasions across spatial scales: intercontinental, regional, and local dispersal of cladoceran zooplankton

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Abstract

The frequency of dispersal of invertebrates among lakes depends upon perspective and spatial scale. Effective passive dispersal requires both the transport of propagules and the establishment of populations large enough to be detected. At a global scale, biogeographic patterns of cladoceran zooplankton species suggest that effective dispersal among continents was originally rare, but greatly increased in the past century with expanded commerce. Genetic analysis allows some reconstruction of past dispersal events. Allozyme and mitochondrial DNA comparisons among New World and Old-World populations of several exotic cladocerans have provided estimates for likely source populations of colonists, their dispersal corridors, and timing of earlier dispersal events. Detecting the Old-World tropical exotic *Daphnia lumholtzi* early in its invasion of North America has allowed detailed analysis of its spatial spread. Twelve years of collection records indicate a rapid invasion of reservoirs in the United States, by both regional spread and long-distance jumps to new regions. Combining landscape features with zooplankton surveys from south-central US reservoirs revealed higher colonization rates of *D. lumholtzi* at lower landscape positions, a result which can be explained by either greater propagule load or by higher susceptibility of these downstream reservoirs. Because invaded reservoirs provide a source of propagules for nearby floodplain ponds, the rarity of this species in ponds suggests limitation by local environments. Such analyses of invading species over multiple spatial scales allow a better understanding of ecological processes governing invasion dynamics.

Introduction

Spatial scaling influences a wide variety of processes as well as human perception of patterns in nature. For instance, plant distributions are often patchy at a coarse scale, but random within habitat patches. Failure to recognize scaling effects has contributed to several controversies in ecology, including the relative importance of physical and biological processes on the distribution of marine phytoplankton (Wiens 1989). The frequency of dispersal in freshwater

zooplankton communities is another area of current disagreement (Bohonak and Jenkins 2003; Louette and De Meester 2005). In particular, differences of opinion exist on how common are fast-dispersing species in nature and how quickly communities develop resistance to invasion. For small invertebrates like zooplankton, detecting a new population requires that a species has already established large numbers; thus descriptions of their dispersal are ordinarily referring to effective dispersal (colonization). As pointed out by (Bohonak and Jenkins 2003),

colonization depends on time scale and the perspective of the investigation. Similarly, spatial scale affects invasion dynamics (Shigesada and Kawasaki 1997) and the resulting patterns of species richness (Shurin et al. 2000). Development of dispersal theory can thus benefit from empirical data at different scales of time and space. The widespread occurrence of exotic species in aquatic communities provides a useful tool for such studies.

Freshwater lakes and ponds are ideal systems for studying the ecology of invasions. Their borders are more distinctive than those of terrestrial communities (Forbes 1925), which makes populations easier to delineate. Lakes and ponds are unevenly distributed around the world; in some regions ("lake districts") lakes are numerous and closely spaced, whereas in other regions lakes are more distant from one another (Hutchinson 1957). Lakes show tremendous variation in age, ranging from ancient tectonic basins (10^7 years)

and glacial lakes (10^4 years) to recently built reservoirs (decades) (Wetzel 2001). Lakes thus provide a template for studies over multiple temporal and spatial scales. Long-term research by limnologists has provided extensive environmental data and species lists for many lakes (e.g., LTER 2004). Such background data on species composition, together with re-analysis of archived samples, allow recreating the history of biological invasions. Hydrologic connections add another important variable contributing to the susceptibility of lakes to invasion (Figure 1). In cases where lakes and ponds are linked through connecting streams, measurement of a few variables allows estimating the flux rates of individuals and hence the renewal rate via immigration (Cottenie and De Meester 2004).

Passively dispersing zooplankton provide a good model for studying invasion patterns and processes. As a group, zooplankton are widespread and diverse, occurring in all but the

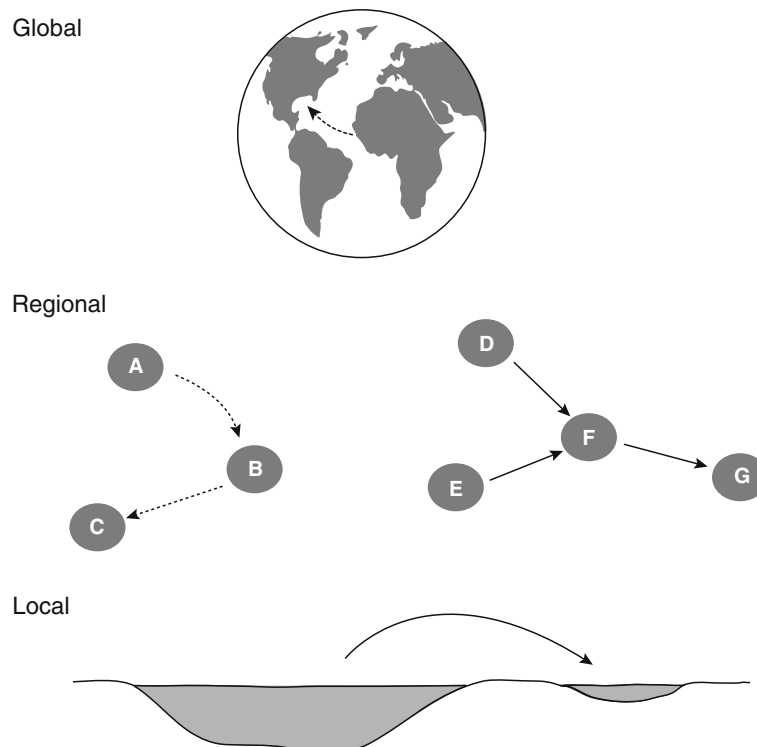


Figure 1. Scale dependence of zooplankton dispersal between lakes. At global and regional scales, dispersal between disconnected sites requires long distance hops over land and ocean barriers (dotted lines). In lakes connected by flow (D, E, F, G), dispersal rates may be increased by transport with water (solid lines). At the local scale, flooding or inundation may also introduce populations into local ponds.

