

Complementary population dynamics of exotic and native *Daphnia* in North American reservoir communities

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With 4 figures and 3 tables

Abstract: During its invasion of North America, the exotic *Daphnia lumholtzi* has rapidly colonized numerous reservoirs, natural lakes, and large rivers. In the current study, we examine the overlap between *D. lumholtzi* and native *Daphnia* species through analysis of two data sets: co-occurrence in reservoirs of the south-central United States and population dynamics in one reservoir. In 171 reservoirs and oxbow lakes, *D. lumholtzi* was among the most prevalent species and its distribution was independent of other *Daphnia* species. Over a 28-month period in Stockton Lake, Missouri, *D. lumholtzi* was abundant only in late summer, a period when the epilimnion was warm (25–30 °C) and cyanobacteria were common. Native *Daphnia* (*D. mendotae*, *D. parvula*, and *D. retrocurva*) complemented this pattern, being generally rare in summer and most abundant during winter and spring. Peak densities and average fecundities of native *Daphnia* during the cooler months were typically greater than densities and fecundities of *D. lumholtzi* in summer. The complementary population dynamics between native and exotic species may be significant for the food webs in warm reservoirs, with *D. lumholtzi* providing another food resource when the abundance of large zooplankton is ordinarily low.

Key words: Biological invasions, *Daphnia lumholtzi*, exotic species, phenology, population dynamics, seasonal succession, zooplankton.

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Introduction

The invasion of exotic species into aquatic environments has become increasingly common over the past few decades, and concern over their effects has led to increased awareness by the scientific community and general public (BRIGHT 1998). Although some species have caused extensive ecological or economic damage (ELTON 1958, KOLAR & LODGE 2000), the majority of exotic species likely have limited or neutral effects on the communities they invade (WILLIAMSON 1996). Numerous zooplankton species now are known to have invaded both marine and freshwater environments (CARLTON & GELLER 1993, BOLLENS et al. 2002), and probably many other cryptic invaders remain undiscovered (e. g., TAYLOR et al. 1998). Two cladocerans that are easily recognized by their distinctive spiny appearance have offered the opportunity to study invasion processes and impacts on communities. The Eurasian predator *Bythotrephes longimanus* appeared in the Laurentian Great Lakes during the late 1980s (THERRIAULT et al. 2002), spread to other lakes in the region (MACISAAC et al. 2004), and has been associated with reduced zooplankton abundances and species richness in a number of these lakes (LEHMAN & CÁCERES 1993, YAN et al. 2002).

Daphnia lumholtzi SARS 1885 is endemic to Africa, the Middle East, the Indian subcontinent, and Australia (BENZIE 1988). This species appeared in a small Texas reservoir in 1990 (SØRENSEN & STERNER 1992) and within 12 years had spread from coast to coast and extended from the deep south (Florida) to the Laurentian Great Lakes (HAVEL & SHURIN 2004). In both native and North American ranges, this species is widespread in both reservoirs and large rivers (SHIEL 1985, HAWKINS 1988, HAVAL et al. 2005 b). The tropical origin of *D. lumholtzi* may pre-adapt this species to tolerate hot summer conditions, which can be challenging to temperate zooplankton (MOORE et al. 1996). Consistent with such tolerances are early North American studies on phenology that showed *D. lumholtzi* populations to have a short period of abundance during summer (HAVAL et al. 1995, WORK & GOPHEN 1999). In contrast, native *Daphnia* (*Daphnia parvula*, *Daphnia galeata mendotae*) have been reported to decline in summer (THRELKELD 1986 b, DETTMERS & STEIN 1992). *Daphnia* have broad diets and high grazing rates, and efficiently transmit energy up the food chain (STOCKNER & PORTER 1988). Because lake fishes require zooplankton during early life stages and are often limited by food of the right size (DETTMERS & STEIN 1992), the addition of this exotic *Daphnia* species is potentially important to the food webs of these warm-water reservoirs.

