

# Do Reservoirs Facilitate Invasions into Landscapes?

JOHN E. HAVEL, CAROL EUNMI LEE, AND M. JAKE VANDER ZANDEN

*The extensive construction of reservoirs over the past century has radically altered the environmental landscape on a global scale. Construction of dams on most large rivers has interrupted the connectivity of water flow and greatly increased the abundance of standing freshwater habitats. Reservoirs act as stepping-stones for the dispersal of exotic species across landscapes. A variety of passively dispersing species have invaded reservoirs, spread through interconnected waterways, and been transported to nearby disconnected habitats. We hypothesize that reservoirs are more readily invaded than natural lakes, because of their physiochemical properties, greater connectivity, and higher levels of disturbance. Here we summarize properties of reservoirs that would make them prone to invasions and discuss cases in which reservoirs have facilitated rapid range expansion. Our overview illustrates linkages between two important forms of global environmental change: the widespread manipulation of river flows and the accelerating spread of exotic species.*

*Keywords: dispersal, disturbance, exotic species, range extensions, species invasions*

**O**ver the past century, human activity has promoted invasions both by creating new transport vectors and by changing the environment. A notable example of environmental manipulation is the widespread construction of reservoirs. In many regions of the world, reservoirs offer an enormous increase in the number, area, and spatial distribution of standing waters, providing new opportunities for colonization and stepping-stones for the spread of invaders into new regions.

Worldwide, the rate of reservoir construction peaked by the 1970s and then slowed as the number of sites that could be economically dammed became fewer (Rosenberg et al. 2000). Impoundments range from small watering ponds for cattle to large hydropower reservoirs hundreds of kilometers (km) long. Whereas most natural lakes (e.g., those formed by glaciers) have been extant for thousands of years, the vast majority of reservoirs are young (< 50 years). The advent of reservoirs represents a major change in the patchwork of standing water in landscapes where lakes and ponds were formerly rare. For example, in the state of Oklahoma, much of which lies in the arid American West, standing water was historically restricted to natural oxbow and playa lakes. The construction of reservoirs led to a 228-fold increase in area of standing water, with the current area (1.5 percent of land area; [www.owrb.state.ok.us](http://www.owrb.state.ok.us)) approaching that found in glaciated regions of high lake density (e.g., 2.8 percent of land area in Wisconsin; <http://facts.wisconsin.com>). A similar expansion of standing surface water is common worldwide, and continues to grow, especially in developing countries (Rosenberg et al. 2000).

Reservoirs have well-known detrimental effects on native stream communities, fisheries, and terrestrial streamside habitats. Aside from converting extensive reaches of stream habitat into standing water, reservoirs flood large areas of land, change the magnitude and timing of water flows, reduce the sediment load, form barriers for fish migration, and extirpate shallow-water species through fluctuating water levels (Malmqvist and Rundle 2002). Reservoirs also lead to the replacement of spatially heterogeneous stream habitats with habitats more similar among regions. This habitat modification, combined with stocking practices, causes displacement of unique local assemblages with widespread species that are better able to tolerate human activities, leading to the homogenization of freshwater biota (Rahel 2002).

The role of reservoirs in accelerating biological invasions into new landscapes has not previously been explored (but see Kolar and Lodge 2000). Reservoirs provide new habitats for passively dispersing organisms that cannot persist in strong unidirectional flow, such as numerous zooplankton species, aquatic plants, and planktonic larvae of benthic invertebrates. This article examines how reservoirs might facilitate the spread of invaders across landscapes. We present several hypotheses on why reservoirs may be particularly

---

*John E. Havel (e-mail: [johnhavel@smsu.edu](mailto:johnhavel@smsu.edu)) is a professor in the Department of Biology at Southwest Missouri State University, Springfield, MO 65804. Carol Eunmi Lee is an assistant professor in the Department of Zoology, and M. Jake Vander Zanden is an assistant professor in the Center for Limnology, at the University of Wisconsin, Madison, WI 53706. © 2005 American Institute of Biological Sciences.*



**Figure 1.** Distribution of *Daphnia lumholtzi* Sars. Old World distribution, as reported in Havel and Hebert (1993), is shown on the right; North American distribution in 1992 and 2002, from Havel and Shurin (2004), is shown on the left. Scale bars on maps = 1000 kilometers. Drawing of *D. lumholtzi* after Havel and Hebert (1993); scale bar = 0.5 millimeter.

susceptible to invasions, and examine the role reservoirs may play in allowing adaptation of brackish species to fresh water. We then discuss how reservoirs can serve as stepping-stones for invading new landscapes. Finally, we describe several areas in which future research would be especially fruitful.

