



## Hydrologic connections and overland dispersal in an exotic freshwater crustacean

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### Abstract

Organisms living in lakes face the problem of dispersing through an uninhabitable matrix in order to reach suitable habitat. One possible mechanism for moving between lakes is by surface water connections. We used a seven-year data set to investigate the spread of the exotic cladoceran *Daphnia lumholtzi* among Missouri reservoirs with respect to stream connections. Reservoirs that were downstream of known populations of *D. lumholtzi* were more likely to become invaded than those that were not. However, invasion likelihood was only weakly related to the presence of upstream source populations, and reservoirs without potential upstream sources were colonized at a rate of 7.3% per year. The difference in invasion rate between lakes with and without upstream sources varied among years, and was significant in only two of the six years of study. In addition, the higher invasion rate of downstream lakes could be explained by their greater surface area. These patterns suggest that surface water connections may form one means of dispersal for *D. lumholtzi*, although overland movement is also important. The ability to utilize several modes of dispersal may explain the rapid expansion of this species' range since its arrival in North America.

### Introduction

Living in discrete habitat patches such as lakes and islands poses the problem of dispersal for many organisms. The terrestrial matrix can form a significant barrier to movement and constrain the number or identity of species found in a particular local habitat (Wiens 2001). Dispersal appears to be particularly problematic for aquatic species such as fish or zooplankton that have no obvious means of moving between lakes. Because of the potential difficulty of dispersal, the ability to colonize a site may be important for limiting species distributions, local diversity, or the spread of invasive species.

Three lines of evidence suggests that dispersal may strongly limit zooplankton distributions. First, genetic variation among freshwater crustacean populations suggests low levels of gene flow as even nearby

lakes show strong among-site differentiation (Boileau and Hebert 1991; Boileau et al. 1992; De Meester 1996). Second, Jenkins and Buikema (1998) found that 57 species of rotifers and crustaceans colonized 12 newly constructed experimental ponds in one year, indicating that dispersal events for many species occur on the order of weeks to months. However, the 12 ponds differed considerably from one another in species composition, suggesting that species were unable to reach all of the ponds. Finally, a global-scale survey of local and regional crustacean taxonomic richness found that local richness increased as a linear function of the size of the regional species pool (Shurin et al. 2000). Such patterns may suggest that dispersal, and not local interactions, places upper limits on local richness (Cornell and Lawton 1992). Dispersal may therefore play a major role in structuring zooplankton populations and communities.

However, alternative explanations may be invoked to account for all of the above results. For instance, if lakes vary in their selective environments, then local adaptation may provide an alternative explanation for high genetic differentiation (De Meester 1996; DeClerck et al. 2001). Second, the large differences in species composition among ponds observed by Jenkins and Buikema (1998) may arise because local communities set up barriers to colonization early in the assembly process. A transplant experiment supporting this interpretation (Shurin 2000) found that 11 natural fishless pond communities resisted invasion by >90% of the species in the regional pool. Biotic interactions played a major role in repelling invaders as perturbing the local community promoted colonization by many species that were otherwise excluded. Finally, predator-mediated coexistence may give rise to linear patterns of local and regional diversity by promoting species coexistence at both local and regional scales (Shurin and Allen 2001). The importance of dispersal for generating geographic patterns in community structure and genetic variation in zooplankton therefore remains an open question.

One reason so little is known about the importance of dispersal in zooplankton is that the mechanisms by which these species move among lakes is poorly understood. Several classic studies showed that animal vectors, particularly birds, are capable of carrying viable zooplankton resting stages (Proctor 1964; Proctor and Malone 1965; Proctor et al. 1967). Some evidence for wind dispersal has been reported (Jenkins and Underwood 1998; Brendonck and Riddoch 1999; Cohen and Shurin, under review); however, the importance of wind relative to other mechanisms remains unknown. Recreational boats have been shown to move aquatic weeds among distant lakes (Johnstone et al. 1985) and recent evidence suggests that boaters move live zooplankton as well (Havel and Stelzleni-Schwent 2000). In addition, diapausing stages of many species may be transported by humans or surface water. The dormant eggs of many species have long been assumed to be the primary stage for dispersal (Maguire 1963; Pennak 1978). Patterns of post-glacial colonization suggest that some species (particularly copepods) may have used rivers as dispersal corridors (Stemberger 1995). In addition, the exotic cladoceran *Daphnia lumholtzi* Sars has been shown to sustain viable populations in large rivers (Thorpe et al. 1994; Stoeckel et al. 1996). Flowing water may therefore be an important vector for the dispersal of this and other species.