Understanding the community impacts of invasion by *D. lumholtzi* on lake and reservoir communities requires examination of its co-occurrence with native *Daphnia*. In the current study, we first examine data on distributions of *D.*

lumholtzi and native *Daphnia* species from a broad survey of reservoirs in the south-central United States. This survey allows us to determine the prevalence of *D. lumholtzi* in the region and to see if species distributions were independent of one another. We then examine population dynamics of four *Daphnia* species in a Missouri reservoir sampled over a 28-month period. This second survey provides a view of the differences in timing of the abundance, fecundity, and population growth rates of *Daphnia* species (herein referred to as “complementary population dynamics”). These data allow an exploration of the environmental conditions of warm-water reservoirs that control population dynamics by exotic and native *Daphnia* and the potential implications for reservoir food webs.

Material and methods

Co-occurrence of *Daphnia* in reservoirs of the south-central United States

To determine the overlap between *D. lumholtzi* and native *Daphnia*, we examined co-occurrence patterns in the south-central United States (Missouri, Arkansas, and Oklahoma), a region where *D. lumholtzi* is common (HAVEL et al. 2005 b). During June–August 1995, we collected zooplankton from 171 reservoirs and oxbow lakes (herein, we refer to both water body types as “lakes”). A distribution map and detailed descriptions of these lakes are given in HAVEL et al. (2005 b). To ensure that all lakes were sampled during the hot summer season, we sampled lakes following a south-to-north progression.

For each lake, zooplankton were collected from two locations using a 200- μ m mesh tow net and then pooled into a single sample. Oxbows were sampled near the middle, small reservoirs near the dam, and large reservoirs in the riverine-lacustrine transition zone. Each sample was anaesthetized with cold carbonated water and preserved in cold, buffered formalin (PREPAS 1978). Either the entire sample or subsamples totaling at least 200 cladocerans were examined at 25 \times magnification. Cladocerans were identified to species using EDMONDSON (1959) and other keys (listed in: <http://www.cnas.missouristate.edu/zooplankton>). Identification of *Daphnia* species followed HEBERT (1995).

We used Chi Square tests of independence to examine if *D. lumholtzi* was associated with the presence or absence of any of the native *Daphnia* species over the region and whether native *Daphnia* species were associated with one another. Similar analyses were performed to see if these trends could be associated with latitude.

Population dynamics in a Missouri reservoir

Study site

We conducted a detailed study of *Daphnia* population dynamics in Stockton Lake, Missouri (37.69° N, 93.76° W) from June 1994 to September 1996. Stockton Lake is a

mesotrophic multi-use reservoir, which drains a 3,003-km² watershed in the Ozark Highlands region of Missouri (JONES & KNOWLTON 1993, HAVEL et al. 1995). Land use in this region is primarily rural, with low-density livestock grazing. The lake has an average retention time of 1.2 years, although retention fluctuates depending upon rainfall in the watershed and power generation at the dam. At conservation pool (managed level above which flood waters are stored), Stockton Lake has a surface area of 101 km² and average and maximum depths of 9.5 and 26 m, respectively. Typically stratified between May and September, Stockton Lake has, in most years, a warm-monomictic circulation pattern. Summer surface temperatures commonly reach 30 °C, and the hypolimnion becomes anoxic (<0.5 mg L⁻¹) by mid-June. As is typical in other medium-large reservoirs (THORNTON et al. 1990), Stockton Lake shows a longitudinal gradient along an up-reservoir to down-reservoir transect, with a decrease in nutrient levels and an increase in water clarity toward the dam (N. Youngsteadt, pers. com.). *D. lumholtzi* was first detected in Stockton Lake in 1990 (HAVEL et al. 1995), and examination of qualitative samples collected from 1990 to 2000 reveals that this species has since been a regular member of the zooplankton community during late summer and fall.

Field sampling

We collected field samples weekly during June–October 1994 and May–October 1995 and monthly during November 1994–April 1995 and November 1995–September 1996. On the basis of a previous study of the lake, we visited two sites along the Sac River arm on each sampling date (see map in HAVEL et al. 1995). Sites #2 and 4 are, respectively, 17 and 26 km from the dam and have maximum depths (in the main channel at conservation pool) of 16 and 20 m. On each date at each site, we measured physical properties in the main channel. Temperature and dissolved oxygen were measured with a YSI model 50B oxygen meter and transparency with a Secchi disk.