harshest freshwater environments. Because of their commonness, small size, and ease of collection and culture, the life history and ecology of crustacean zooplankton are well known (Kerfoot 1980; Dodson and Frey 2001; Williamson 2001). They are thus favorite subjects of both surveys and experimental studies. The storage of preserved samples allows reanalysis for invading species, which may have been overlooked earlier. Finally, in contrast to the common practice of intentionally translocating fishes (Rahel 2002), humans have deliberately introduced zooplankton into lakes on only rare occasions (e.g., mysids in Flathead Lake (Spencer et al. 1991)).

The purpose of this paper is to analyze the scale dependence of biological invasions by cladoceran zooplankton. We first examine the history of several cladoceran invasions, reviewing in some detail the ecology and dynamics of the tropical exotic *Daphnia lumholtzi* Sars. We then use two new datasets together with landscape variables to analyze the relationship of hydrology to dispersal of this species at local and regional scales. Finally, we review the perspectives gained on dispersal of exotic species through methods carried out at different spatial scales. The answer to the question “Is dispersal common?” is clearly dependent on the scale of reference.

Dispersal ecology of exotic cladocerans

Dispersal: another planktonic paradox?

The distribution of cladoceran zooplankton presents an interesting paradox about dispersal. On the one hand, cladocerans have several life history traits which should favor their capability for high dispersal rates. Cladocerans, like many other freshwater invertebrates, are capable of asexual reproduction and hence a single individual can found a new population (Dodson and Frey 2001). Cladocerans also form resting eggs and, in many genera, these are encased in a hard capsule (“ephippium”). Ehippia can resist freezing and desiccation, which allows surviving hostile terrestrial conditions. Furthermore, several studies have demonstrated viable gut passage in fish and birds (Proctor and Malone 1965; Mellors 1975; Figuerola et al. 2003). Resting eggs

thus allow cladocerans and other zooplankton to take advantage of a number of potential transport vectors (Havel and Shurin 2004), as well as persist in the sediments for centuries (Cáceres 1998). Nevertheless, several lines of evidence provide clues to the limits of effective dispersal by cladocerans.

Biogeographic patterns at the global scale reveal that most species of cladocerans and copepods have regional or continental distributions (Frey 1982; Hebert 1995; Reid 1998). This modern perspective is strikingly different from previously reported cosmopolitan distributions, which were likely due to a naive taxonomy. It was quite natural for freshwater biologists in North America, making the assumption that zooplankton are good dispersers, to identify species with names from Europe where many of the established taxonomic keys originated (Frey 1982). Nevertheless, even before the recent explosion of exotic species, some species of cladocerans had intercontinental distributions. For instance, *D. lumholtzi* has its native range in tropical regions of Africa, the Indian subcontinent, and Australia (Benzie 1988).

Regional studies of biogeography and population genetics also suggest restricted effective dispersal in many zooplankton species. For example, species distributions of freshwater copepods from the northern USA and Canada have remained near their glacial refuges and likely dispersed along with postglacial meltwaters (Hebert and Hann 1986; Stemberger 1995). Further studies of numerous species of microcrustaceans (anostracans, cladocerans, copepods, and ostracods) using genetic markers have revealed strong spatial structuring of genotypes, even at small spatial scales (Boileau et al. 1992). Such data suggest that gene flow among populations is very slow, although it is not yet clear if this restricted effective dispersal is due to limitation in getting propagules from one place to another or to the failure of propagules to persist in the new environment. Spatial structure may be linked to habitat properties, such as water chemistry (Weider and Hebert 1987), or to resistance of previously arriving genotypes to invasion through priority effects (De Meester et al. 2002). Similar mechanisms may also operate at the community level (see “Scale and perspectives on zooplankton dispersal” below).

Studies of dispersal in natural zooplankton are complicated by the potential presence of a hidden population of dormant eggs in the sediments. For example, long-term studies of population dynamics reveal that different *Daphnia* species may become common in the plankton after being absent for a decade (Mills and Forney 1988). Thus, the absence of a species in the plankton community, followed by its appearance, might represent dispersal from other populations in the region or simply “resurrection” of a long-lost population from dormant eggs (Cáceres 1998). Exotic species offer a way around this problem since, being new to the region, they would be less likely to have an egg bank prior to the discovery of their populations.

Recent invasions of exotic zooplankton

Over the past 20 years, a variety of exotic zooplankton have invaded new continents and captured the attention of freshwater ecologists. Morphological and genetic studies have revealed that at least six species of cladocerans have invaded North American lakes and five others have colonized other continents (Table 1). Similarly, 21 species of copepods have invaded from other continents into freshwater and estuarine environments (Reid and Pinto-Coelho 1994).