In the present study, we examined patterns in the invasion of Missouri reservoirs by *D. lumholtzi* over seven years to ask whether surface water connections promote the spread of this species. *D. lumholtzi* was first reported from a Texas lake in 1990 (Sorensen and Sterner 1992), and expanded its range rapidly in the US over the next ten years (Havel and Hebert 1993; Havel et al. 1995; Muzinic 2000). During the seven years of the current study, the cumulative prevalence of *D. lumholtzi* increased from 6% to 34% in 153 Missouri lakes. Previous work (Havel et al. 2002) found that invasion likelihood was positively related to lake surface area, epilimnetic temperature, and geographic proximity to source populations. The present study combined the data on the incidence of *D. lumholtzi* in these lakes with geographic data on hydrologic connections to ask whether lakes downstream of known populations of *D. lumholtzi* were more likely to become invaded than ones that were not. If movement via surface water is an important mode of transport, then we expect invasion probability to be greater for lakes that receive surface water flow from invaded lakes. Alternatively, if overland or upstream movement (perhaps via wind, birds, or humans) are most important, then we expect invasion likelihood to be unrelated to the presence of upstream sources.

## Methods

Most reservoirs were sampled yearly during 1992–1998, while 16 floodplain lakes were sampled only in 1994 and 1995. All samples were collected in daylight hours, during July and August, the period when *D. lumholtzi* is most abundant in this region (Havel et al. 1995). Zooplankton samples were collected with two or more vertical tows (total length 20 m), using a 25 cm diameter zooplankton net (mesh = 200  $\mu$ m). The tows were pooled into one sample and preserved with buffered sugar–formalin. The entire sample from each site was screened for the presence of *D. lumholtzi* at 30 $\times$ , using the characteristics illustrated in Havel and Hebert (1993).

We used ArcView v. 3.2 (1999) to create a Geographical Information System (GIS) to establish the pattern of surface water connections between the reservoirs in our survey, as well as the direction of flow. Hydrologic connections were determined from stream coverages for the state of Missouri using Census TIGER 1995 stream line files (<http://www.esri.com/>).

After downloading all the files for each county, the maps were merged to create a continuous stream line coverage for the entire state. The lakes fell within three major drainage basins: the Mississippi, Missouri, and White River basins. Some lakes were reservoirs or oxbows on major rivers that receive flow from many watersheds, while others were on low order streams that drain surface water from much smaller areas (Figure 1). For each lake, all upstream lakes in the survey were identified. In addition, we used GIS to identify whether each lake received surface water from any upstream lakes that were not sampled as a part of our survey, but that were apparent in the GIS. Each sampled lake was then classified for each year as either downstream or not from any other lakes in the GIS. Of the 153 lakes in the survey, 83 were not downstream of any other lake. Figure 2 shows the progression of the invasion during the study along with watershed boundaries.

We tested whether the probability that *D. lumholtzi* colonized lakes varied among three categories of lakes: (1) lakes not downstream of any other lake that was apparent in the GIS, (2) lakes downstream of other lakes without known *D. lumholtzi* populations, and (3) lakes downstream of known source populations. We distinguished between categories 1 and 2 because lakes may have been downstream of invaded lakes that we did not sample. Category 2 includes both lakes that were sampled where *D. lumholtzi* was not detected and ones that were not sampled. Any previously-sampled lake where *D. lumholtzi* was not found was considered susceptible to invasion. All lakes where *D. lumholtzi* was found in any earlier year were considered potential sources of colonists for all subsequent years. Although the species sometimes disappeared from lakes where it was previously found (Figure 2), we assumed that lakes with the species present could provide propagules to other lakes in every year after the first year in which