Phytoplankton

To assess food resources, phytoplankton was sampled during the first year of the study (June 1994–May 1995). We collected duplicate depth-integrated phytoplankton samples in the main channel using a 5-m-long tygon tube (inner diameter = 12 mm), providing samples that encompassed the entire photic zone (2.1–4.5 m, on the basis of three times the Secchi depth) (HORNE & GOLDMAN 1994). The two samples were pooled and then preserved with Lugol's iodine (EDMONDSON 1959). Phytoplankton was identified to genus at 400 × magnification using the key in PRESCOTT (1978). One 10-mL subsample from each sample was settled in an Utermöhl chamber and algae enumerated by genus using a Whipple disk.

Zooplankton

We collected zooplankton during the entire 28-month study. To account for spatial heterogeneity, three samples were collected at random locations in the pelagic region

(> 10 m offshore) at each site. For all sampling dates, the station depths among locations (measured with a sounding line) ranged from 6 to 23 m (site 2) and 5 to 18 m (site 4), with about 25% of sample stations < 12 m. Zooplankton was collected by taking 10-m vertical tows with a 153 μm -mesh Wisconsin net (25 cm diameter). This mesh size was selected to avoid clogging with filamentous algae; a preliminary study showed that this net has a high efficiency for collecting *Daphnia*, although it is biased against smaller crustaceans such as *Bosmina* and copepod nauplii. If sample locations were < 12-m deep, tows extended from 2 m above the bottom to avoid disturbing bottom sediments. The three zooplankton samples from each site were later analyzed separately. Samples were preserved and identified as previously described. We enumerated in a Bogorov tray by examining either the entire sample or subsamples until at least 200 *Daphnia* were counted.

Population growth rate (r , in days^{-1}) was calculated by a standard modification of the exponential growth equation:

$$r = (\ln N_2 - \ln N_1) t^{-1}$$

where N_1 and N_2 are densities on successive sampling dates and t is the number of days between samples (LAMPERT & SOMMER 1997). To test for complementary patterns in the dynamics of exotic and native *Daphnia*, time-series graphs and pair-wise correlations between species in their population growth rates at each sample site were examined. Additional pair-wise correlations were used to examine the associations between *Daphnia* densities and features of the environment (temperature and phytoplankton densities).

To estimate fecundities, we counted eggs (including embryos) carried by mature females of each species. Mature size was defined as the minimum size observed to carry eggs in a preliminary analysis of dates when each species was common. Although some prematurely released eggs may have been lost from samples by passing through the net, ballooned carapaces and loose eggs were rarely observed in the samples, and so we expect that this bias is small. Summary statistics are presented only for species and dates where a minimum of 20 mature females had eggs counted. Because of small sample sizes, egg counts were pooled from the three replicate samples. Since data were lacking on vertical migration behavior of the *Daphnia* and thus the temperatures for egg development, we did not attempt to estimate birth rates. Fecundity was used simply as another measure of the performance of each *Daphnia* species over time.

Results

Co-occurrence of *Daphnia* in the south-central United States

The summer zooplankton samples from 171 warmwater reservoirs and oxbow lakes in the south-central United States showed *Daphnia* to be present in 88% of these lakes. Eleven *Daphnia* species were detected in the region (Table 1). Five *Daphnia* species were widespread and abundant, including the exotic *D. lumholtzi*. Although this species was first detected in North America only five

years before the current survey (SORENSEN & STERNER 1992), *D. lumholtzi* occurred in 33 % of the study lakes. Among the natives, *D. parvula* was the most prevalent (65 %), followed by *D. mendotae* (33 %), *D. ambigua* (15 %), and *D. retrocurva* (12 %). Over 50 % of the lakes contained two or more *Daphnia* species, with up to five co-occurring species. The co-occurrence matrix indicated that, except for two pairs of native species that showed facilitation (*D. parvula* with *D. ambigua* and *D. retrocurva* with *D. mendotae*), frequencies of *Daphnia* species were not significantly associated with one another (Table 1). *D. lumholtzi* occurred alone in only 20 % of the lakes it inhabited ($n = 56$); it commonly co-occurred with *D. parvula* (62 %) and *D. mendotae* (27%), as well as with *D. ambigua* and *D. retrocurva* (Table 1). The co-occurrence data indicate that, at least for the warm summer months, *D. lumholtzi* co-occurs and potentially interacts with the native *Daphnia* in these reservoirs and oxbow lakes.