Some of the cladoceran invasions are clearly recent events. Particularly well studied are the cladocerans *D. lumholtzi* and *Bythotrephes*

cederstroemi Schoedler (discussed below). Their distinctive morphologies helped researchers to notice these species quickly and initiate time series (prospective) studies of their invasions. Invasions by less-conspicuous species (“cryptic invasions”) are more difficult to detect and the time course of their spread is unknown. Some of these cryptic invasions are being detected by improved taxonomy and new molecular techniques. For example, *Eubosmina coregoni* Baird is endemic to Eurasia and first appeared in the Laurentian Great Lakes in 1966, apparently introduced with ballast water (Lieder 1991). The species spread to numerous smaller lakes, but has so far been reported only in lakes within 100 km of the Great Lakes. Subsequent morphological and allozyme analyses have confirmed that these populations are the same as the species reported in Europe (DeMelo and Hebert 1994b). Similar genetic analyses allowed detection of other European species in the Great Lakes, including *Eubosmina maritima* (DeMelo and Hebert 1994c) and *Daphnia galeata* (Taylor and Hebert 1993), although the dates of their introductions are unknown.

Recent introductions of easily recognizable cladoceran species has allowed detailed studies on the sources, vectors, and rates of spread. *B. cederstroemi* invaded the Laurentian Great Lakes in 1984 (Bur et al. 1986), and was likely transported from the Baltic Sea in ship ballast water (MacIsaac et al. 2000). Over the 20 years

Table 1. Documented examples of intercontinental invasions by cladoceran zooplankton.

Species	Year invaded	Native range	Location where first population was reported	References ^a
<i>Alona weinecki</i>	1774	Antarctica	Rano Raraku, Easter Island	1
<i>Bythotrephes cederstroemi</i>	1984	Eurasia	Laurentian Great Lakes (Lake Huron)	2
<i>Cercopagis pengoi</i>	1998	Eurasia	Laurentian Great Lakes (Lake Ontario)	3
<i>Daphnia ambigua</i>	1947	North America	Kew Gardens, England	4
<i>Daphnia galeata*</i>	????	Eurasia	Laurentian Great Lakes (Lake Erie)	5
<i>Daphnia lumholtzi</i>	1990	Africa, Asia, and Australia	Joe Pool Lake, Texas	6
<i>Daphnia obtusa</i>	1994	Europe and North America	Australia	7
<i>Daphnia parvula</i>	1973	North and South America	Ponds and Lake Constance, Germany	8
<i>Daphnia pulicaria</i>	1988	North America	Fish pond in Macedonia	9
<i>Eubosmina coregoni</i>	1960s	Eurasia	Laurentian Great Lakes (Lake Michigan)	10
<i>Eubosmina maritima*</i>	????	Eurasia (Baltic Sea)	Laurentian Great Lakes	11

^aReferences: 1 – Dumont et al. (1998); 2 – Bur et al. (1986); 3 – MacIsaac et al. (1999); 4 – Scourfield (1947); 5 – Taylor and Hebert (1993); 6 – Sorensen and Sterner (1992); 7 – Benzie and Hodges (1996); 8 – Flossner and Kraus (1976); 9 – Petkovski (1990); 10 – Lieder (1991); 11 – DeMelo and Hebert (1994c).

Species marked with an asterisk (*) are cryptic invaders detected by molecular methods.

since its introduction, *B. cederstroemi* has invaded all the Great Lakes and about 50 nearby inland lakes (Yan et al. 2002). Contributing to this invasion success is its broad diet of other zooplankton (Schulz and Yurista 1999) and large tailspine, which deters feeding by some predatory fish (Barnhisel and Harvey 1995). The appearance of *B. cederstroemi* has created some concern, as high densities and selective predation have lowered densities and species richness of some native zooplankton communities (Yan et al. 2002) and may thus impact food webs. Another cladoceran which likely arrived with ships from the Baltic Sea is *Cercopagis pengoi* Ostroumov, which recently appeared in the Great Lakes (MacIsaac et al. 1999). Genetic analysis has provided a view into the source and sequence of these invasions. Comparisons of allozyme diversity among Great Lakes and European populations narrowed the source of *B. cederstroemi* to lakes in Finland (Berg and Garton 1994) and suggested that founding populations were small. Comparisons of mitochondrial DNA gene sequences from *C. pengoi* in the Great Lakes with multiple Old World populations confirmed that the pathway of invasion for this species likely followed a corridor from the Black Sea to the Baltic Sea, before invading the Great Lakes (Cristescu et al. 2001). Another exotic cladoceran appears to have taken a different route for invading North America.

The dispersal ecology of a tropical exotic

D. lumholtzi was first detected during 1990 in an eastern Texas reservoir (Sorensen and Sterner 1992) and quickly invaded the southeastern United States (Havel and Hebert 1993). Allozyme and mitochondrial DNA data, together with anecdotal evidence, point toward a lake in Africa as the source of this invasion (Havel et al. 2000a). Unlike the zooplankton invasions of the Great Lakes, no link can be made between the appearance of *D. lumholtzi* and ship ballast. Instead, the likeliest explanation is that dormant eggs were transported with introduced fish (Sorensen and Sterner 1992). Using archived zooplankton samples from over 100 reservoirs, Havel et al. (1995) showed that *D. lumholtzi* had already invaded Missouri by 1990 and quickly

spread to a dozen other reservoirs in the state. A subsequent seven-year series of zooplankton collections indicated a rapid increase to about 34% of these Missouri reservoirs, with multiple instances of long-distance jumps in distribution (Havel et al. 2002).