### Case study: Rapid and widespread invasion of reservoirs by a tropical cladoceran

The cladoceran *Daphnia lumholtzi* is an outstanding example of a rapidly dispersing invader of reservoirs. This species is native to natural lakes, reservoirs, and floodplains of the Old World tropics, with its prior range extending over three continents (figure 1). Following invasion of a Texas reservoir in 1990 (Sorensen and Sterner 1992), the species quickly spread across the southeastern United States (Havel and Hebert 1993). In only a decade, *D. lumholtzi* dispersed throughout 125 reservoirs in the Midwest and into the arid western states (figure 1; Havel and Shurin 2004). *Daphnia lumholtzi* has since made another intercontinental jump by appearing recently in a Brazilian reservoir (Zanata et al. 2003). Although present in large rivers and natural lakes, the vast majority of US populations of *D. lumholtzi* are in reservoirs.

As an invader from the tropics, *D. lumholtzi* is probably physiologically adapted to hot summer conditions in the southern United States. During this season, *D. lumholtzi* becomes abundant while native *Daphnia* species decline (Havel et al. 1995). The fact that some Missouri populations now

persist during winter suggests the species has now adapted to cooler temperatures. Such an adaptation following invasion of reservoirs might have facilitated its subsequent invasion of the Great Lakes (Muzinic 2000) and may allow the invasion of other glacial lakes.

### Are reservoirs particularly susceptible to invasions?

Ecologists have identified several attributes of the abiotic environment and receiving biotic community that may influence the success of exotic introductions (Elton 1958). These include (a) habitat connectivity and propagule pressure, (b) disturbance and environmental variability, and (c) species diversity and biotic interactions (Elton 1958, Davis et al. 2000). Reservoirs and natural lakes differ with respect to these properties (table 1) in a way that would make reservoirs especially vulnerable to invasions (table 2).

**Connectivity and propagule pressure.** The magnitude of immigration by new individuals (propagule pressure) is a major factor for predicting the success of invaders in colonizing new ecosystems (Kolar and Lodge 2001). For aquatic organisms, the physical connection between water bodies provides an important conduit for immigration. Because of their sequential placement in riverine networks, reservoirs are highly connected to river systems and to other reservoirs. Thus, the downstream transport of water has great potential for enhancing colonization rates of invasive species. Two examples

**Table 1. Characteristics of reservoirs in relation to natural (glacial) lakes.**

Characteristic	Description of reservoir (in comparison with natural lakes)
<b>Geographic and geological</b>	
Geographic distribution (Northern Hemisphere)	More in southern latitudes
Climate	More in warm and arid regions
Age	Much younger
Life span	Shorter
<b>Physical</b>	
Depth (average)	Lower
Location of maximum depth	Near dam versus center
Watershed area-to-volume ratio	Much higher
Shape	More irregular (greater edge-to-area ratio)
Zonation <sup>a</sup>	Much more longitudinal (river channel)
Water-level variation <sup>a</sup>	Larger and more irregular
Flushing rate	Much higher and more variable
Outflow level <sup>a</sup>	Subsurface versus surface
Connectivity among lakes <sup>b</sup>	Higher
Thermal stratification	Weaker and more irregular
Turbidity	Higher and more variable
Suspended solids (inorganic)	Much higher
Sedimentation rate	Much higher
<b>Chemical</b>	
Total dissolved solids	Higher and spatially more variable
Nutrient loading	Higher
<b>Biological</b>	
Phytoplankton biomass and production	More variable (along longitudinal axis)
Allochthonous input	Much greater
Littoral zone development <sup>a</sup>	Lower
Benthic invertebrate biomass <sup>a</sup>	Lower
Zooplankton biomass	Similar, but spatially more variable
Fish biomass	Higher when new, then similar
<p>a. These characteristics apply primarily to large hydropower and flood-control reservoirs.                      b. Refers to the rate of water exchange via surface flow from upstream to downstream lakes.                      Source: Adapted from Wetzel (1990).</p>	

illustrate this process: invasions by *D. lumholtzi* and by zebra mussels (*Dreissena polymorpha*).

Numerous zooplankton species can survive in large rivers, providing inocula for downstream habitats (Van den Brink et al. 1994, Havel et al. 2000). For instance, a study of the exotic cladoceran *D. lumholtzi* in Missouri revealed higher invasion rates in downstream reservoirs than in those upstream or those isolated from potential source populations (Shurin and Havel 2002). Nevertheless, other factors could also explain the higher invasibility of downstream reservoirs. These reservoirs tend to be larger in surface area and are visited by more recreational boaters. The intensive recreational use of reservoirs may also contribute to their connectivity, as boater movement among systems is also a vector for the spread of invaders such as *D. lumholtzi* and zebra mussels (Johnson and Carlton 1996, Havel and Stelzleni-Schwent 2000).