We divided the lakes into three similar-sized groups on the basis of latitude (36–39, 40–42, and 43–44° N) and reexamined these patterns. Although lakes were purposefully sampled during summer conditions over the entire range, surface water temperature was significantly different among these groups of lakes ($F = 3.23$, $p = 0.043$), with the southern lakes (sampled earlier in the summer) being slightly cooler than the mid-latitude lakes (mean 28.9 and 29.9 °C, respectively). Nevertheless, all but 3 of the 171 lakes had epilimnetic temperatures > 25 °C, such as characterized summer conditions in Stockton Lake (below). *Daphnia lumholtzi* occurred more frequently in the southern lakes (50 %) than in the other regions (29 %). On average, *D. lumholtzi* co-occurred with one other *Daphnia* species in each lake (range 0–3), and this

Table 1. Pairwise co-occurrence of common *Daphnia* species from 171 reservoirs and oxbow lakes in Missouri, Arkansas, and Oklahoma, sampled in summer 1995. Omitted are the rarer *Daphnia* species: *D. rosea* (10 sites), *D. pulicaria* (8), *D. laevis* (6), *D. catwba* (1), *D. pulex* (1), and *D. schoedleri* (1). Shown on the diagonal (shaded) is the number of lakes in which a species was found alone. Above the diagonal is the number of lakes in which a species pair co-occurred. Because some lakes had three or more co-occurring species, the sum of pair-wise occurrences can exceed the total frequency for each species. Chi Square statistics are shown below the diagonal; boldface statistics represent p-values of $p = 0.022$ and $p = 0.007$, both showing facilitation between species.

	Total freq. (lakes)	Dpar	Dmen	Dlum	Damb	Dret
<i>D. parvula</i> (Dpar)	111	30	38	35	22	13
<i>D. mendotae</i> (Dmen)	57	0.12	4	15	12	12
<i>D. lumholtzi</i> (Dlum)	56	0.21	1.61	11	6	6
<i>D. ambigua</i> (Damb)	26	5.23	2.27	1.30	1	2
<i>D. retrocurva</i> (Dret)	20	0.00	7.25	0.08	0.48	2

pattern did not vary with latitude. Two native species were common enough to allow regional comparisons of co-occurrence with *D. lumholtzi*. *D. mendotae* did not show a regional pattern and 30% of lakes in each region had co-occurring populations. In contrast, *D. parvula* showed a significant pattern in co-occurrence among regions ($X_2^2 = 9.99$, $p = 0.007$); 55% of lakes in the south had co-occurring populations, compared to 27% in other regions.

Population dynamics in a Missouri reservoir

During the 28-month study of Stockton Lake, the water column was stratified from early May through September and mixed during the rest of the year (Fig. 1). An exception occurred for a six-week period during January–February 1996, when ice covered site 4. During June–August of both years, epilimnetic temperatures typically ranged from 25 to 30 °C. As the summer progressed, the thermocline extended from 9 m up to a minimum depth of 5 m. The bottom of the hypolimnion became anoxic ($<0.5 \text{ mg L}^{-1}$) by June and this anoxic layer progressed to the thermocline by the end of July. However, oxygen was intermittently replenished in the hypolimnion, perhaps through river underflows (THORNTON et al. 1990). During the study period, Secchi transparency was highly variable among sampling dates, ranging from 0.3 to 2.5 m (Fig. 1). Secchi depths tended to be greater at the down-reservoir site 2 (median 1.6 m) than at the up-reservoir site 4 (median 1.2 m) (paired Wilcoxon test, $W = 1176$, $p < 0.001$, $n = 55$). No significant association was found between Secchi depth and total phytoplankton density (Pearson correlation, $r = 0.00$, $p = 0.92$, $n = 33$), a result consistent with JONES & KNOWLTON'S (1993) findings that the turbidity of most Missouri reservoirs is due primarily to inorganic suspended solids.