Using published records and personal communications, we have since documented the distribution of *D. lumholtzi* in the United States to include 152 water bodies, ranging from Florida to California and Louisiana to Lake Erie (Figure 2). This range expansion has included long distance jumps across arid environments (e.g., Texas to Arizona). Recently, *D. lumholtzi* has been reported from a reservoir in Brazil (Zanata et al. 2003), indicating another intercontinental hop in its distribution. Invaded habitats primarily include reservoirs, and also large rivers, swamps, and natural lakes. Studies of population dynamics reveal most populations peak in late summer (Havel et al. 1995), a period when reservoirs in the south-central USA are quite warm. Such dynamics may be linked to a high tolerance of both warm temperatures (Lennon et al. 2001) and cyanobacteria (Pattinson et al. 2003), and may pre-adapt *D. lumholtzi* to successfully colonize such habitats during a period when most native cladocerans are in low abundance. Their high thermal tolerance may also allow *D. lumholtzi* to survive during transport in live wells of recreational boats (Havel and Stelzleni-Schwent 2000), using these as a vector for long-distance hops into new regions. Similarly, its high abundance in large rivers (Thorp et al. 1994; Stoeckel et al. 1996) and tolerance of turbidity (Gittinger-Soeken and Havel unpublished manuscript) may allow *D. lumholtzi* to use rivers as corridors for migration into downstream reservoirs and river floodplains.

Effects of hydrologic connections on invasions

River connections among reservoirs may greatly increase dispersal rates of zooplankton over background rates among disconnected habitats. Increased connectivity in fluvial systems has been previously shown to promote high community diversity for fishes and aquatic insects (Magnuson et al. 1998; Amoros and Bornette 2002).

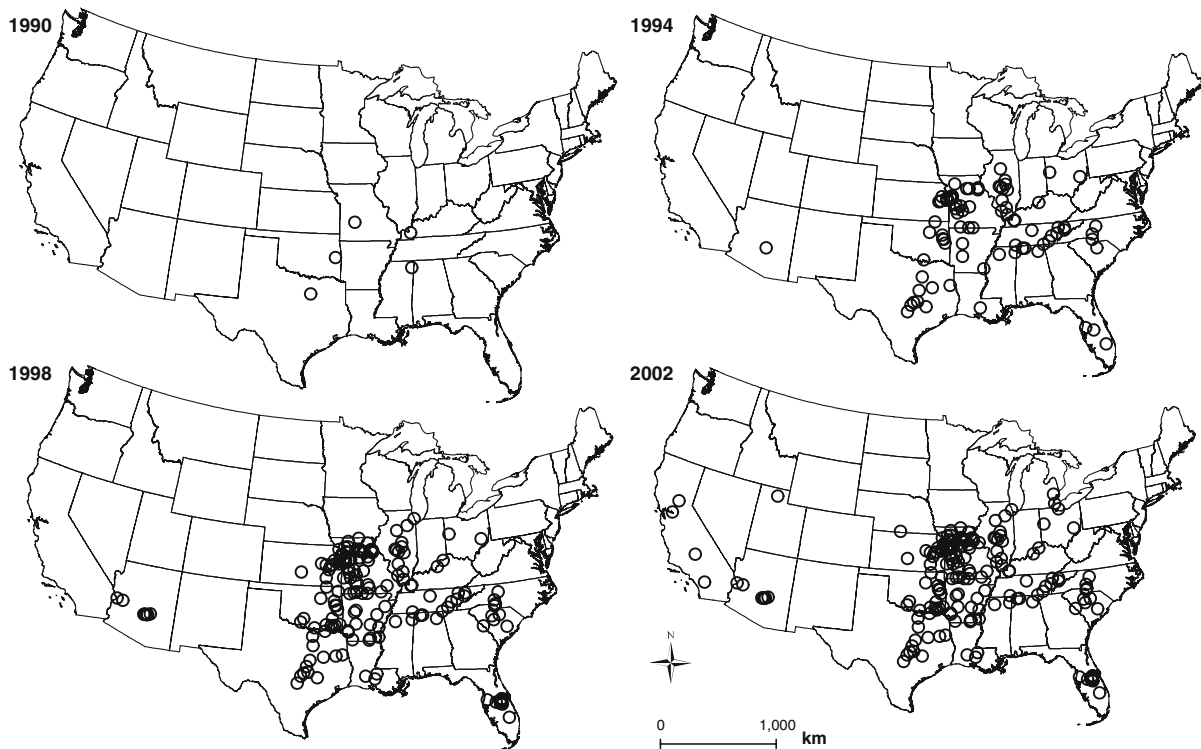


Figure 2. Cumulative distribution of *Daphnia lumholtzi* Sars in the United States. Although the first published record was from Texas, examination of archived samples indicated that in 1990 populations were already widespread. Over the next 12 years, the species expanded its range and increased its prevalence in lakes and reservoirs. Site names and credit to sources are listed in a web site (Havel and Shurin 2004); GPS coordinates, elevations, and stream connections are available through the senior author.

Nevertheless, such effects for zooplankton are less clear. In a complex of ponds connected by streams, dispersal of zooplankton was shown to occur at a high rate but, because of large population sizes in the resident ponds, dispersal contributed little to local population dynamics (Michels et al. 2001). Nevertheless, results from *in situ* experiments in the same system suggest that dispersal increased species richness of cladocerans and increased their responsiveness to biotic factors (Cottenie et al. 2003). In an effort to see if hydrologic connections enhanced the invasion rates of *D. lumholtzi* into reservoirs and floodplain ponds, we employed GIS analysis with two new datasets.

Lake level and invasion of floodplain ponds

Prior surveys revealed that *D. lumholtzi* is typically absent from ponds, even in the vicinity of established reservoir and river populations

(Dzialowski et al. 2000; Havel et al. 2000b). We do not know if this absence is because dispersal vectors (e.g., birds or boaters) are missing, if the conditions of ponds are unfavorable for colonization after dispersal, or if some combination of these factors prevents colonization.