The importance of hydraulic transport is shown by the rapid spread of the zebra mussel in North American waterways. Within only seven years of their introduction into the Laurentian Great Lakes, zebra mussels were transported into 18 states in the United States and two provinces in Canada through interconnected waterways (Johnson and Padilla 1996). In contrast, overland transport to inland waters via small recreational fishing boats has been much slower. Surveys for zebra mussel larvae from 140 isolated lakes in the Upper Midwest indicated invasion rates considerably lower than rates for interconnected water bodies (Kraft et al. 2002). Interestingly, the life cycle of this invader is such that its distribution and dispersal through river systems is heavily dependent on the spatial positioning of standing waters, such as reservoirs.

In contrast to native unionid mussels, zebra mussels have an obligate planktonic larval (veliger) stage. Although this attribute certainly facilitates rapid horizontal dispersal in lakes and downstream transport in streams, it also provides a challenge to population persistence in flowing waters. Since their planktonic larvae cannot swim against currents, long-term maintenance of zebra mussel populations in river systems requires propagule inputs from an upstream site with standing water. Reservoirs should greatly enhance this process, particularly in highly modified rivers with disconnected floodplains. Indeed, in a study of commercially available waterways of the Mississippi River drainage, Allen and Ramcharan (2001) found that the presence of impoundments significantly enhanced the likelihood of zebra mussel occurrences in downstream river reaches.

**Table 2. Processes that regulate passive invasions of exotic species into lakes and reservoirs.**

Process of dispersal (primary vector) <sup>a</sup>	Characteristics of reservoirs that may increase invasibility
Intercontinental transport (humans)	Higher physical disturbance
Long-distance hops within continents (humans)	Higher and more variable fertility
Connectivity within landscapes (streamflow)	Higher salinity
Short hops without connections (humans, wind, or birds)	Altered food webs

a. All dispersal processes are probably enhanced by the additional standing water provided by reservoirs, particularly in arid regions. Reservoirs have much higher connectivity than natural lakes.

**Disturbance and environmental variability.** Anthropogenic disturbance is well known to increase the susceptibility of communities to invaders (Orians 1986). Several ideas about the roles of enrichment and disturbance on invasibility were recently integrated by Davis and colleagues (2000) into the fluctuating resource availability (FRA) hypothesis. This hypothesis predicts that communities become more susceptible to invasions whenever and wherever there is an increase in the amount of unused resources. Disturbance may temporarily reduce the abundance of native species and the intensity of biotic interactions, thus opening a “resource gap” for potential invaders. Similarly, nutrient inputs may temporarily increase resource availability, also creating opportunities for invaders. The FRA hypothesis specifically predicts that systems with fluctuating resources or elevated productivity will be more invasible.

How does this theory relate to the potential invasibility of reservoirs? Although limited supporting data are available, we hypothesize that the properties of reservoirs (table 1) should increase their susceptibility to invasion relative to natural lakes. Larger reservoirs are extensively manipulated by humans, through controlled water releases for hydropower and flood control. Such drawdowns produce a high degree of disturbance and environmental variability through time. Reservoirs also tend to have a much faster hydrologic flushing rate than natural lakes (Wetzel 1990), and reservoir flushing rates are more variable over time than those of lakes. Fluctuating water levels in flood-control and hydropower reservoirs lead to the death of many vascular plants, to such an extent that the nearshore (littoral) zone tends to be poorly developed (Wetzel 1990). With little root structure for preventing erosion of sediments, winds readily resuspend sediments and nutrients, resulting in considerable turbidity and recycled nutrients for phytoplankton growth.

Reservoirs also have much higher watershed areas relative to their volume than those of natural lakes (Wetzel 1990). As a consequence, reservoirs receive high loads of organic materials, nutrients, and other dissolved solutes relative to natural lakes. Loading results in increased ionic concentration in reservoirs (see discussion of adaptation below). High loading from the watershed also creates an increased potential for eutrophication and related nuisance algal blooms.

Reservoirs are characterized both by a high degree of disturbance and by resource enrichment (eutrophication). On the basis of Davis and colleagues' (2000) FRA hypothesis, we would expect both of these factors (hydrologic disturbance and nutrient loading) to enhance the invasibility of reservoirs. Few studies test aspects of this theory for freshwater systems. An experimental study of *D. lumholtzi* introductions along a nutrient gradient found decreased invader success with nutrient enrichment (Lennon et al. 2003), a result that seems contrary to the FRA hypothesis. Such a result implies that systems that are already productive (eutrophic) may not become any more invasible with further enrichment. Watershed-scale analysis of fish invasions in California revealed positive associations between invaders and anthropogenic landscape

alterations, such as urbanization and hydrological alterations (Marchetti et al. 2004), a result consistent with the FRA hypothesis.

