

Invasion of the exotic cladoceran *Daphnia lumholtzi* into North American reservoirs

John E. Havel, William R. Mabee, and John R. Jones

Abstract: *Daphnia lumholtzi*, a large cladoceran native to Africa, Asia, and Australia, has recently invaded reservoirs of the southern United States. We examined its distribution, history of invasion, and population dynamics in Missouri reservoirs. Surveys detected the species in 7 of 112 reservoirs in 1992 and 11 of 119 reservoirs in 1993. Analysis of quantitative zooplankton samples from two reservoirs over a 7-year period indicated that *D. lumholtzi* first reached detectable densities in 1990 and persisted during 1991–1993. Population maxima typically occurred in late summer, with the species absent from the plankton during winter and spring. Based on its current distributional patterns, *D. lumholtzi* appears to be capable of colonizing most reservoirs in the southern regions of North America.

Résumé : *Daphnia lumholtzi*, cladocère de grande taille indigène d'Afrique, d'Asie et d'Australie, a depuis peu envahi des plans d'eau du sud des États-Unis. Nous avons examiné sa répartition, l'histoire de l'invasion et la dynamique des populations dans les réservoirs du Missouri. Les relevés ont permis de repérer cette espèce dans 7 des 112 réservoirs en 1992 et dans 11 des 119 réservoirs en 1993. L'analyse des échantillons quantitatifs de zooplancton prélevés dans deux réservoirs sur une période de sept ans a révélé que *D. lumholtzi* a atteint des densités repérables en 1990, et a persisté en 1991–1993. Les maximums de population apparaissaient de façon caractéristique à la fin de l'été, l'espèce étant absente du plancton pendant l'hiver et le printemps. D'après son profil actuel de répartition, *D. lumholtzi* semble en mesure de coloniser la plupart des plans d'eau des régions méridionales de l'Amérique du Nord.

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Introduction

Freshwater habitats have been invaded by a wide range of exotic species. For instance, at least 139 exotic species have invaded the Laurentian Great Lakes, and the rate of invasions has increased in recent years (Raloff 1992; Mills et al. 1993). Although some species have invaded North America by natural means, most have been purposeful or accidental human introductions (Mooney and Drake 1986). Some exotics have caused enormous problems in freshwater environments. The Nile perch, intentionally introduced to Lake Victoria, East Africa, has severely disrupted the food web and is driving native cichlids to extinction (Baskin 1992). Exotic plants, such as water hyacinths and *Hydrilla*, have clogged waterways and crowded out native

plants in the United States (Culotta 1991). Zebra mussels, introduced only a decade ago to the Laurentian Great Lakes through ballast water of large freighters (Carlton 1993; Mills et al. 1993), have exploded in numbers, covering bottom substrates and clogging water intakes for industry and boats (Nalepa and Schloesser 1993).

Exotic species provide opportunities to examine the ecology and evolution of new populations (Mooney and Drake 1986). Of particular interest are characteristics of species which make them effective invaders (Ehrlich 1986), characteristics of habitats which make them susceptible to invasion ("invasibility", Ewel 1986), and influence of invaders on native food webs (Baskin 1992). Species discovered in the early stage of invasion provide unique opportunities to document these processes and their consequences.

One such species is the cladoceran *Daphnia lumholtzi* Sars, recently discovered in reservoirs of the southern United States (Sorensen and Sterner 1992; Havel and Hebert 1993). *Daphnia lumholtzi* is native to Africa, the Mideast, the Indian subcontinent, and Australia (Green 1971; Gophen 1979; Swar and Fernando 1979; Benzie 1988), where it lives in a variety of habitats ranging from deep tectonic lakes to turbid temporary ponds. *Daphnia lumholtzi* has several features which distinguish it from other *Daphnia*: a large pointed helmet and tailspine, distinctive lateral fornices, and prominent spines along the