To test the importance of hydrology, we examined a system where water level fluctuations of a reservoir inundated ponds in its floodplain and provided connections for redistributing zooplankton. Truman Lake, a 227 km² reservoir in Missouri USA, has had a detectable population of *D. lumholtzi* every year since its invasion in 1993 (J. Havel, pers. obs.). Accessible ponds adjacent to the reservoir were located, mapped with GPS, and surveyed for elevation. We obtained daily lake levels over a 10-year period (1993–2002) from the US Army Corps of Engineers (Kansas City District). These data were then organized in a GIS to reconstruct the flood history of 29 ponds. All but one of the ponds

were inundated by the lake over this period and most of the ponds were inundated more than once a year (Figure 3). Using standard techniques (Havel et al. 2000b), we collected zooplankton from the water column and hatched resting eggs from the sediments. Over all the 29 ponds, we detected 41 species of crustacean zooplankton, 20 of them present in both the lake and the ponds. *D. lumholtzi* was present in only two of the ponds. Since *D. lumholtzi* tends to be most common in local reservoirs during July–September (Havel et al. 1995), we re-analyzed the 10-year flooding data restricted to those three months and found that 28 of the ponds experienced at least two inundation events. *D. lumholtzi* in the water column or their dormant eggs in the near-surface sediments should have been available to invade the ponds during these

periods. Since it appears likely that *D. lumholtzi* propagules would have been transported from the lake into most floodplain ponds, the absence of this species suggests limitation by local environmental conditions. For instance, the ponds might lack deepwater refuges from UV radiation or from fish predators introduced during high water periods. Future manipulative experiments are required to better elucidate the environmental limits to invasion of floodplain ponds.

Watershed areas, connectivity, and invasion success

When posing the question “does hydrology matter” in determining invasion success, we would predict that reservoirs with a greater number or total area of upstream sources should have a greater propagule load. Furthermore, since a higher propagule load would provide more opportunities for successful colonization, we would expect a positive association between source density and the frequency of invasions. Some sources have previously detected populations. Others, because of insufficient sampling, may have populations which had not been detected. It thus seems reasonable to measure both the number and area of known source populations plus the number and area of potential sources in the watersheds of susceptible reservoirs, and see if these variables are positively associated with invasions.

To investigate this question, we analyzed data from a 1995 survey of 174 reservoirs in the south-central USA (Missouri, Oklahoma, and Arkansas), 57 of which contained *D. lumholtzi* (Havel et al. unpublished manuscript). We counted and mapped locations of all reservoirs using GPS coordinates (at the dam). Reservoir elevations were determined using topographic maps on the internet (<http://www.topozone.com>) or by using digital elevation data. For larger watersheds, we used USGS 10- and 14-digit hydrologic-unit-codes coverage to determine watershed area. The ArcHydro data model was used within the Spatial Analyst extension of ArcGIS 8.3 (ESRI, Redlands, California, USA) to delineate individual watersheds and calculate watershed area for smaller watersheds. Coverages representing hydrology and locations of all detectable

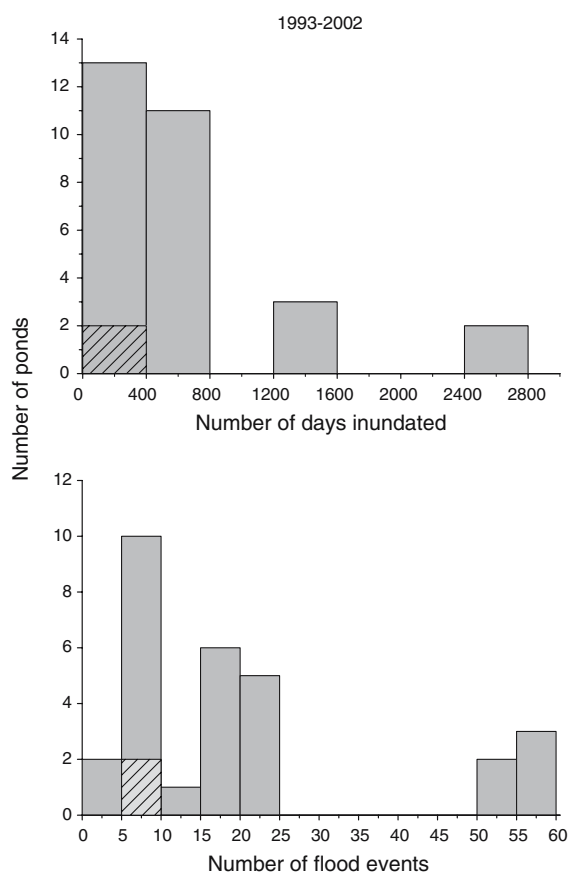


Figure 3. Hydrology of 29 ponds in the Truman Lake watershed over a 10-year period (1993–2002). Two of the ponds invaded by *Daphnia lumholtzi* are shown with hatching.

reservoirs ($\geq 1 \text{ km}^2$) were obtained from internet resources (<http://msdisweb.missouri.edu>), and placed within the GIS to count the number of reservoirs upstream from the surveyed reservoirs.