Phytoplankton samples collected during 1994–95 revealed that this community included at least 52 genera, although on individual sampling dates only a few genera were dominant. Total cell density ranged from 5,000 to 70,000 cells mL^{-1} and showed no significant difference between sites (paired t-test, $t = 0.83$, $p = 0.44$, $n = 33$). Major peaks occurred at both sites in early August and mid-October (Fig. 1). Cyanobacteria (primarily *Oscillatoria* and *Raphidiopsis* filaments) dominated at both sites by late summer (up to 50% of cell density) and were common throughout the fall (Fig. 2). Edible chlorophytes and cryptophytes (primarily *Ankistrodesmus* and *Chroomonas*, respectively) maintained high densities all year, with densities $>10,000$ cells mL^{-1} in late summer and fall (Fig. 2). Diatoms (mainly *Cyclotella* and *Synedra*) were most common during winter and early spring. Thus, food resources for zooplankton included abundant edible genera during most of the study period, although the high cyanobacteria densities indicate the presence of potentially-interfering filaments during summer and early fall.

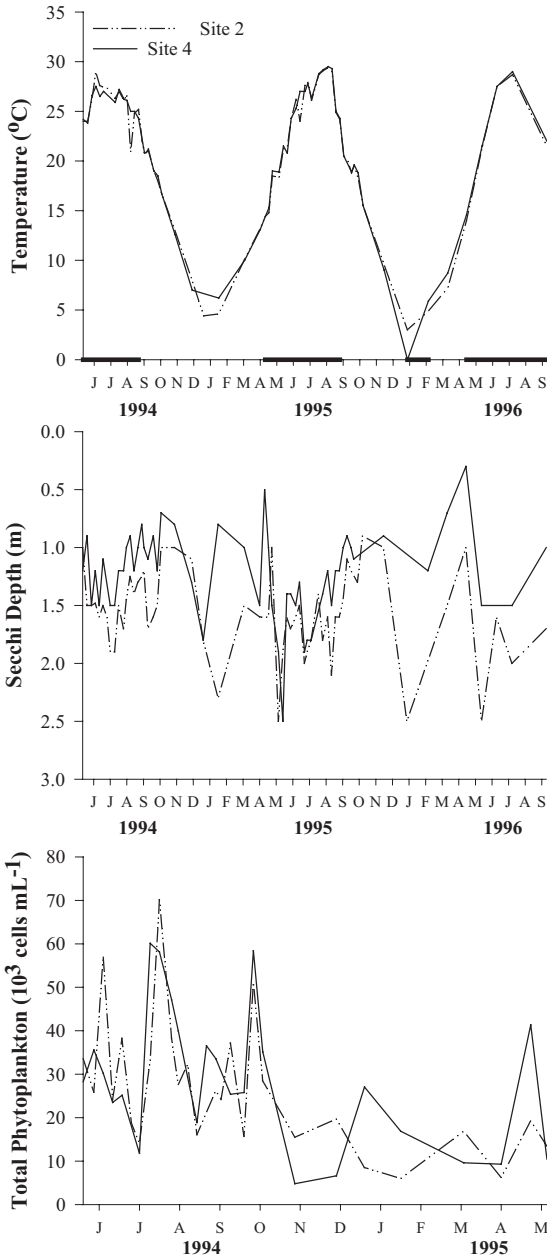


Fig. 1. Environmental variation at two sites in Stockton Lake, Missouri, 1994–96. In all figures, letters denote the midpoints of each month. Temperatures displayed in the top panel are averages from the top 5 m of the water column. Periods during which the lake was stratified are indicated by the solid bars on the horizontal axis. The hypolimnion was intermittently anoxic during stratified periods. Note that the duration of phytoplankton sampling (bottom panel) is shorter than the total study period.