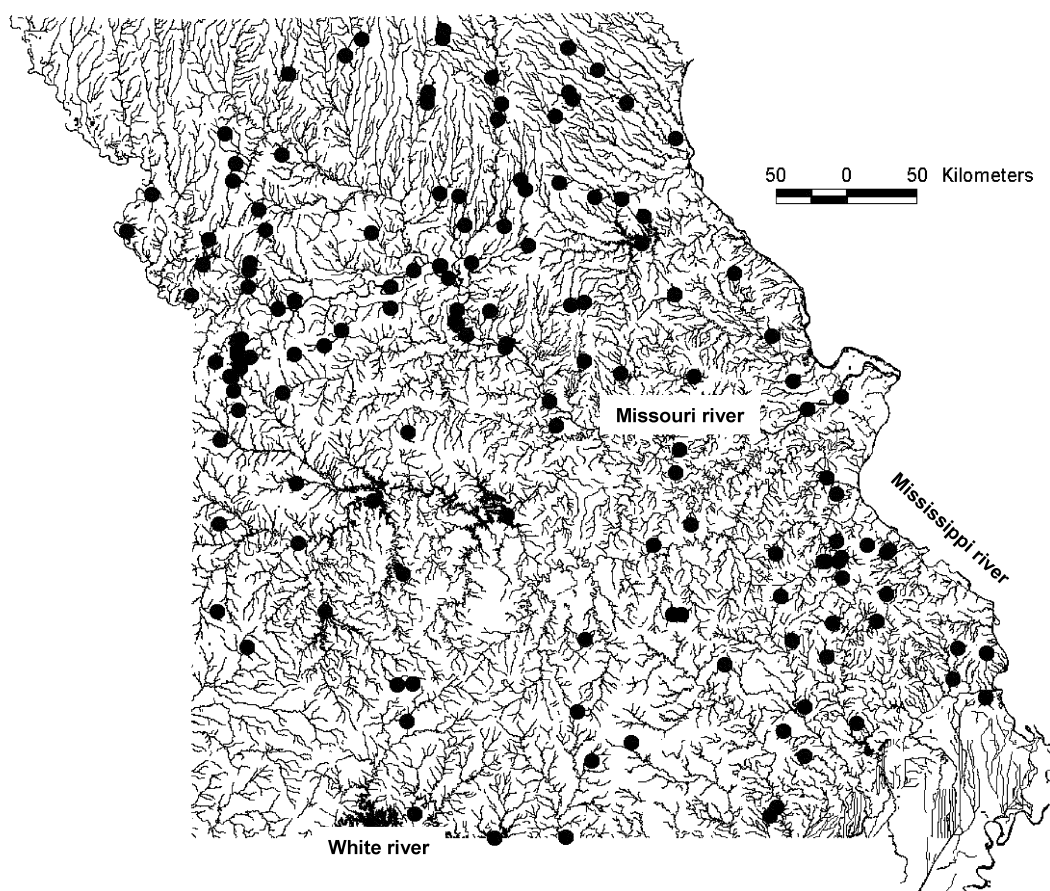


Figure 1. Map of the 153 Missouri (USA) lakes in the survey (circles) and their river and stream connections.