For the 1995 survey in the south-central USA, watershed areas for reservoirs invaded by *D. lumholtzi* were considerably greater than for those reservoirs which were not invaded ($T = 8.36$, $P < 0.001$, on log-transformed data) (Figure 4, top). The variance in watershed areas was also higher for invaded reservoirs than those not invaded ($F = 4.4$, $P < 0.001$), indicating that invaded sites encompassed a broader range of watershed sizes than non-invaded sites. Reservoirs which were invaded had a significantly

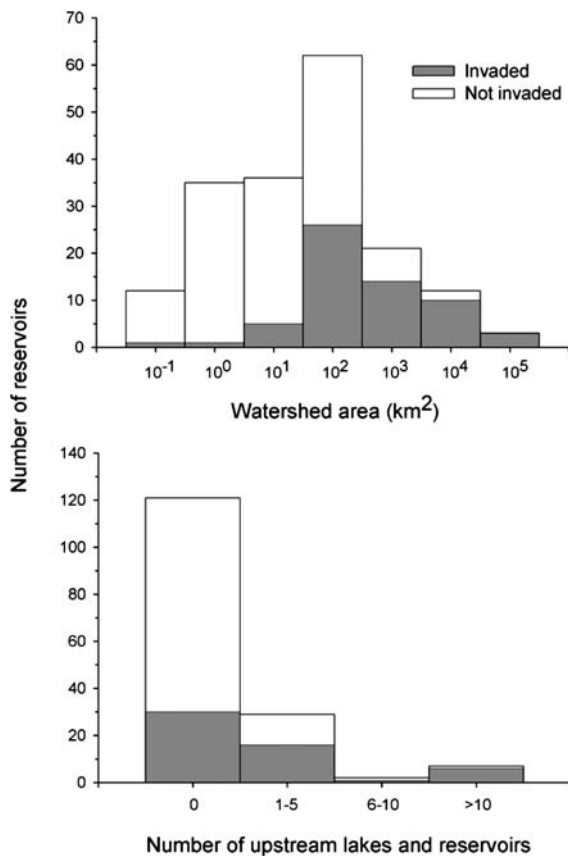


Figure 4. Relationship between landscape position of 174 reservoirs in Arkansas, Missouri, and Oklahoma and presence ($n = 57$) or absence of *Daphnia lumholtzi* in the 1995 survey. Top figure: watershed areas for each of the surveyed reservoirs, presented on a log scale. Bottom figure: number of lakes and reservoirs upstream from the surveyed reservoirs (range 0–96).

greater number of upstream source populations and total number of lakes and reservoirs (potential sources) than those reservoirs which were not invaded ($T = 3.20$ and $T = 3.29$, $P = 0.002$, respectively, on square-root transferred data) (Figure 4, bottom).

The data clearly show that reservoirs lower in the landscape had a greater chance of being invaded than those higher up. Nevertheless, many reservoirs higher in the landscape do occasionally get invaded. Indeed, 55% of the reservoirs invaded by *D. lumholtzi* did not have lakes higher in the landscape. These results are consistent with an earlier analysis of time-series data from Missouri (Shurin and Havel 2002). Their hydrologic analysis revealed that reservoirs downstream from source populations of *D. lumholtzi* had an average probability of invasion of 27% per year, whereas those without upstream connections had an average probability of invasion of only 7% per year (Shurin and Havel 2002). Both the 1995 and Missouri data sets are consistent with the importance of landscape position for colonization of zooplankton, although other explanations must be invoked for long-distance and upstream jumps in distribution.

We also examined the 2002 distribution of *D. lumholtzi* in the USA (152 invaded reservoirs, Figure 2) to explore the timing of invasions with watershed position. This dataset includes the location, year each reservoir was invaded, and stream connections and direction of flow. We used GIS to examine each watershed where multiple reservoirs were invaded and, for each watershed, compared the connections and elevation of the reservoir which was invaded first with that of the reservoir which was invaded second. Of the 15 watersheds sampled in multiple years and with more than one invaded reservoir, we asked the question “Was the second reservoir invaded downstream from the first?” The data show no significant tendency in either direction (5 yes vs. 10 no; Binomial test, $P = 0.15$). If anything, the larger low-elevation reservoirs tended to be invaded earlier than those at higher elevation. Nevertheless, we need to be cautious with interpreting these data for the entire US. In contrast to the detailed surveys in the south-central USA, we pooled observations from numerous other observers and thus had incomplete

information. For instance, we do not know the other locations sampled and lacking *D. lumholtzi* populations. Furthermore, we do not know the sampling intensity for different groups of reservoirs; it's entirely possible that larger reservoirs are sampled more frequently and would thus have a higher likelihood of detecting new species.

In summary, a variety of data are consistent with the importance of landscape position for colonization of zooplankton into reservoirs. Because many zooplankton can survive in large rivers, it seems reasonable that hydrologic connections provide a source of propagules for downstream reservoirs. However, several other explanations are consistent with these observations. First, downstream reservoirs also tend to be larger in area (correlation between surface area and watershed area, $r = 0.60$, $P < 0.001$). These larger reservoirs may serve as a bigger target for vectors, such as having more shallow areas for waterfowl and more boat ramps to attract boaters. Second, these larger downstream reservoirs may have more available habitats for invaders. Other environmental features of reservoirs, such as fertility, are also known to differ

with landscape position (J.R. Jones, pers. com.), and may be linked to invasibility.

Scale of perspective on zooplankton invasions

The global transport and subsequent regional spread of exotic species offer a large spatial template for studying dispersal. However, our methods have clear constraints. Intercontinental movements of exotic species are generally rare events and thus extremely difficult to study experimentally. We are left with the indirect approaches of surveys and such descriptive data can often yield more than one explanation. Regional and local spread of exotic species can be addressed with either surveys or experiments. Zooplankton, in particular, have many properties which make them useful models for such studies (*see* introduction above), and a wide variety of survey and experimental procedures have been used to address questions about dispersal of both exotic and native species (Table 2). An overarching question is: "Is colonization limited primarily by movement of viable propagules into new

Table 2. Empirical methods for studying biological invasions in freshwater.