Reservoirs are also spatially heterogeneous in their habitats for colonization. A variety of physiochemical properties exhibit a longitudinal gradient from up-reservoir (riverine) to down-reservoir (lacustrine) zones. For instance, at the riverine end, thermal stratification tends to be unstable, and turbidity and sedimentation rates are high (Thornton et al. 1990). Here, nutrient loading is high and recycling from the sediments provides extra material to supply algal growth. However, the high turbidity often leads to light limitation. In contrast, the lacustrine zone is more similar to natural deep lakes, with high water clarity and pronounced stratification and nutrient limitation during summer (Thornton et al. 1990). Phytoplankton and zooplankton densities and composition also differ along the riverine-to-lacustrine gradient (Wetzel 1990). This spatial and temporal heterogeneity in physiochemical environment and food resources within reservoirs should provide multiple niches for colonizers.

**Species diversity and biotic interactions.** Elton (1958) argued that “natural” ecosystems should be better able to resist invasions than simplified, anthropogenically altered systems. His argument was that the interspecific interactions (predation, competition, and parasitism) within natural systems, which were more intense than in humanmade or human-altered systems, provided a barrier to successful colonization. Studies have subsequently indicated that high species diversity increases the resistance of a community to invaders (Kennedy et al. 2002), although evidence for this relationship remains equivocal (Levine and D'Antonio 1999). There are few tests of this hypothesis for aquatic systems, although Shurin (2000) found that reducing the intensity of interspecific interactions, by experimentally reducing the density and diversity of native species, resulted in increased success for introduced species of zooplankton.

How do reservoirs differ from natural systems in terms of species diversity and biotic interactions? Since reservoirs are recent features on landscapes, we would expect them to be in the early stages of community succession, when the likelihood of successful colonization should be higher (MacArthur and Wilson 1967). We would expect there to be fewer species in reservoirs than in natural lakes. Passively invading zooplankton would make a good test, since these species are typically not deliberately introduced by humans. We would expect there to be fewer species in reservoirs than in natural lakes. Since species richness strongly depends on area (Dodson 1992), the best test would be a comparison of richness across a wide range of sizes of both natural lakes and reservoirs, testing the hypothesis that the slope of the species–area curve for lakes is greater than the slope for reservoirs.

Food web interactions in reservoirs are also likely to differ from those in lakes. Reservoirs are often characterized by a high degree of nutrient and sediment loading and phytoplankton productivity, although high turbidity in some sys-

tems reduces light penetration, thereby limiting algal production (Wetzel 1990) as well as grazing rates on algae and feeding by visual fishes. Furthermore, the fact that reservoirs contain recently assembled stocked fish communities suggests that their food web interactions should be highly unstable (Stein et al. 1995). For example, in central US reservoirs, omnivorous gizzard shad can dominate fish community biomass, exerting strong effects on zooplankton, bluegill, and largemouth bass populations (Stein et al. 1995). Yet high temporal variability in gizzard shad populations is also likely to provide occasional periods when successful establishment of zooplankton invaders is enhanced.

### Reservoirs as havens for adaptation to freshwater environments

Slightly elevated salinities, resulting from higher loading of solutes, offer opportunities for species native to brackish-water habitats to adapt to lower salinities (Lee and Bell 1999) and possibly extend their ranges into natural freshwater lakes. Indeed, reservoirs located in arid climates commonly have average salinity levels (i.e., conductivity of approximately 1000 microsiemens [ $\mu\text{S}$ ] per centimeter [ $\text{cm}$ ]) about five times higher than those typical of natural lakes. Although this salinity is considerably lower than that of seawater (approximately 43,000  $\mu\text{S}$  per  $\text{cm}$ ), the range in some lakes extends to hypersaline conditions (Wetzel 2001).

Some freshwater invaders are recent immigrants from saline habitats. The construction of canals and reservoirs provided transport pathways and habitats for a wide variety of exotic invertebrates from the Ponto-Caspian seas to invade Europe (Jazdzewski 1980, Lee and Bell 1999). Many of these invaders, including zebra mussels, have reached brackish waters of the Baltic Sea and subsequently invaded the Great Lakes of North America (Ricciardi and MacIsaac 2000). Another example of a saline invader is the coastal copepod *Eurytemora affinis*. This copepod is broadly distributed in saline estuaries and salt marshes in the Northern Hemisphere, and has repeatedly invaded fresh water within the past century (figure 2; Lee 1999). These invasions occurred through various means, such as the impoundment of saline water bodies followed by reduction in salinity, the incidental introduction of the copepods with sport fish, and possibly the release of bilge and ballast water (see Lee 1999).