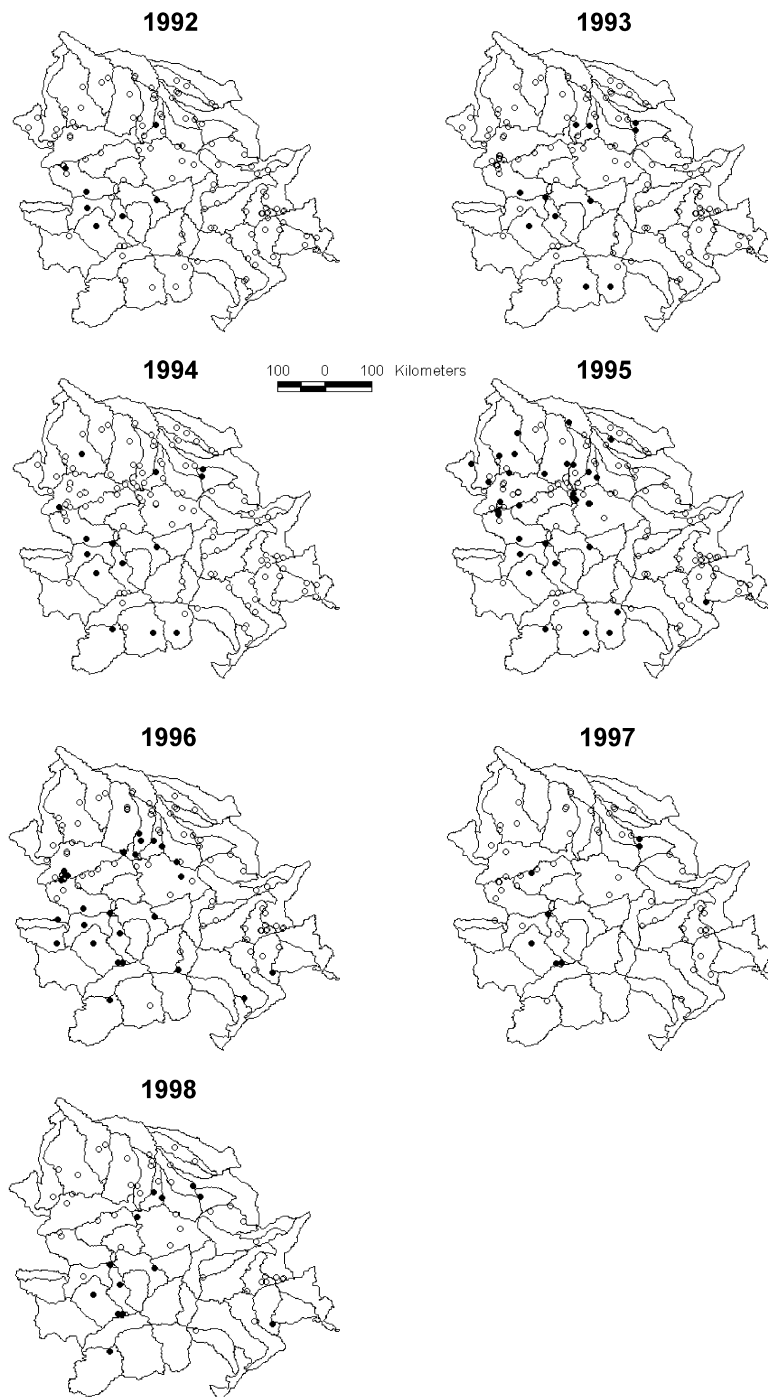


Figure 2. Map showing the watershed boundaries (dark lines) and the location of the lakes (circles) sampled in each year. Lakes where *D. lumholtzi* was found are solid black circles and uninfected lakes are open circles. Lakes fell within 48 separate watersheds.

*D. lumholtzi* was detected. We made this assumption because *D. lumholtzi* produces viable dormant eggs (J.E. Havel, pers. obs.) that may persist in the sediments for many years (Cáceres 1998). Lakes with a dormant population but without planktonic individuals could potentially export resting eggs, and were therefore considered potential sources of colonists. In addition, individuals may have been present at densities below the detection limits of our sampling regime ( $1/m^3$ ).

To test whether the three categories of lakes differed in their likelihood of invasion, we used a three-by-two contingency table with a Fisher's exact test (Sokal and Rohlf 1995). In each year, we identified all susceptible lakes in the survey (those with no known population in any previous year). GIS was used to identify lakes that were downstream from potential source populations, or from lakes that were not sampled. We then determined the numbers of susceptible lakes in each of the three categories where *D. lumholtzi* was detected for each year after 1992, the first year of sampling. The categories in the contingency table were therefore lake type (three categories) and the presence or absence of *D. lumholtzi* (two categories). We also analyzed data for all susceptible lakes grouped together for the six years of study. Because there were a total of 439 susceptible lake-years (potential invasions), a chi-square test was used to test differences among the three lake categories for the pooled data, rather than a Fisher's Exact test as in the individual years (Sokal and Rohlf 1995). If surface waters are important routes for dispersal of *D. lumholtzi*, then we expect to find a significant dependence of invasion probability on the presence of upstream sources. Because we predicted that upstream sources would increase invasion likelihood, one-tailed tests of significance were used.