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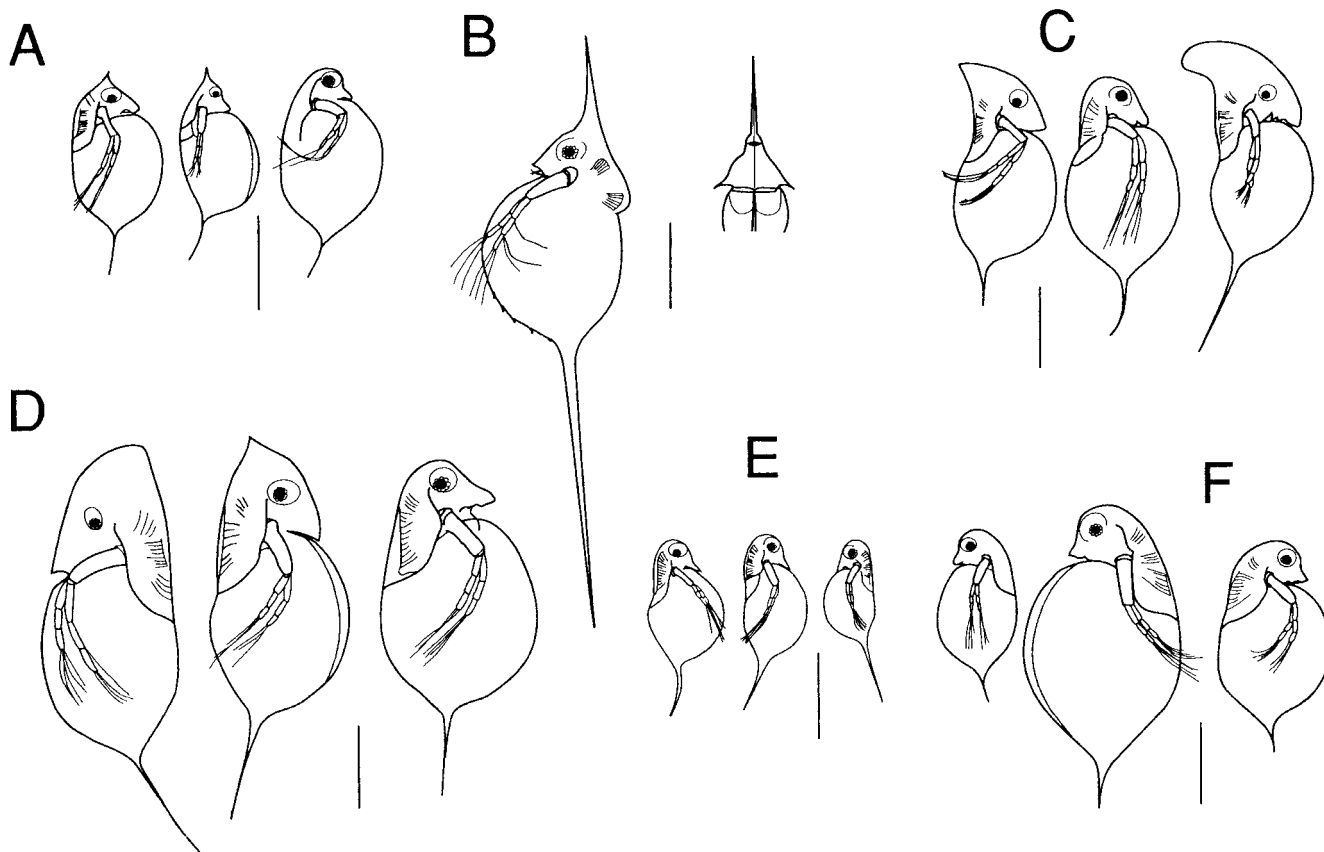
J.E. Havel.¹ Department of Biology, Southwest Missouri State University, Springfield, MO 65804, USA.

W.R. Mabee. Missouri Department of Conservation, Fish and Wildlife Research Center, 1110 S. College Ave., Columbia, MO 65201, USA.

J.R. Jones. School of Natural Resources, University of Missouri, Columbia, MO 65201, USA.

¹ Author to whom correspondence should be addressed.

Fig. 1. Morphology of *D. lumholtzi* and other *Daphnia* common in Missouri reservoirs. A, *D. ambigua*; B, *D. lumholtzi*; C, *D. retrocurva*; D, *D. galeata mendotae*; E, *D. laevis*; F, *D. parvula*. *Daphnia lumholtzi* modified from Havel and Hebert (1993); other *Daphnia* from Brooks (1957). Length of scale bar = 0.5 mm.



ventral carapace margin (Sars 1885; Havel and Hebert 1993) (Fig. 1).

The invasion of *D. lumholtzi* is peculiar for several reasons. First, biogeographic and genetic data suggest that intercontinental dispersal of most Cladocera is ordinarily rare. Although the resistant resting eggs and parthenogenetic mode of reproduction provide a good mechanism for dispersal (Dodson and Frey 1991), most species are restricted to single continents (Frey 1982; P.D.N. Hebert, University of Guelph, Guelph, Ont., personal communication). Second, the dispersal vector is unknown. In contrast with other invertebrates which have invaded the Great Lakes via ballast of large ships (Roberts 1990; Raloff 1992; Carlton 1993), restriction of *D. lumholtzi* to inland reservoirs suggests that *D. lumholtzi* used another vector, such as introduced fishes or the aquarium trade (Havel and Hebert 1993). Finally, the species appears to have invaded numerous sites within a short time period. Recent surveys in several regions indicated that *D. lumholtzi* achieved detectable densities in early 1991 and has since invaded reservoirs in Texas, Missouri, Tennessee, and Florida (Sorensen and Sterner 1992; Havel and Hebert 1993). The recency of this invasion, together with archived zooplankton samples, provided the opportunity for a detailed study of this exotic species.

The objectives of the current study were to determine the regional distribution and population dynamics of

D. lumholtzi, through detailed collections from Missouri reservoirs. Besides providing an early history of this invading zooplankton, these data provide a foundation for later study of range expansion and predictions of effects on native reservoir communities.