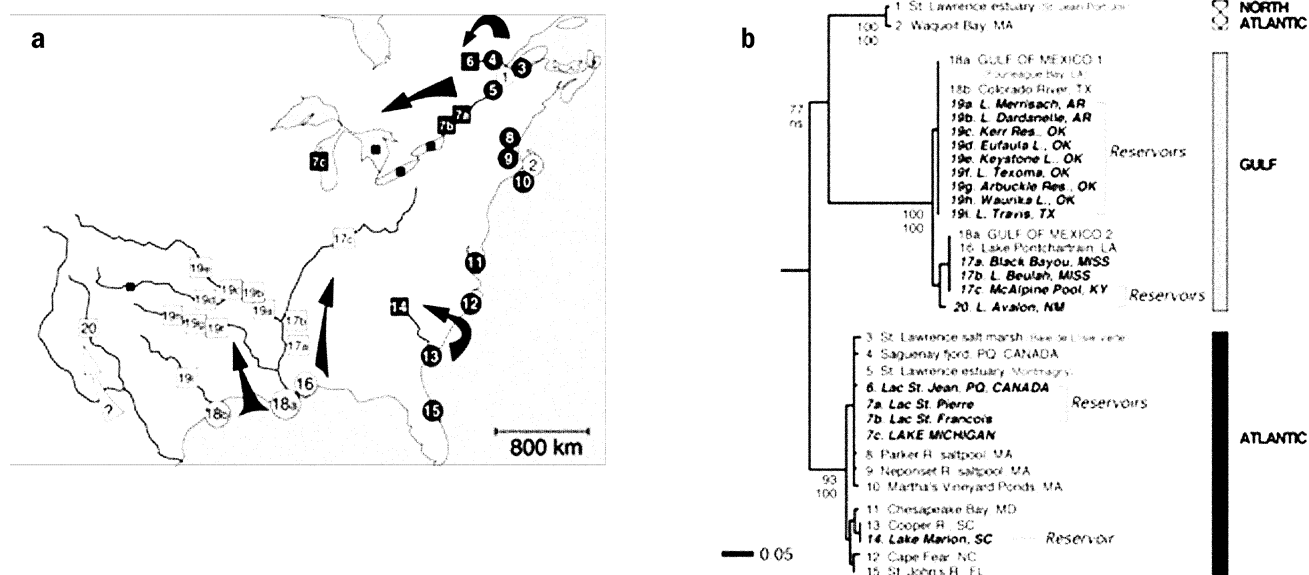
Genetic analysis has shown that invasions of reservoirs by *E. affinis* occurred multiple times independently from genetically distinct coastal source populations (figure 2b; Lee 1999). Once a population invades a drainage system, dispersal proceeds rapidly among the interconnected reservoirs (figure 2). For example, populations containing one mitochondrial haplotype spread to at least eight reservoirs within the Mississippi River drainage within decades of reservoir construction, indicating dispersal among these reservoirs from a common source (figure 2; Lee 1999). In fact, all freshwater habitats in which *E. affinis* is known to occur are connected to a river system or a marine bay, and consist predominantly of reservoirs (Lee 1999).

Numerous invaders from brackish-water habitats are likely to undergo natural selection on physiological tolerance and performance following invasion into reservoirs. Many invaders from the Ponto-Caspian Basin, such as zebra mussels (Dietz et al. 1986) and the amphipod *Corophium curvispinum* (Taylor and Harris 1986), are poor osmoregulators compared with native freshwater species. In the case of *E. affinis*, freshwater invasions occurred through natural selection and evolutionary shifts in osmotic tolerance (Lee et al. 2003), rather than through acclimation or broad tolerance. Thus, reservoirs, with their slightly elevated salinities, could provide havens for adaptation to freshwater habitats (Lee 2002).

### Reservoirs as stepping-stones for invading landscapes

Once a population is established in a new landscape via long-distance dispersal, it can serve as a stepping-stone for further invasions. Theoreticians have pointed out that such processes (known as stratified diffusion) greatly enhance invasion rates (Shigesada and Kawasaki 1997). Can reservoirs serve as stepping-stones for freshwater exotics? The rapid invasion of the cladoceran *D. lumholtzi* into reservoirs across the United States (figure 1) has provided populations that could supply inocula for natural lakes. Adaptation to lower temperatures may have allowed its subsequent invasion of the Great Lakes. Similarly, the adaptation of *E. affinis* to intermediate osmotic concentrations in reservoirs may provide opportunities for this species to invade freshwater habitats. Another zooplankton that has invaded natural lakes may also be able to use a reservoir to jump into a new landscape. The spiny water flea, *Bythotrephes longimanus*, is native to much of Eurasia and invaded the Laurentian Great Lakes in the early 1980s. By 2003, *B. longimanus* had been reported in inland lakes in five adjacent states and provinces (MacIsaac et al. 2000). Once *B. longimanus* colonizes an inland system, it can spread rapidly to nearby lakes via boat movement. Interestingly, this species rarely makes long-distance jumps ( $> 150$  km) across the landscape (MacIsaac et al. 2004), indicating poor long-distance dispersal ability. The recent invasion of this species into a reservoir in northern Wisconsin (Pieter Johnson, University of Wisconsin, Madison, personal communication, 21 April 2005) increases its potential for invading a landscape with thousands of natural lakes (<http://limnosun.limnology.wisc.edu>).