Because lakes with low landscape positions tend to be larger, we also analyzed whether any apparent effects of hydrologic connectivity could be explained by lake surface area. Lake surface area and hydrologic connectivity category were entered together into multiple logistic regression models to predict which susceptible lakes became invaded in each year. If statistical effects of stream connections to source populations are really due to correlation between landscape position and surface area, then adding hydrologic connectivity should not improve the fit of the model relative to that with only surface area. Alternatively, if river connections promote dispersal by *D. lumholtzi*, then

connectivity should have effects on invasion likelihood that are independent from those of surface area.

## Results

Lakes downstream of known populations of *D. lumholtzi* were more likely to be invaded than those not downstream from source lakes, as well as those downstream of lakes outside the survey (Figure 3). This result was evident in every year except 1994 when only three new invasions were recorded, none of which were downstream of potential sources. The probability of invasion differed significantly among the three categories of lakes in 1993 and 1996, but not in the other individual years (Figure 3). The rate of invasion for downstream lakes varied from 0% in 1994 to 50% in 1998, with downstream lakes having an overall average probability of invasion of 26.7% per year (8/30 lake-years invaded). The rate of invasion for lakes downstream of lakes either without *D. lumholtzi* or outside of the survey (category 2) ranged from 0% (1997 and 1998) to 20.7% (1995), with an overall average of 8.2% (12/147 lake-years, Figure 3). For lakes with no possible upstream source lakes (i.e. that did not receive

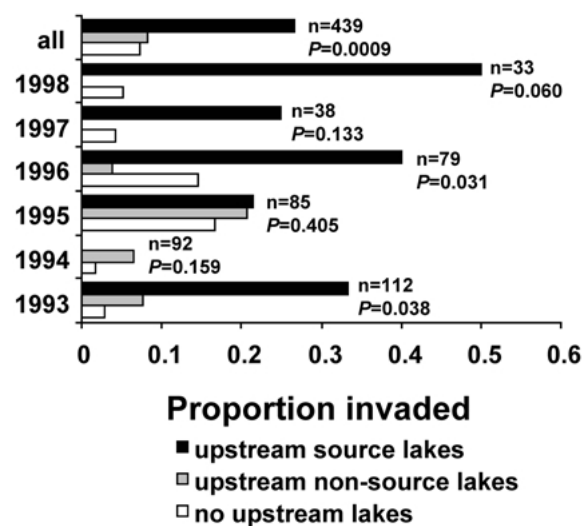


Figure 3. Proportion of susceptible lakes colonized by *D. lumholtzi* that were downstream of known source populations (black bars), downstream of lakes either without *D. lumholtzi* or not in the survey (gray bars) and not downstream of any other lakes (white bars) for 1993–98. One-tailed *P*-values are based on a three-by-two contingency table with a Fisher's exact test (individual years) or a chi-square test (combined data). 'n' is the number of susceptible lakes sampled.