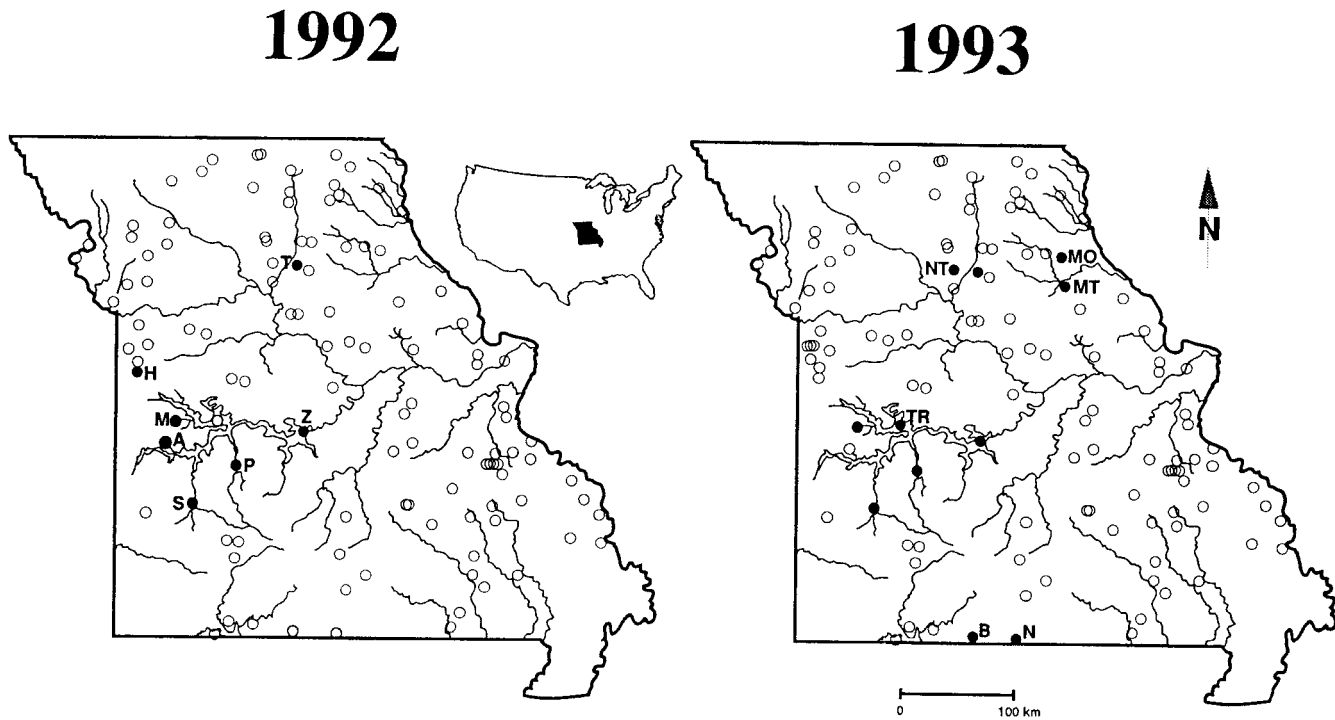
Materials and methods

Distribution in Missouri reservoirs

The distributional study involved collections from Missouri reservoirs (Fig. 2), ranging from mainstem impoundments to small tributary storage reservoirs used for water supply and recreation. The reservoirs are located in all physiographic regions of the state and exhibit a large variation in limnological characteristics (Table 1) (Jones and Knowlton 1993).

One hundred and twelve reservoirs were visited once during June 1992 and 119 were visited three times during May–August 1993. Each sample was collected near the dam, during daylight hours, by two vertical tows with a 25-cm-diameter zooplankton net (mesh = 200 μm). The two samples were pooled and preserved with buffered formalin. In order to avoid transmitting *D. lumholtzi* between reservoirs, special care was taken to thoroughly rinse collecting nets at each site. The entire sample from each site was later screened at 30 \times for *D. lumholtzi*. Because the sampling was not quantitative, no attempt was made to

Fig. 2. Results of Missouri reservoirs surveys for *D. lumholtzi* in 1992 and 1993. Solid circles, present; open circles, absent. Lake codes: A, Atkinson; B, Bull Shoals; H, Harrisonville; M, Montrose; MO, Monroe; MT, Mark Twain; N, Norfolk; NT, Nehai Tonkayea; P, Pomme de Terre; S, Stockton; T, Thomas Hill; TR, Truman; Z, Lake of the Ozarks.



compare densities among reservoirs. Other common cladoceran species were identified in a subset of 1992 samples, using Brooks (1957) for *Daphnia* and Edmondson (1959) for other Cladocera.

Study sites

Detailed studies of *D. lumholtzi* population dynamics were carried out in two reservoirs: Stockton and Pomme de Terre (Figs. 2 and 3; Table 2). Like most reservoirs in the Ozark Highlands, these waterbodies exhibit a warm-monomictic circulation pattern and a decrease in nutrients and increase in water clarity along an up-lake to down-lake transect (toward the dam) (Youngsteadt and Gumucio 1991). Although the two reservoirs are similar in conservative ions (alkalinity $115 \text{ mg}\cdot\text{L}^{-1}$ as CaCO_3 , conductivity $260 \mu\text{S}\cdot\text{cm}^{-1}$), Pomme de Terre has a shorter hydraulic retention time, higher watershed to volume ratio (5.3 vs. 2.7), and higher fertility than Stockton Lake (Table 2).

Population dynamics

Population dynamics of *D. lumholtzi* were studied through a series of quantitative zooplankton samples collected in each of seven years. On each date, four zones were sampled from Stockton Lake (Nos. 1–4, Fig. 3) and three from Pomme de Terre (Fig. 3). Within each zone, zooplankton were collected from two to four locations randomly chosen from a grid. Depth was $\geq 18 \text{ m}$ in most of zone 1 for both lakes and $\leq 6 \text{ m}$ for zones 2–4. During 1987–1991, zooplankton were collected weekly from May until the middle of June and then biweekly until October. During 1992–1993, samples were collected monthly from April to October. Because these zooplankton collections were made as part of an investigation of the interactions between zooplankton,

gizzard shad, and sport fish (P. Michaletz, Missouri Department of Conservation, Columbia, Mo., personal communication), data on fish diets were also available for April–October of each year.

Zooplankton were collected with an $80\text{-}\mu\text{m}$ -mesh Wisconsin net, with vertical hauls to the surface, from either the bottom or 9 m, whichever distance was smaller. Recorded volume was determined by assuming that the total column of water passed through the net. Because net hauls were not calibrated with meters and net efficiency is expected to decline with increasing seston levels, the densities reported below are likely underestimates. The entire contents of each sample were examined at $25\text{--}50\times$ and *D. lumholtzi* counted.