Method	Scale	Example	References ^a
1. Manipulative experiments			
(i) colonization of open habitats	L	Zooplankton invasion sequence in newly dug ponds	1
(ii) invasion resistance of communities	L	Invaders and native communities in pond enclosures	2
(iii) survivorship in vectors	L	<i>Daphnia</i> in live wells of recreational boats	3
2) Field surveys			
(i) direct interception	L	Isolation of seeds and resting eggs from waterfowl feces	4
(ii) current spatial patterns:			
(a) biogeography, paleolimnology, and history	G	Comparison of fauna in sediment cores on isolated islands with history of human exploration	5
(b) genetic structure	G, R	Allozyme and mtDNA differentiation among North American <i>Daphnia</i> populations	6
(c) habitat characteristics	R	Predicting North American sites susceptible to invasion by Zebra Mussels based on their European distribution	7
(d) species-area curves	R	Slope of species-area curve depends on dispersal rate	8
(e) local vs. regional species richness	R	Linear patterns imply regional limitation of colonists	9
(iii) distribution of an exotic species over time	R	Pattern and rate of spread of invading <i>Daphnia</i>	10
(iv) distribution of an exotic species in the past (paleolimnology, paleogenetics)	L	Timing of appearance of <i>Daphnia curvirostris</i> in sediment cores	11

^aReferences: 1 – Jenkins and Buikema (1998); 2 – Shurin (2000); 3 – Havel and Stelzl-Schwent (2000); 4 – Figuerola et al. (2003); 5 – Dumont et al. (1998); 6 – Taylor et al. (1993); 7 – Ramcharan et al. (1992); 8 – Dodson (1992); 9 – Shurin et al. (2000); 10 – Havel et al. (2002); 11 – Duffy et al. (2000).

Scales (Figure 1): G – global; R – regional; L – local.

habitats, by physiological constraints to conditions in the new environment, or by community resistance to invasion?" The first part of this question can be addressed by examining the colonization of open environments and the mechanisms whereby new individuals can be transported. The second and third parts of the question require study of the characteristics of environments and communities which tend to be invaded. Here we discuss these questions with respect to zooplankton and how they have been addressed at different spatial scales.

Colonization: natural and manipulative experiments

The colonization experiment measures the time course of invasions in open environments, exploring community succession at one place. Classic examples have been described for plants colonizing the island of Krakatoa following its sterilization by a volcano (Brown and Lomolino 1998) and for insects colonizing small Caribbean islands following experimental defaunation (Simberloff 1981). Similar experiments have been conducted with ponds and lakes. The Great Midwest Flood of 1993 destroyed hundreds of levees along the lower Missouri River, creating new lakes ("scour basins") (Galat et al. 1998). Their rapid (<2y) colonization by zooplankton revealed the importance of large rivers as corridors for zooplankton dispersal (Havel et al. 2000b). Newly constructed ponds have also been used to explore colonization processes. Jenkins and Buikema (1998) followed the succession of rotifers, cladocerans, and copepods over a one-year period following the construction of 12 artificial ponds. In that time, 57 species had invaded, 60% of them in half or more of the ponds. A similar experiment over a broader area rich in natural aquatic habitats revealed an even-higher invasion rate by cladoceran zooplankton (Louette and De Meester 2005). Experiments using playpools and different filter meshes have further discriminated the invasion dynamics by different species of zooplankton, as well as the likely vectors transporting them (Cáceres and Soluk 2002). Overall, these colonization experiments have shown large differences among taxa in their ability to colonize the ponds, indicating either that

species varied in their abilities to move propagules to the ponds or that local communities quickly developed a resistance to invasion to some but not all of the species.

Vectors for moving propagules

Results from colonization experiments are partially explained by the transport of propagules by natural or human vectors (Havel and Shurin 2004). For instance, direct interception surveys with sticky traps suggest that wind is generally a weak agent for dispersing fairy shrimp resting eggs (Brendonck and Riddoch 1999). In contrast, collections of feces from waterfowl include viable seeds (plants) and dormant eggs (zooplankton), indicating the potential for long-distance dispersal via migrating birds (Figuerola et al. 2003). Several manipulative experiments have verified viable gut passage of a variety of invertebrates (e.g., Proctor and Malone 1965). Similarly, surveys and experiments have examined the role of human vectors for transporting exotic and invasive species. Surveys of recreational boats for weeds (Johnston et al. 1985), zebra mussels (Johnson and Padilla 1996), and zooplankton (Havel and Stelzleni-Schwent 2000) have revealed that boaters can effectively move exotics between invaded and susceptible lakes. Experiments with two species of adult *Daphnia* in live wells during summer conditions revealed that a high percentage of individuals could survive three days, a period during which many boaters move between lakes in different states (Havel and Stelzleni-Schwent 2000). Presumably dormant eggs are even more tolerant of conditions in the boats. Such data strongly suggest that recreational boats can move propagules of invasive species a long distance.

Invasibility experiments and surveys

If the biogeographic barrier between lakes were broken and propagules could be introduced to a new environment, under what conditions would we expect the invasion to succeed or fail? This invasibility question has been widely addressed in both terrestrial and aquatic systems (e.g., see Ramcharan et al. 1992; Moyle and Light 1996; Lonsdale 1999). The surveys for

exotic zooplankton described above have revealed possible limiting factors to invasions over broad spatial scales. However, confirming the mechanisms for these patterns requires experiments, which to date have been more local in their scale. A recent series of experiments from Michigan showed convincingly the resistance of local zooplankton communities to invasion. Shurin (2000) introduced invaders from the regional species pool into zooplankton communities of 11 fishless ponds held in large field enclosures. Most species failed to invade intact communities, whereas native communities reduced in density allowed four-fold more novel invaders. Similar experimental methods might be applied to long-distance processes. However, such deliberate introductions outside of “naturally-invaded” regions are impractical or unethical, limiting the geography of invasibility experiments. For instance, adding exotic species to enclosures in lakes not yet invaded would entail too high a risk of escape or later release of resting eggs.