The widespread creation of reservoirs on a global scale has provided potential stepping-stones for invasion by a variety of nuisance species. Reservoirs may play a role in facilitating the spread of passively dispersing nuisance exotic plants such as Eurasian watermilfoil and *Hydrilla* in North America. Both reservoirs and natural lakes can be heavily invaded with these exotic weeds, so increasing the area of standing water may accelerate their spread across landscapes. Reservoirs have also been linked to parasitic disease. Reservoirs have facilitated the spread of the *Schistosoma* parasite by greatly expanding its habitat and allowing the spread of this parasite's snail host (Morgan et al. 2001). The consequence has been an increased incidence of deadly schistosomiasis throughout



**Figure 2.** Invasions by the copepod *Eurytemora affinis* from saline sources into freshwater reservoirs. (a) Geographic pathways of invasions within North America. Circles represent saline populations and squares represent freshwater populations. Names of sites and clades are shown in (b); patterns of circles and squares correspond to genetically distinct clades. Arrows indicate independent invasions into freshwater habitats. Small black squares are reservoir populations that have not been genotyped. Details on the timing of invasions are presented in Lee (1999). (b) Phylogeny showing genetic relationships among source and invading populations of *E. affinis* (based on 652 base pairs of the COI gene). Freshwater populations, which occur primarily in reservoirs, are shown in bold and italics. Branch lengths reflect genetic distance (maximum likelihood), with scale bar indicating 5 percent genetic distance. Phylogeny indicates that invasions into fresh water occurred rapidly and repeatedly from genetically distinct saline sources. Adapted from Lee (1999, 2000).

the tropics, where it affects 200 million people. The link between reservoir construction and the spread of disease to new regions is an important area for future research. The bloom-forming cyanobacterium *Cylindrospermopsis* has rapidly expanded its range from India into the tropical and temperate waters of Africa, Europe, the Americas, and Australia. Strains of this species have been reported to produce potent toxins, dangerous to both humans and livestock, and the deep-dwelling (metalimnetic) algae are sometimes difficult to detect. *Cylindrospermopsis* is closely associated with reservoirs (Bouvy et al. 2000), so it is important to assess whether reservoirs are facilitating their global spread.

Reservoirs have also prevented the spread of at least some exotic species, since dams act as important barriers to dispersal by fishes. The presence of low-head dams prevents upstream migration and reproduction of the exotic (and highly destructive) sea lamprey in tributary streams of the Great Lakes (Dodd et al. 2003). The presence of dams may also retard the dispersal of several introduced Asian carp species invading large rivers of the midwestern United States. In sum, dams may interfere with some species migrating through waterways, while their impounded reservoirs provide new habitats for invaders capable of reaching them.

### Directions for future research

Our discussion of passive invasions in reservoir systems aims to promote research at the interface of two major threats to flowing-water ecosystems: widespread hydrological alterations and the rapid spread of exotic species (Kolar and Lodge 2000). Most major river systems have been extensively modified by humans, and the many costs and benefits of reservoirs are well known (Rosenberg et al. 2000, Malmqvist and Rundle 2002). However, the ways in which these two human impacts on natural ecosystems interact are currently unknown, and the outcomes are likely to be complex and highly context dependent. We have argued that construction of reservoirs is likely to increase invasions of exotic species into freshwater habitats. Reservoirs provide stepping-stones into new landscapes, particularly in arid regions, where standing water is less abundant. We expect that the high connectivity among reservoirs should enhance dispersal into other reservoirs and eventually into natural aquatic landscapes.

**Invasibility.** We have further hypothesized that the high level of physical disturbance, solute loading, and unstable food webs should enhance the invasibility of reservoirs over that of natural lakes. Do invasions of reservoirs occur at higher rates than

invasions of natural lakes? Unfortunately, few empirical data are available to allow a test of this hypothesis. The principal problem with studies to date is that invasions of reservoirs and those of lakes have been conducted in different geographic regions. We would predict that, in landscapes with a combination of lakes and reservoirs, invasions would occur at higher rates in reservoirs than in lakes. The northern prairie region of the United States and Canada is one place where such a comparison could be made. In addition, we have few comparative data on patterns of species richness between natural lakes and reservoirs. We thus cannot compare invasibility as a function of species richness in the two types of water bodies. Further data on richness of exotic and native fauna from regions with high concentrations of both reservoirs and natural lakes would be particularly helpful to address these questions.