An additional zone on Stockton Lake (No. 5, Fig. 3) was sampled from May 1991 through December 1993 on a monthly basis, by taking three 13-m vertical tows with a $200\text{-}\mu\text{m}$ -mesh zooplankton net (total volume sampled approximately 1900 L). Prior to October 1991, subsamples were examined; thereafter, the entire contents of each sample were screened at $25\times$ for the presence or absence of *D. lumholtzi*.

Statistical analyses

Statistical comparisons of limnological characteristics between reservoirs were carried out with Wilcoxon two-sample tests, by the methods of Sokal and Rohlf (1981), using Minitab, PC version, release 8 (Minitab 1991).

Results

Distribution in Missouri reservoirs

Examination of 1992 reservoir samples revealed nine species of *Daphnia*, of which six were common (Fig. 1).

Table 1. Limnological characteristics of Missouri reservoirs. For each reservoir, samples were collected during summer 1992 from the surface and Secchi depth and averaged. Shown are the median (and range) among reservoir samples with ($n = 13$) and without ($n = 101$) *Daphnia lumholtzi* (*D.l.*). p -values, based on Wilcoxon two-sample tests: ns, $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Details on methods are presented in Jones and Knowlton (1993).

Variable	With <i>D.l.</i>	Without <i>D.l.</i>	p -value
Area (ha)	19 274 (49–147 148)	217 (25–56 833)	***
Water temperature (°C)	25.1 (23.1–27.2)	24.1 (11.6–28.1)	**
Secchi depth (m)	1.46 (0.3–2.97)	1.2 (0.2–5.3)	ns
SiO ₂ (mg·L ⁻¹)	7.6 (6.5–8.9)	7.4 (4.9–11.1)	ns
Total nitrogen (mg·L ⁻¹)	0.72 (0.35–1.30)	0.73 (0.17–3.23)	ns
Dissolved nitrogen (mg·L ⁻¹)	0.60 (0.26–1.16)	0.51 (0.11–1.42)	ns
NO ₂ ⁻ + NO ₃ ⁻ (µg·L ⁻¹)	48 (4–543)	5 (1–768)	***
NH ₄ ⁺ (µg·L ⁻¹)	31 (10–62)	31 (6–278)	ns
Total phosphorus (µg·L ⁻¹)	32 (13–174)	34 (6–369)	ns
Total dissolved phosphorus (µg·L ⁻¹)	14 (6–30)	14 (4–84)	ns
Chlorophyll <i>a</i> (µg·L ⁻¹)	14.9 (1.5–90.6)	12.7 (0.9–212.7)	ns
Nonvolatile suspended solids (mg·L ⁻¹)	4 (1–43)	2.7 (0.3–26.5)	ns
Volatile suspended solids (mg·L ⁻¹)	2.5 (1–11.8)	2.5 (0.5–25.4)	ns
Ca ²⁺ (mg·L ⁻¹)	31 (19–62.6)	23.5 (1.7–91.7)	ns
Mg ²⁺ (mg·L ⁻¹)	12.6 (4–19.3)	10.8 (1.8–82)	ns
Na ⁺ (mg·L ⁻¹)	4.4 (2.1–26.7)	4.6 (1–36.1)	ns
K ⁺ (mg·L ⁻¹)	3.9 (1.6–11.1)	3.3 (0.7–8.8)	ns
Conductivity (µS·cm ⁻¹)	298 (196–718)	253 (31–935)	*
Color (Pt units)	25 (15–32)	24.3 (13–56)	ns

Pelagic species richness ranged from 1 to 10 cladocerans, with up to six species of *Daphnia* coexisting in single reservoirs.

Daphnia lumholtzi was detected in 3 of the 112 reservoirs sampled in June 1992: Atkinson, Pomme de Terre, and Montrose lakes. Each of these lakes is on a separate drainage (Fig. 2). Atkinson and Montrose lakes are small (areas approximately 144 and 2675 ha, respectively), eutrophic, and turbid (Secchi depths 0.2–0.5 m). Although few individuals were detected in Atkinson and Pomme de Terre, *D. lumholtzi* was the most common zooplankton in the sample from Montrose Lake. Four additional populations

were detected in samples collected in July–October 1992: Lake of the Ozarks (Niangua River arm), Stockton Lake, Thomas Hill Reservoir, and Harrisonville Lake (Fig. 2). Lake of the Ozarks is a large impoundment on the Osage River, which receives water from Stockton and Pomme de Terre lakes. Thomas Hill and Harrisonville lakes are located on separate drainages.

During May–August 1993, 119 reservoirs were each visited on three occasions. Over this period, much of the midwestern United States received exceptionally large rainfalls, resulting in widespread flooding. No *D. lumholtzi* were detected in May and June samples. During July and

Fig. 3. Sampling zones on Stockton and Pomme de Terre. Zones 1–4 were collected by the Missouri Department of Conservation and zone 5 by Springfield City Utilities.