Time course of invasions over multiple spatial scales

From the extensive work reported on zooplankton, it is clear that (effective) dispersal occurs more rapidly at short spatial scales (a few meters) than over greater distances (e.g., across a continent). At what intermediate spatial scale does this transition occur? Study of range expansion, together with new statistical techniques, offers a way to assess the effect of spatial scale on invasion success. In particular, we would like to estimate the shape of the dispersal probability-with-distance function (“dispersal kernel”) (Clark 1998). Prospective studies of new invaders provide a useful source of data for such an analysis. The invasion literature has a large number of invasion case histories, ranging from starlings in North America and muskrats in central Europe (Elton 1958) to recently emerging diseases at the global level (e.g. SARS and West-Nile virus, NCID 2004). The recent invasions of exotic cladocerans into North American lakes offer the opportunity to examine the scale of effective dispersal by planktonic organisms.

A seven-year data set on range expansion of *D. lumholtzi* and lake characteristics in Missouri

USA allowed modeling the features most important in controlling its range expansion. Havel et al. (2002) combined local environmental variables and spatial position of all invaded and susceptible reservoirs into multiple logistic regression models. First, potential dispersal was included through a variable describing the propagule load experienced by each susceptible lake, based on its position relative to all known potential source lakes (those invaded in previous years). The shape of the dispersal kernel is unknown and was estimated from the data, using both exponential and Gaussian models. After varying the value of the dispersal parameter over a wide range, maximum likelihood techniques were used to find which value of the parameter offered the best agreement between the model and the data. Next, in order to compare the importance of dispersal (propagule load) relative to local environmental constraints (water chemistry, temperature, and lake morphometry), Havel et al. (2002) compared logistic regression models containing only local variables, only the dispersal parameter, and both together. The results showed that physico-chemical factors (particularly area and temperature) were more important than distance for predicting invasion likelihood. However, including the dispersal term along with the local terms improved the fit of the model in most years studied and the shape of the dispersal kernel was highly consistent among years. The probability of invasion declined sharply up to about 20 km from a source, and remained relatively constant at greater distances (Havel et al. 2002). These results provide a useful contrast to the colonization experiments in artificial pools (Cohen and Shurin 2003), which generally showed a lack of distance effects on colonization within smaller spatial scales (10s of meters).

A related approach toward modeling dispersal has been to use gravity models, which require a firm understanding of dispersal vectors. These have been applied to dispersing zebra mussels (Buchan and Padilla 1999), where a clear link has been made to macrophytes carried by boats (Johnson and Carlton 1996). Once we have a better picture of the relative roles of birds and boats in transporting zooplankton, such an approach could be extended to studies of exotic zooplankton.

Conclusions and questions for future study

Use of multiple methods at different scales (Table 2) has provided deeper insights into the spatial scale of effective dispersal by zooplankton. The data imply that colonization is rapid into empty habitats, particularly at short spatial scales, but strong limitation can be imposed by local communities. Tracking the exotic *Daphnia lumholtzi* reveals that long-distance jump dispersal can occur quite rapidly (Figure 2). The fact that other recently studied cladoceran invaders (*B. longimanus*, *E. coregoni*) have more restricted distributions implies that these species are less invasive, but the underlying causes are less clear. Such a pattern could be due to differences among species in the density of individuals in contact with boats, with their survival in transit, or with their ability to survive and reproduce in their new environments. Since *B. longimanus*, *E. coregoni* have been invading different kinds of landscapes (natural lakes) than *D. lumholtzi* (reservoirs), it is also possible that the higher invasion rate of *D. lumholtzi* is simply a consequence of reservoirs being more invasible than natural lakes. For instance, the greater relative area of watershed to lake volume in reservoirs provides higher nutrient loading and variation in resource levels (Thornton et al. 1990), conditions which theory predicts should increase invasibility (Davis et al. 2000). Perhaps future invasion experiments could mimic these differences between lakes and reservoirs.

At the scale of watersheds, hydrologic connections appear to be linked to increased colonization rates of exotics into reservoirs. Nevertheless, it is unclear whether this correlation is due to differences in propagule load or to other effects of landscape position. Such studies would benefit from a better understanding of hydrologic processes. Stream ecologists have used drainage networks to explain distribution patterns of aquatic insects and fish (Amoros and Bornette 2002). For lakes and reservoirs, using historical data on water levels with topographic features allows discerning the effect of inundation on dispersal of freshwater invertebrates between ordinarily discontinuous habitat patches. Such approaches could also be applied to other passively dispersed taxa. Furthermore, the history of community

changes can be explored by coring the sediments, assigning dates, and hatching dormant eggs (Cáceres 1998).

One question which is poorly understood is the commonness of intercontinental invasions of exotic species. Descriptive studies documenting new invasions (e.g., Elton 1958; Mills et al. 1993), are certainly important, but are biased towards easily recognized species. As revealed by recent studies with genetic markers (e.g., DeMelo and Hebert 1994a; Taylor and Hebert 2000), numerous cryptic invasions likely occur but are missed because of morphological similarity between populations in source and recipient regions. Applying this approach to a wider range of taxa and communities should uncover additional invaders. Genetic markers can also be applied to dormant eggs in the sediments (e.g., Duffy et al. 2000), providing an additional dimension for uncovering and dating past invasion events. An understanding of freshwater invasions ultimately requires a continued appreciation for basic taxonomy and biogeography. Only against this backdrop are we prepared to recognize the invader in our midst.

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