**Evolutionary ecology of reservoir invasions.** Reservoirs are artificial and unstable habitats analogous to disturbed terrestrial habitats, such as agricultural fields and industrial landscapes. Disturbed terrestrial habitats tend to be colonized by ruderal and weedy species that are adapted to disturbance (Altieri and Liebman 1988). Reservoirs might also be dominated by such species assemblages. For example, zebra mussels are successful as early colonizers, but tend to become displaced by quagga mussels over time (Mills et al. 1999). To what extent are reservoirs colonized by populations that are preadapted to disturbance, and to what degree do conditions in reservoirs promote the evolution of ruderal species? What characteristics evolve in response to the nonequilibrium conditions in reservoirs: elevated levels of phenotypic plasticity or elevated levels of genetic variance for phenotypic traits? Are specific traits selected for in reservoirs? What effect would adaptation in reservoirs have on subsequent range expansions? Addressing these questions requires further research on the community ecology, physiological performance, and genetic architecture of reservoir populations.

## Conclusions

Developing an understanding of the linkages between reservoirs and the passive invasion of exotic species provides a broader perspective on the widespread impacts of human alteration of natural flow regimes. The ultimate impact of reservoirs on dispersal of invasive species will depend on landscape context and the spatial positioning of aquatic habitats. Reservoirs may be located in such a way as to bridge gaps between standing-water systems, thus facilitating movement across landscapes, by homogenizing habitats and serving as stepping-stones for invasive species. As is the case with zebra mussels, reservoirs have vast potential to alter source-sink dynamics and can provide the critical upstream conditions that sustain downstream populations of invaders.

## Acknowledgments

Partial support for this synthesis was provided by a sabbatical leave to J. E. H. from Southwest Missouri State University,

The Wisconsin Sea Grant Institute and the National Science Foundation (DEB-0130543) provided support to C. E. L. The Wisconsin Department of Natural Resources provided support to M. J. V. Z. We thank Stanley Dodson, Jack Jones, David Strayer, and two anonymous reviewers for comments on earlier versions of this paper.

## References cited

- Allen YC, Ramcharan CW. 2001. *Dreissena* distribution in commercial waterways of the US: Using failed invasions to identify limiting factors. Canadian Journal of Fisheries and Aquatic Sciences 58: 898–907.
- Altieri MA, Liebman MZ. 1988. *Weed Management in Agroecosystems: Ecological Approaches*. Boca Raton (FL): CRC Press.
- Bouvy M, Falcao D, Marinho M, Pagano M, Moura A. 2000. Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. Aquatic Microbial Ecology 23: 13–27.
- Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology 88: 528–534.
- Dietz TH, Wilcox SJ, Byrne RA, Lynn JW, Silverman H. 1986. Osmotic and ionic regulation of North American zebra mussels (*Dreissena polymorpha*). American Zoologist 36: 364–372.
- Dodd HR, Hayes DB, Baylis JR, Carl LM, Goldstein JD, McLaughlin RL, Noakes DL, Porto LM, Jones ML. 2003. Low-head sea lamprey barrier effects on stream habitat and fish communities in the Great Lakes basin. Journal of Great Lakes Research 29 (suppl. 1): 386–402.
- Dodson SI. 1992. Predicting crustacean zooplankton species richness. Limnology and Oceanography 37: 848–856.
- Elton CS. 1958. *The Ecology of Invasions by Animals and Plants*. Chicago: University of Chicago Press.
- Havel JE, Hebert PDN. 1993. *Daphnia lumholtzi* from North America: Another exotic zooplankton. Limnology and Oceanography 38: 1823–1827.
- Havel JE, Shurin JB. 2004. Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnology and Oceanography 49: 1229–1238.
- Havel JE, Stelzleni-Schwent J. 2000. Zooplankton community structure: The role of dispersal. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 27: 3264–3268.
- Havel JE, Mabee WR, Jones JR. 1995. Invasion of the exotic cladoceran *Daphnia lumholtzi* into North American reservoirs. Canadian Journal of Fisheries and Aquatic Sciences 52: 151–160.
- Havel JE, Eisenbacher EM, Black AA. 2000. Diversity of crustacean zooplankton in riparian wetlands: Colonization and egg banks. Aquatic Ecology 34: 63–76.
- Jazdzewski K. 1980. Range extensions of some gammaridean species in European inland waters caused by human activity. Crustaceana 6 (suppl.): 84–107.
- Johnson LE, Carlton JT. 1996. Post-establishment spread in large-scale invasions: Dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. Ecology 77: 1686–1690.
- Johnson LE, Padilla DK. 1996. Geographic spread of exotic species: Ecological lessons and opportunities from the invasion of the zebra mussel *Dreissena polymorpha*. Biological Conservation 78: 23–33.
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P. 2002. Biodiversity as a barrier to ecological invasion. Nature 417: 636–638.
- Kolar CS, Lodge DM. 2000. Freshwater nonindigenous species: Interactions with other global changes. Pages 3–30 in Mooney HA, Hobbs RJ, eds. *Invasion Species in a Changing World*. Washington (DC): Island Press.
- . 2001. Progress in invasion biology: Predicting invaders. Trends in Ecology and Evolution 16: 199–205.
- Kraft CE, Sullivan PJ, Karatayev AY, Burlakova YE, Nekola JC, Johnson LE, Padilla DK. 2002. Landscape patterns of an aquatic invader: Assessing dispersal extent from spatial distributions. Ecological Applications 12: 749–759.
- Lee CE. 1999. Rapid and repeated invasions of fresh water by copepod *Eurytemora affinis*. Evolution 53: 1423–1434.