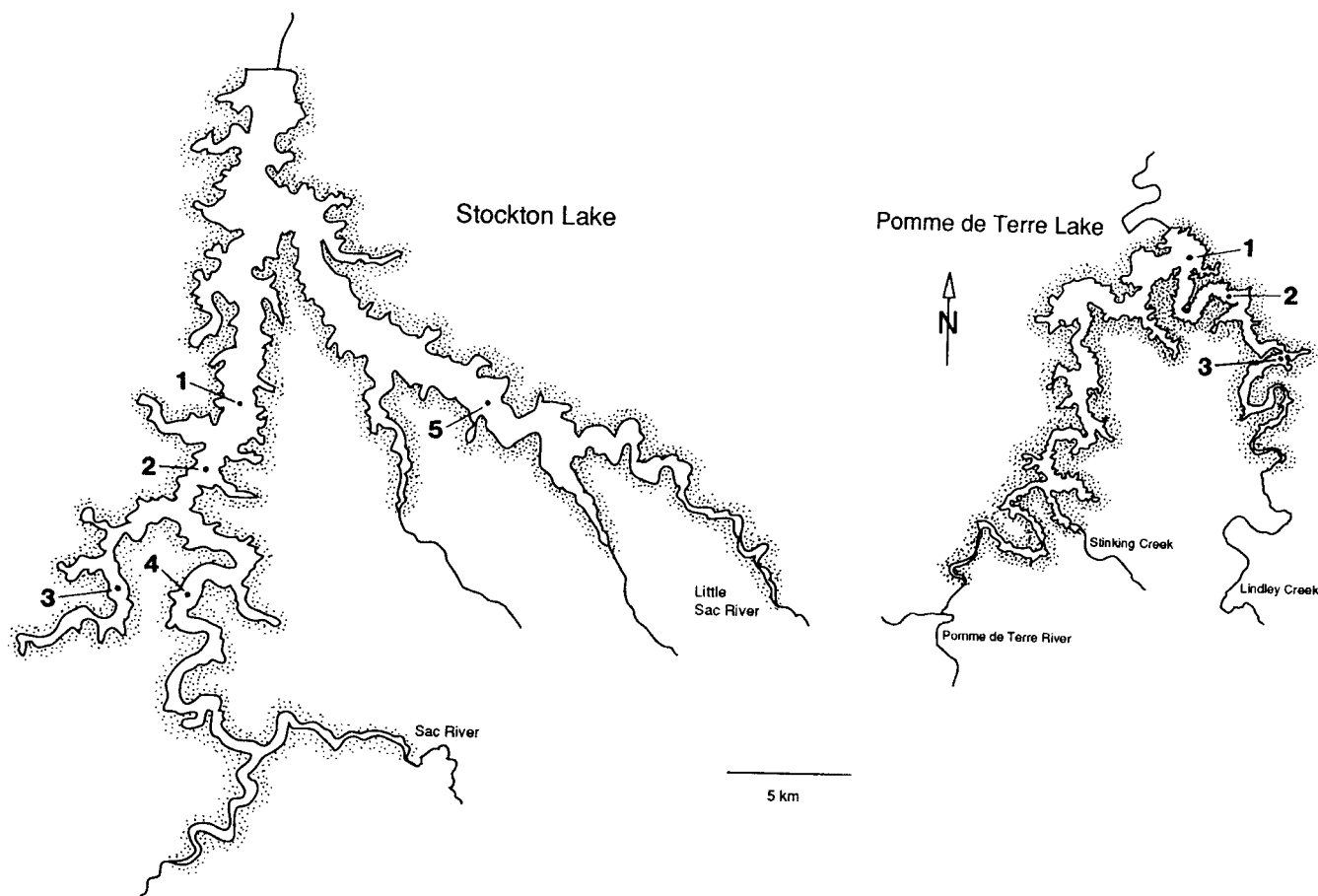


Table 2. Limnological characteristics of Stockton and Pomme de Terre lakes. For each reservoir, the water chemistry data were collected from a single site near the dam in summer 1992.

	Area (ha)	Mean depth (m)	Retention time (years)	Chlorophyll <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	Total P ($\mu\text{g}\cdot\text{L}^{-1}$)	Total N ($\mu\text{g}\cdot\text{L}^{-1}$)	Secchi depth (m)
Stockton	10 031	10.9	1.20	5.1	13	400	3.0
Sac River arm	2 072	7.3	0.31				
Little Sac arm	3 423	10.8	1.12				
Pomme de Terre	3 194	9.3	0.60	13.9	20	520	1.7
Lindley Creek arm	672	8.8	0.46				
Pomme de Terre arm	950	12.6	0.42				

August, populations were detected in 11 reservoirs. Six of these represented populations not detected in 1992, although one reservoir (Mark Twain) had not been sampled in 1992. Five populations were detected in both 1992 and 1993 (Fig. 2). Despite the extensive sampling, no *D. lumholtzi* were detected in Atkinson or Harrisonville Lake, indicating that these populations were either locally extinct or extremely rare.