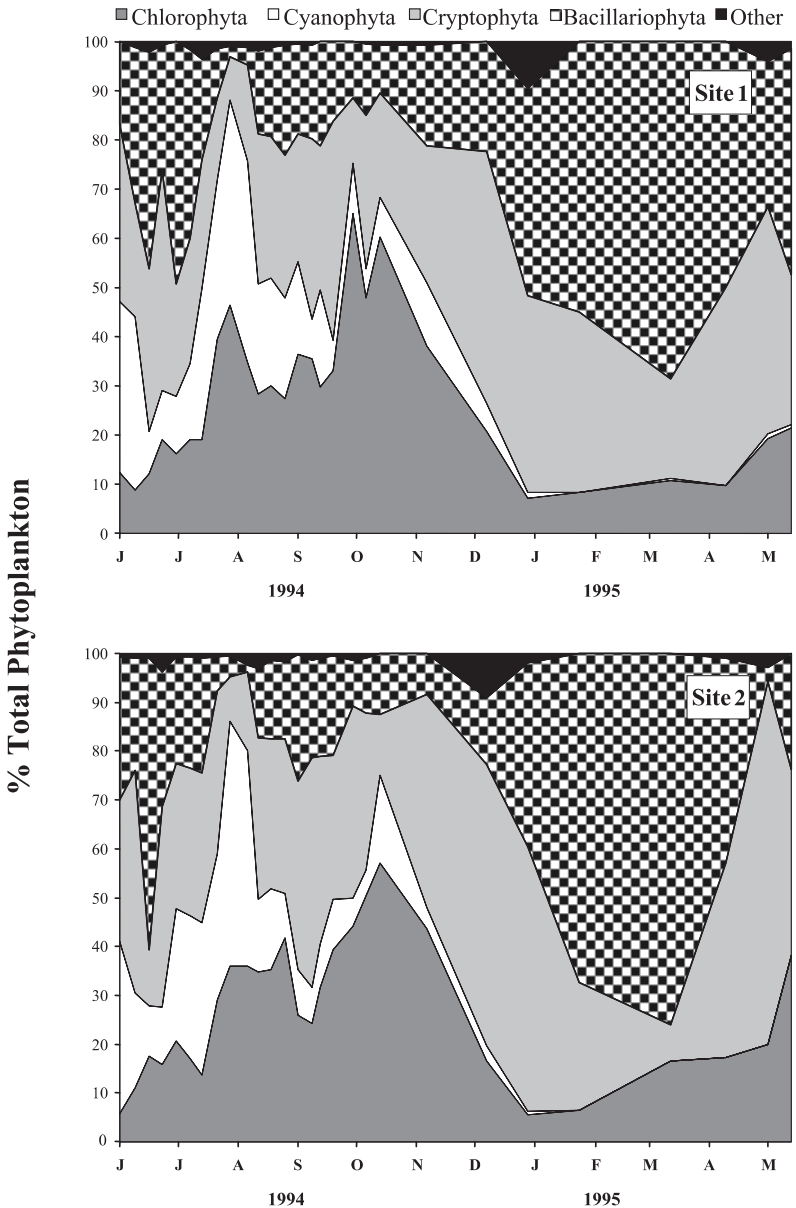


Fig. 2. Phytoplankton composition at two study sites in Stockton Lake, Missouri, 1994–95. Top – site 2, bottom – site 4. Other taxa include dinoflagellates, euglenoids, and chrysophytes.