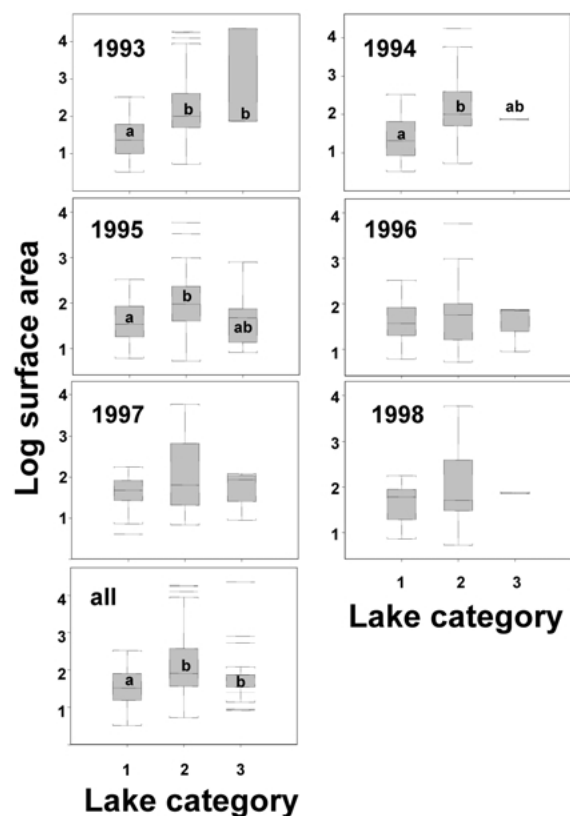


Figure 4. Box plots of lake surface area by connectivity category for each year and for all six years together. Category 1 is no upstream lakes, 2 is with upstream non-source lakes, and 3 is with upstream source lakes. Letters indicate significant differences between connectivity categories as indicated by Tukey's test.

surface water from any other lakes), the rate of invasion ranged from 1.7% (1994) to 16.7% (1995) and averaged 7.3% (19/262) among years. When data from all 439 susceptible lake-years are analyzed together, the three lake categories differed significantly in their probability of invasion (one tailed  $P = 0.0009$ , Figure 3). Lakes downstream from sources were the most likely to become invaded (Figure 3).

Lakes without upstream sources were generally smaller than those downstream of other lakes, although the difference in surface area among hydrologic connectivity categories varied between years (Figure 4). When included along with surface area in multiple logistic regression models to predict invasion, the presence of upstream source populations was not a significant predictor of invasion (Table 1). Thus, the apparent effect of hydrologic connectivity (Figure 3) could be explained as a consequence of lake surface area.

Table 1. Results of logistic regression analyses to predict invasion of *D. lumholtzi* based on surface area and hydrologic connectivity to source populations.

Source	Coefficient	<i>t</i>	<i>P</i>
<i>1993</i>			
Constant	-7.57	-4.37	<0.0001
Area	2.23	2.87	0.004
Connectivity	-1.12	-0.82	0.41
<i>1994</i>			
Constant	-8.37	-3.36	0.0008
Area	2.52	2.21	0.03
Connectivity	-1.42	0.70	0.48
<i>1995</i>			
Constant	-1.61	-1.90	0.06
Area	-0.009	-0.02	0.98
Connectivity	0.31	0.79	0.43
<i>1996</i>			
Constant	-2.53	-2.14	0.03
Area	0.39	0.58	0.56
Connectivity	-0.42	-0.62	0.54
<i>1997</i>			
Constant	-4.34	-1.89	0.06
Area	0.42	0.40	0.69
Connectivity	0.95	1.00	0.32
<i>1998</i>			
Constant	-3.72	-1.56	0.12
Area	0.05	0.04	0.97
Connectivity	1.25	1.14	0.26
<i>All</i>			
Constant	-3.85	-8.21	<0.0001
Area	0.69	3.07	0.002
Connectivity	0.36	1.24	0.22

The independent variable 'connectivity' is a categorical variable with three levels referring to the lake's position within the river network. The three levels of connectivity are (1) no upstream lakes, (2) upstream lakes without known populations of *D. lumholtzi*, and (3) upstream lakes with known populations of *D. lumholtzi*. Entering connectivity into the model before surface area did not qualitatively affect the conclusions (i.e. connectivity was never significant when area was in the model, regardless of the order in which the variables were entered).

## Discussion

The patterns of spread of *D. lumholtzi* among Missouri reservoirs suggest that surface water connections may form one route for the dispersal of this species. *D. lumholtzi* spread rapidly among lakes over seven years, increasing its cumulative prevalence from 6% to 34% of the reservoirs sampled (Havel et al. 2002). Reservoirs downstream from potential source populations were more likely to be invaded, although the effect of connectivity varied among years

(Figure 3). Large rivers such as the Ohio and Illinois can sustain viable populations of *D. lumholtzi* (Sorensen and Sterner 1992; Thorp et al. 1994), suggesting that rivers may transport live individuals as well as resting stages. Indeed, floodplain lakes along the Missouri River were rapidly invaded by *D. lumholtzi* following the Great Midwest Flood of 1993 (Havel et al. 2000). Nevertheless, the rate of invasion of downstream lakes was quite variable among years (Figure 3), averaging 26.7% across the survey. The upstream presence of source populations therefore does not insure that a lake will be colonized.