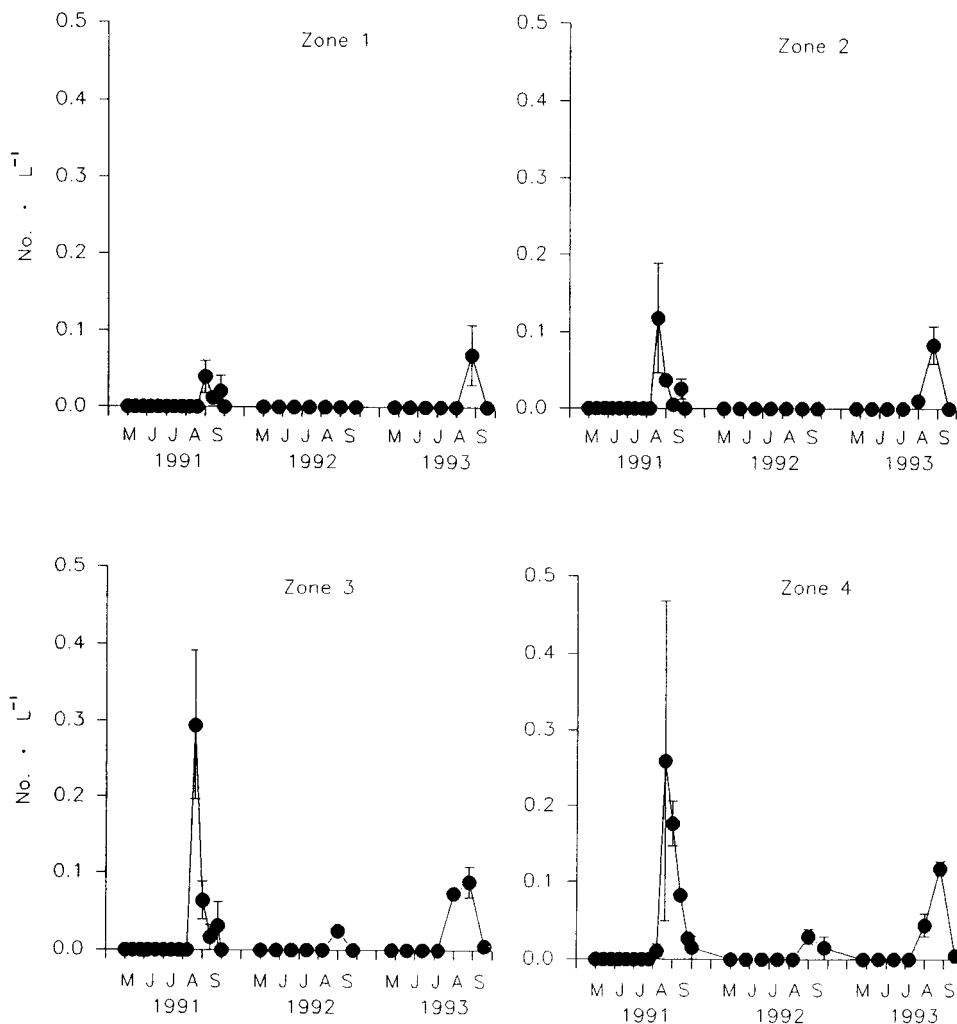
Based on both years, at least 13 Missouri reservoirs have been invaded so far by *D. lumholtzi*. There were no significant differences in median values for most limnological

characteristics of the 13 invaded reservoirs and 101 others which have not been invaded (Table 1). However, invaded reservoirs tended to be larger in area, to have a higher water temperature, and to have higher conductivities and higher concentrations of nitrite and nitrate than noninvaded reservoirs.

Population dynamics in Stockton and Pomme de Terre

The zooplankton communities of the two lakes consisted of 29 species, including six species of *Daphnia* (Fig. 1).

Fig. 4. Population dynamics of *D. lumholtzi* in Stockton Lake (mean \pm 1 SE ($n = 3$)).
Stockton Lake—West Arm



Native *Daphnia* species typically reached their maximal abundances during spring and early summer and *Ceriodaphnia* and *Diaphanosoma* species during late summer (J. Havel and W. Mabee, personal observation).

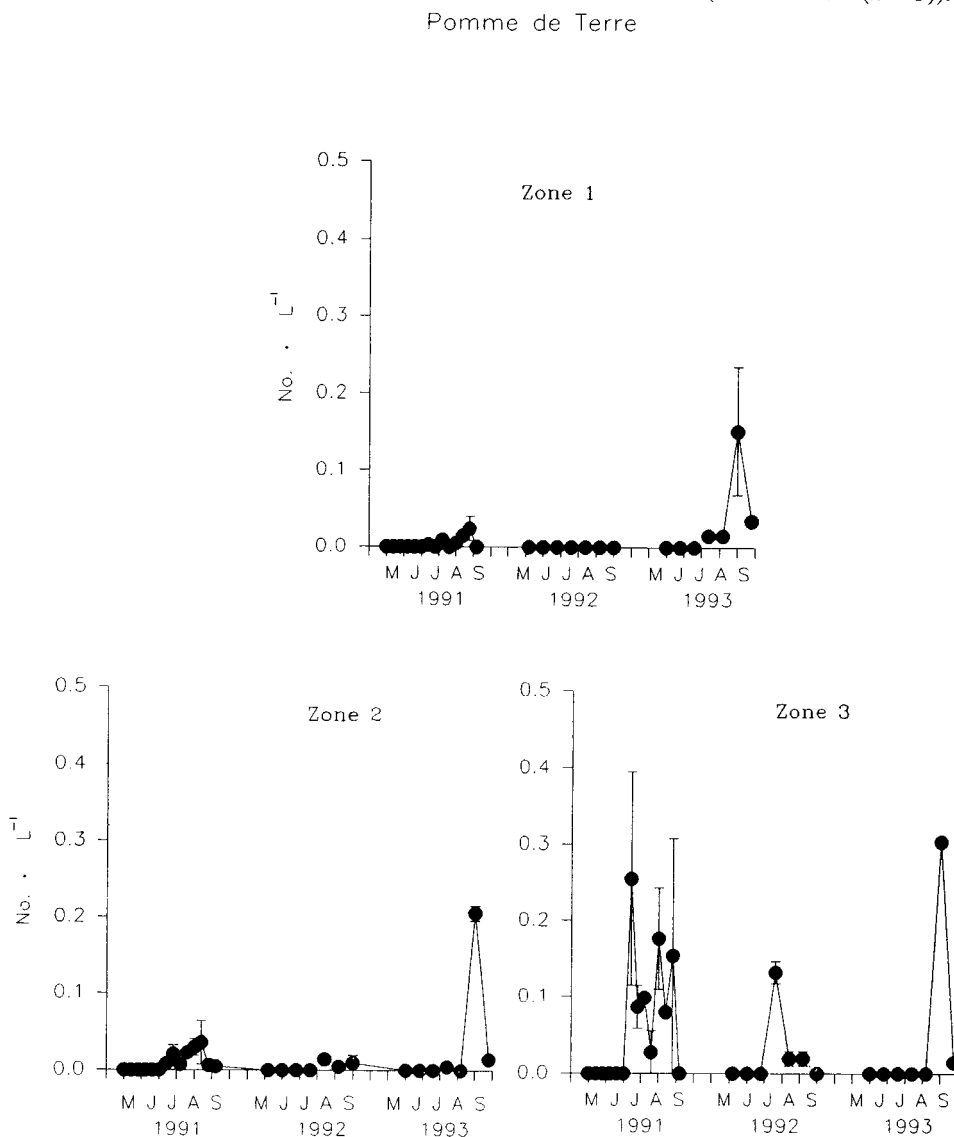
Daphnia lumholtzi was not observed in any sample in 1987, 1988, 1989, or early 1990. In Stockton Lake, this species first appeared in a stomach sample from a white crappie (*Pomoxis annularis*) on August 14, 1990, and in a zooplankton sample on October 1, 1990. In Pomme de Terre, *D. lumholtzi* first appeared in a white crappie stomach sample on October 11, 1990, and in a zooplankton sample on October 3, 1990, when it was the dominant cladoceran.