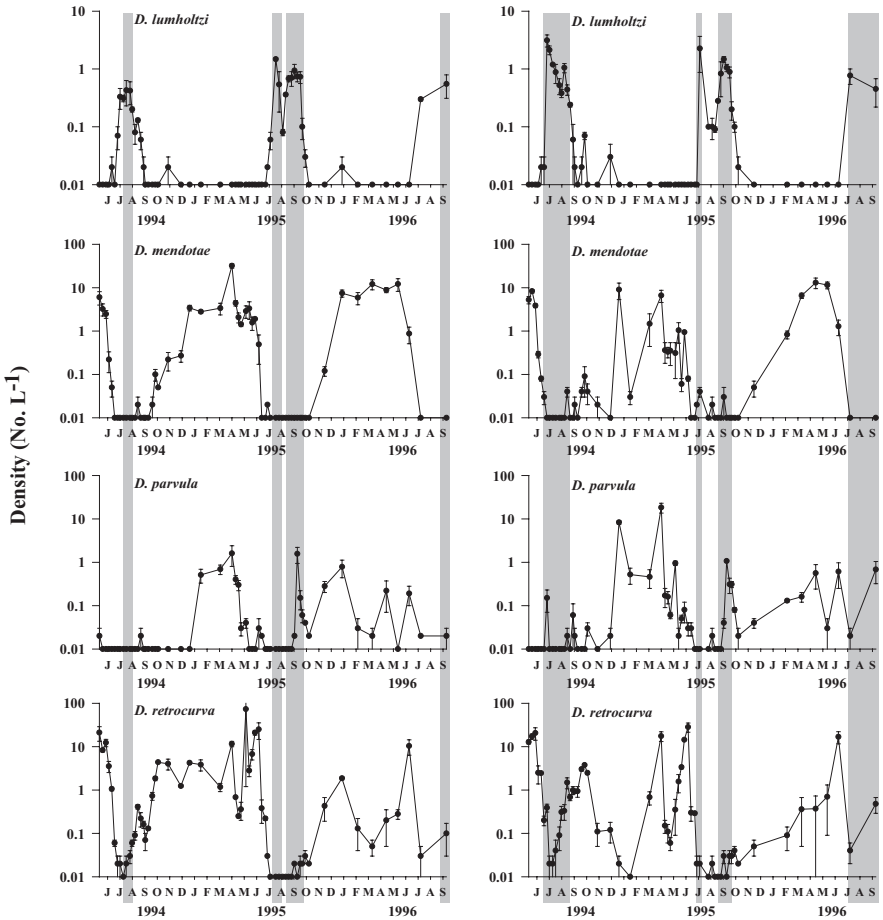


Fig. 3. *Daphnia* population dynamics at two sites in Stockton Lake, Missouri, 1994–96 (left panel – site 2, right panel – site 4). Mean \pm 1 SE, based on three replicate samples on each date. Shaded bars indicate periods when *D. lumholtzi* density exceeded 0.4 per liter. Note different scales on the y-axes.

The zooplankton community included 37 species of cladocerans, with four common *Daphnia* species (*D. lumholtzi*, *D. mendotae*, *D. parvula*, *D. retrocurva*) and two others that were rare (*D. ambigua* and *D. pulicaria*). Densities of *D. lumholtzi* and *D. parvula* both tended to be greater up-reservoir (site 4) than down-reservoir (site 2) (Sign tests, both $p < 0.01$), whereas those for *D. mendotae* and *D. retrocurva* appeared similar between sites ($p = 0.39$ and $p = 0.09$, respectively).

Daphnia lumholtzi was common only in July–September, with a maximal density (3 L^{-1}) at site 4 during July 1994 and summer peaks again in each of the following two years (Fig. 3). The same trends were observed at the down-

reservoir site 2, although the peak each year tended to occur about a month after site 4 (Fig. 3). *D. lumholtzi* generally was absent in the water column through spring and early summer, before temperatures rose to 25 °C (Fig. 1). Following its appearance in July, *D. lumholtzi* maintained positive rates of population increase for a brief period until early fall. After the lake cooled below 20 °C, the population declined. Nevertheless, a smaller peak occurred each year in late fall (Fig. 3), and low densities ($<0.1\text{ L}^{-1}$) of *D. lumholtzi* remained in the water column of site 2 into December, when temperatures had cooled to 7 °C. Males and ephippial females were observed intermittently during summer and fall; however these stages were never common.

In contrast to the late-summer dominance of *D. lumholtzi*, all three native *Daphnia* typically had their peak abundances during the cooler periods (exception *D. parvula* in 1995). Thus their dynamics appeared to show a complementary pattern to that of *D. lumholtzi* (Fig. 3). *D. mendotae* had overwintering populations and maximal abundances during spring of each year (Fig. 3), when temperatures rose from 9 to 21 °C. Their peak abundances during spring were generally 10 times greater than the peaks for *D. lumholtzi* in summer. *D. parvula* also peaked during winter-spring, although its densities were highly irregular over time (Fig. 3). For instance, this species had additional population peaks at both sites during September 1995 at the same time that *D. lumholtzi* was abundant. *D. retrocurva* showed peak abundance ($>20\text{ L}^{-1}$) each year in early summer, followed by a rapid decline in July and an increase again in the fall. *D. retrocurva* showed the greatest temporal overlap with *D. lumholtzi*, co-occurring on 32 to 42 % of dates at the two sites (Fig. 3). During their periods of co-occurrence, *D. retrocurva* tended to decline while *D. lumholtzi* was increasing. However, the negative correlations between their population growth rates were only marginally significant at one site (Table 2). By comparison, *D. parvula* and *D. mendotae* only co-occurred with *D. lumholtzi* on 8 to 23 % of the dates at the two sites.