The frequent invasion of lakes high in the landscape with no potential upstream sources indicates that mechanisms of dispersal other than rivers also play an important role. Other modes of dispersal for *D. lumholtzi* may include transport via birds, humans, or wind. The resting stages of some species have been shown to remain viable after passing through the digestive tracts of birds (Proctor 1964; Proctor and Malone 1965; Proctor et al. 1967). Humans are known or suspected to be major agents of dispersal for many aquatic invasive species (Johnstone et al. 1985; Carlton and Geller 1993; Schneider et al. 1998; Buchan and Padilla 1999) and it is likely that *D. lumholtzi* is transported by human traffic as well. *D. lumholtzi* can survive for several days in the live wells of recreational boats, a period during which many boats travel among distant reservoirs (Havel and Stelzleni-Schwent 2000). Dzialowski et al. (2000) provide support for the importance of boaters as isolated ponds in Kansas with no human visitors were never invaded by *D. lumholtzi* whereas reservoirs with boat traffic were frequently invaded. However, it is also possible that small lakes are less invasible to *D. lumholtzi* than reservoirs because of differences in the local environment. Transport via birds or boaters could explain the invasions in our survey of headwater lakes that do not receive surface water flow from any other lakes.

The apparent effect of hydrologic connectivity on the spread of *D. lumholtzi* (Figure 3) could be explained as a consequence of the correlation between landscape position and lake surface area (Table 1). Downstream lakes tended to be larger, although the difference among hydrologic categories in surface area varied among years (Figure 4). Including connectivity along with surface area did not significantly improve the fit of multiple regression models to predict invasion in any of the years, or in the combined data (Table 1). Thus, the presence of upstream sources did not significantly affect the

likelihood of invasion by *D. lumholtzi* once surface area was taken into account. Larger lakes may be invaded more often because they present bigger targets to dispersers (have higher colonization rates), have different local environments (e.g. more pelagic zone), or support larger local populations (lower extinction rates). Large lakes at lower elevations also typically have higher concentrations of dissolved ions and exhibit lower annual variability (Kratz et al. 1991; Webster et al. 1996; Soranno et al. 1999). Therefore, the effect of surface water connections on invasions may be related to differences in the local physical environment as well as surface area. In addition, the observation that reservoirs with no potential upstream sources were invaded at a rate of 7.3% per year indicates that, while transport through rivers may be important, it is certainly not the only mode of dispersal for *D. lumholtzi*.

The frequent invasion of lakes without upstream source populations, coupled with rapid spread of the species across North America (Havel and Hebert 1993; Muzinic 2000), indicate that *D. lumholtzi* is a highly effective disperser over relatively large distances (100s of kilometer). The ability to utilize multiple modes of transport may account for the speed at which *D. lumholtzi* has expanded its range. This conclusion suggests that, once the initial period of range expansion is over, the geographic distribution of this species may ultimately be limited more by tolerance of local physical or biological conditions than by dispersal. If this inference is correct, then it has important implications for the factors limiting the ranges of other zooplankton that utilize similar modes of transport. Previous experimental work suggested that many crustaceans and rotifers have relatively high rates of movement among ponds within a region of around 100 km<sup>2</sup> (Shurin 2000; Cohen and Shurin, under review). The patterns of spread by *D. lumholtzi* support this inference. Lakes in Missouri had an overall probability of colonization of 8.9% per year, while lakes without upstream source populations had a rate of 7.4%. Thus, the species' extinction probability would have to be correspondingly high in order for dispersal to be significantly limiting. Since *D. lumholtzi* forms resting eggs that may persist in lake sediments for many years (Caceres 1998), it is likely that extinction events occur much less frequently than colonization. Understanding the means of transport for different species provides an important link in determining the importance of dispersal in limiting the spread of exotic species and species diversity in zooplankton communities.

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