Population density estimates for Stockton Lake, based on samples collected between 1991 and 1993, indicated that *D. lumholtzi* was rare or absent during each spring, suddenly increased in late summer, and declined in autumn (Fig. 4). The pattern was evident at all four zones. Although population densities appeared to decline from 1991 to 1992, *D. lumholtzi* were still abundant in 1993 (Fig. 4). Monthly

samples collected over three years at an additional up-lake site (No. 5) showed a similar pattern, indicating that this species was absent from the plankton during all months except August–October. Samples collected from Pomme de Terre also indicated a short summer population peak for *D. lumholtzi* in most years, although in one year (1991) the density remained high for most of the summer (Fig. 5). For both lakes, densities were greatest at up-lake zones (Nos. 3 and 4), and this pattern was consistent for most dates (Figs. 4 and 5).

Discussion

We have shown that the exotic *D. lumholtzi* has so far invaded approximately 11% of the reservoirs in Missouri and has persisted in two well-studied reservoirs for at least 3 years. Although the 2-year survey suggests that a range expansion is taking place, the larger number of populations detected could have been an artifact of the increased sampling effort in 1993. The observation that two populations

Fig. 5. Population dynamics of *D. lumholtzi* in Pomme de Terre (mean \pm 1 SE ($n = 3$)).

detected in 1992 were apparently extinct in 1993 suggests that populations are unstable or extremely patchy. Their brief period of population abundance each year may make *D. lumholtzi* sensitive to environmental disturbances. For instance, Atkinson Lake, which had a small population in 1992, was inundated by (the normally downstream) Truman Lake during the severe flooding of 1993, bringing in a large population of gizzard shad (*Dorosoma cepedianum*; D. Cornelius, Missouri Department of Conservation, Sedalia, Mo.). These planktivorous fish or other flood-associated changes may have kept *D. lumholtzi* below detectable limits in 1993.

These reservoirs need monitoring to determine if established populations will persist and if the range of this species will continue to expand. We expect that reservoirs located downstream or in close proximity to established populations will have the highest probability of being colonized. Further, if human activity is the primary vector for moving propagules among sites, as suggested by Havel

and Hebert (1993), then we would expect that reservoirs which receive frequent boat traffic from sites with established populations should also have a high probability of colonization. This "bass-boat hypothesis" could be further tested by sampling live wells of fishermen moving among sites, just as ballast tanks have been sampled from large ships (Carlton and Geller 1993; Locke et al. 1993). Because our study revealed that the population size of *D. lumholtzi* is largest in late summer, such distributional studies should focus on samples collected at this time of year.

Studies of range expansion of new exotics also provide a model system for estimating rates at which zooplankton colonize new habitats. Because of the presence of a long-lasting egg bank in the sediments (Dodson and Frey 1991), it is usually difficult to separate colonization of new habitats from the hatching of eggs from earlier populations. In contrast, all new occurrences of exotic species, because they did not previously occur in the region and did not have an egg bank, would represent true colonization events.

Exotics thus serve as a good marker for determining zooplankton dispersal. Such studies may yield insight into questions about how zooplankton communities are reestablished in previously degraded systems (Keller and Yan 1991).

Successfully invading species often share similar life-history traits. They generally have broad environmental tolerances, short generation times, and are habitat and trophic generalists (Ehrlich 1986). *Daphnia* and other cladocerans have many of these properties, suggesting that this group should be effective at dispersal and colonization. Specifically, they are abundant in their native range, have short generation times, and a single individual (or egg) is able to colonize alone (Dodson and Frey 1991). The observation that most cladoceran species are limited to single continents (Frey 1982) suggests either that long-distance dispersal is usually not very effective or that colonization of filled niches is difficult. *Daphnia lumholtzi* is unusual in having a native distribution over three continents, residing in a wide assortment of habitats, from clear deep lakes and temporary ponds to turbid impoundments and floodplains (Green 1967; Gophen 1979; Geddes 1984). Such a broad habitat range may have contributed to its success in rapidly establishing multiple populations in North America.