- . 2000. Global phylogeography of a cryptic copepod species complex and reproductive isolation between genetically proximate “populations.” *Evolution* 54: 2014–2027.
- . 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* 17: 386–391.
- Lee C, Bell M. 1999. Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology and Evolution* 14: 284–288.
- Lee CE, Remfert JL, Gelembiuk GW. 2003. Evolution of physiological tolerance and performance during freshwater invasion events. *Integrative and Comparative Biology* 43: 439–449.
- Lennon JT, Smith VH, Dzialowski AR. 2003. Invasibility of plankton food webs along a trophic state gradient. *Oikos* 103: 191–203.
- Levine JM, D’Antonio CM. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* 87: 15–26.
- MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton (NJ): Princeton University Press.
- MacIsaac HJ, Ketelaars HAM, Grigorovich IA, Ramcharan CW, Yan ND. 2000. Modeling *Bythotrephes longimanus* invasions in the Great Lakes basin based on its European distribution. *Archiv für Hydrobiologie* 149: 1–22.
- MacIsaac HJ, Borbely JVM, Muirhead JR, Graniero PA. 2004. Backcasting and forecasting biological invasions of inland lakes. *Ecological Applications* 14: 773–783.
- Malmqvist B, Rundle S. 2002. Threats to the running water ecosystems of the world. *Environmental Conservation* 29: 134–153.
- Marchetti MP, Light T, Moyle PB, Viers JH. 2004. Fish invasions in California watersheds: Testing hypotheses using landscape patterns. *Ecological Applications* 14: 1507–1525.
- Mills EL, Chrisman JR, Baldwin B, Owens RW, O’Gorman R, Howell T, Roseman EG, Raths MK. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *Journal of Great Lakes Research* 25: 187–197.
- Morgan JAT, Dejong RJ, Snyder SD, Mkoji GM, Loker ES. 2001. *Schistosoma mansoni* and *Biomphalaria*: Past history and future trends. *Parasitology* 123: S211–S228.
- Muzinic CJ. 2000. First record of *Daphnia lumholtzi* Sars in the Great Lakes. *Journal of Great Lakes Research* 26: 352–354.
- Orians GH. 1986. Site characteristics favoring invasions. Pages 133–148 in Mooney HA, Drake JA, eds. *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Rahel FJ. 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33: 291–315.
- Ricciardi A, MacIsaac HJ. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology and Evolution* 15: 62–65.
- Rosenberg DM, McCully P, Pringle CM. 2000. Global-scale environmental effects of hydrological alterations: Introduction. *BioScience* 50: 746–751.
- Shigesada N, Kawasaki K. 1997. *Biological Invasions: Theory and Practice*. New York: Oxford University Press.
- Shurin JB. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81: 3074–3086.
- Shurin JB, Havel JE. 2002. Hydrologic connections and overland dispersal in an exotic freshwater crustacean. *Biological Invasions* 4: 431–439.
- Sorensen KH, Sterner RW. 1992. Extreme cyclomorphosis in *Daphnia lumholtzi*. *Freshwater Biology* 28: 257–262.
- Stein RA, DeVries DR, Dettmers JM. 1995. Food-web regulation by a planktivore: Exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2518–2526.
- Taylor PM, Harris RR. 1986. Osmoregulation in *Corophium curvispinum* (Crustacea: Amphipoda), a recent coloniser of freshwater, I: Sodium ion regulation. *Journal of Comparative Physiology, B* 156: 323–329.
- Thornton KW, Kimmel BL, Payne FE, eds. 1990. *Reservoir Limnology: Ecological Perspectives*. New York: John Wiley and Sons.
- Van den Brink FWB, Van Katwijk MM, Van der Velde G. 1994. Impact of hydrology on phyto- and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse. *Journal of Plankton Research* 16: 351–373.
- Wetzel RG. 1990. Reservoir ecosystems: Conclusions and speculations. Pages 227–238 in Thornton KW, Kimmel BL, Payne FE, eds. *Reservoir Limnology: Ecological Perspectives*. New York: John Wiley and Sons.
- . 2001. *Limnology: Lake and River Ecosystems*. San Diego: Academic Press.
- Zanata LH, Espíndola ELG, Rocha O, Pereira R. 2003. First record of *Daphnia lumholtzi* (Sars, 1885), exotic cladoceran, in São Paulo state (Brazil). *Brazilian Journal of Biology* 63: 717–720.