Certain communities may be especially prone to invasion by exotic species: disturbed or cultivated habitats have long been recognized to be particularly vulnerable to invasion (Elton 1958). Similarly, the fluctuating water levels, habitat alteration, turbidity, and intentional food web manipulations make reservoirs highly disturbed systems (Thornton et al. 1990) and, we would expect, particularly susceptible to establishment of invading species. It should be no surprise that *D. lumholtzi*, without the ballast-water vector used by Great Lakes exotics (Locke et al. 1993; Mills et al. 1993), should invade reservoirs rather than natural lakes. However, such a pattern could be simply an artifact, since there are few natural lakes in the areas studied.

The current study allowed testing for an association between the occurrence of successful invasion by *D. lumholtzi* and limnological characteristics. There appears to be a broad overlap of most limnological characteristics in the 13 Missouri reservoirs invaded and 101 reference reservoirs not invaded (Table 1). For instance, with the exception of nitrite/nitrate, all measures of fertility were similar between the two groups. In contrast, the area of invaded reservoirs tended to be larger than that of those not invaded. Such an observation is consistent with a variety of expectations from species-area curves (Dodson 1992). For instance, dispersal vectors such as waterfowl or boats should have a higher probability of encountering larger lakes than smaller lakes. Similarly, more open niches might be available in larger lakes than smaller lakes, providing for a lower probability of extinction.

Reservoirs invaded by *D. lumholtzi* were, on average, 1° warmer than those not invaded (Table 1). These survey data are consistent with the population dynamics in Stockton and Pomme de Terre, as populations developed only during the warm summer months and highest densities were found at the shallower (and warmer) up-lake stations. These data suggest that *D. lumholtzi* will be restricted to

lakes that develop warm epilimnetic temperatures during the summer. A large number of temperate and tropical lakes in North America should thus be susceptible to invasion by this exotic.

Community composition should also influence invasibility (Ewel 1986). In the current study, populations of *D. lumholtzi* were most abundant during periods when most native *Daphnia* were rare. Summer maxima for *D. lumholtzi* were considerably lower than those which native *Daphnia* achieved earlier in the year. For instance, whereas we observed a maximum of $<0.5 D. lumholtzi \cdot L^{-1}$ (Figs. 4 and 5), native *Daphnia* during the spring bloom in Stockton Lake (primarily *D. galeata*; J. Havel, personal observation) can often exceed $20 \text{ individuals} \cdot L^{-1}$ (N. Youngstead, City Utilities of Springfield, personal communication). The lower density of *D. lumholtzi* could be due to lower quality food typical of late summer (Wetzel 1983) or to a variety of competitive and predatory interactions with zooplankton and planktivorous fish. It is intriguing to note that coincident with the lower abundances of *D. lumholtzi* in 1992 (Figs. 4 and 5) were large midsummer populations of native *Daphnia* (N. Youngstead, personal communication). Perhaps *D. lumholtzi* is restricted to living during a period in which its competitively superior congeners are normally absent. Clearly, more work is necessary to elucidate the relationship between community composition and population cycles in *D. lumholtzi*.

Some exotics have caused widespread disruption of native freshwater food webs. The best known cases involve the importation of top predators, such as Nile perch in Lake Victoria (Baskin 1992) and peacock bass in Lake Gatun (Zaret and Paine 1973). Few data exist on exotic zooplankton and their impacts on aquatic food webs. *Bythotrephes cederstroemi* is the best-known example of a cladoceran invading North American lakes. This predatory species appears to have invaded the Great Lakes in the late 1970's or early 1980's, and, like zebra mussels, has been linked to the ballast water of ships (Lehman 1987). Although widespread disruption of pelagic food webs has not yet been detected (Sprules et al. 1990), *B. cederstroemi* abundance has been linked to a depression of another predatory cladoceran (*Leptodora kindtii*), as well as two of three common *Daphnia* species living in Lake Michigan (Lehman and Cáceres 1993). A possible collapse of *Daphnia* populations is potentially important because of its role as a "keystone herbivore" in freshwater systems (Stockner and Porter 1988).

Daphnia lumholtzi also has the potential for disrupting community structure. This herbivorous species has both an enlarged pointed helmet and extremely long tailspine (Fig. 1). Similar structures have been experimentally shown to reduce predation by both invertebrates (O'Brien et al. 1979) and small planktivorous fish (Jacobs 1967; Barnhisel 1991). Green (1967) found both helmeted and nonhelmeted ("monacha") morphs of *D. lumholtzi* living in Lake Albert, Uganda. He noted that the monacha morph was rarely found in locations with high densities of planktivorous fish whereas the helmeted morph was commonly found in these locations. Stomach contents from *Alestes baremose* from Buhuka Lagoon, where the two morphs cooccurred, contained a large volume of the monacha morph, but none

of the helmeted morph. Based on these data, Green (1967) concluded that the helmet and/or spines reduced predation on this morph. If North American *D. lumholtzi* should out-compete native zooplankton and become dominant during periods when larval and juvenile fishes are feeding on zooplankton, then this exotic could negatively impact the fisheries of North American reservoirs. So far, however, *D. lumholtzi* has been most abundant late in the summer, after the most active period of planktivory by larval fishes (P. Michaletz, personal communication), so this exotic has so far had no discernable impact.

In conclusion, the rapidity with which *D. lumholtzi* has invaded North America so far suggests that this species will eventually become a common member of the zooplankton in reservoirs of southern North America. Study of its progression, together with possible impacts on native food webs, should provide a fascinating look into the ecology of biological invasions.

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