During the warm periods when *D. lumholtzi* was common, their fecundities were generally low (mean 0.8 eggs per adult, range among dates 0–3.3). Nevertheless, large clutches were occasionally observed (up to 25 eggs). During cooler periods ($<20\text{ °C}$), the rare adults never carried eggs (Fig. 4). The three native species tended to have greater average clutch sizes than *D. lumholtzi* (means of 1.1 to 2.2 eggs per adult, Fig. 4). The fecundity of all *Daphnia* species was variable and distinct patterns among seasons were not discernable. All species showed a slight negative association between fecundity and temperature (Fig. 4), but the correlations were not statistically significant (Spearman-Rank Correlation: all $r \leq -0.34$, $p \geq 0.05$).

Based on the first year of study, when algal abundance data were available, associations were evident between *Daphnia* population dynamics and changes in temperature and phytoplankton community composition (Figs 1–3). As ex-

Table 2. Pearson correlation coefficients (p-values in parentheses) between each pair of *Daphnia* species for intrinsic growth rates (r) at each site of Stockton Lake. The sample size (n) is the number sample dates less one. Species codes as in Table 1. Significant correlations (Bonferroni experiment-wise $\alpha < 0.05$) are shown in bold.

	Dlum	Dmen	Dret
Site 2 (n = 59)			
Dmen	0.021 (0.876)	–	–
Dret	–0.246 (0.060)	0.423 (0.001)	–
Dpar	0.027 (0.837)	–0.005 (0.972)	0.213 (0.105)
Site 4 (n = 55)			
Dmen	–0.039 (0.776)	–	–
Dret	–0.058 (0.672)	0.283 (0.036)	–
Dpar	0.129 (0.347)	–0.006 (0.966)	0.308 (0.022)

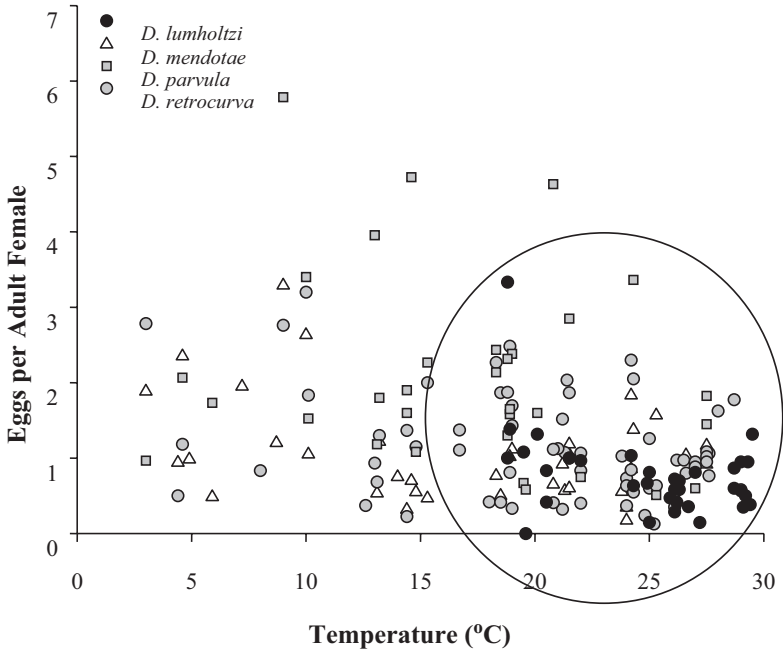


Fig. 4. *Daphnia* fecundity by temperature in Stockton Lake. Data from sites 2 and 4 are pooled. The circle envelopes the range of temperatures where *D. lumholtzi* carried eggs.

pected, phytoplankton densities and composition were associated with temperature. In particular, the density of cyanobacteria showed a strong positive correlation with temperature at both sites (Table 3). *D. lumholtzi* abundance was also positively correlated with temperature, whereas abundance of native

Table 3. Spearman-Rank correlation coefficients (p-values in parentheses) between temperature, density of phytoplankton (by division), and abundance of *Daphnia* (by species) at each sampling site in Stockton Lake, Missouri. Significant correlations (Bonferroni experiment-wise $\alpha < 0.05$)* are shown in bold. Species codes as in Table 1.

	Temperature	Bacillariophyta	Chlorophyta	Cryptophyta	Cyanophyta	Other
Site 2 (n = 28)						
Temperature	–	0.278 (0.160)	0.370 (0.058)	0.412 (0.033)	0.740 (<0.001)	0.347 (0.076)
Dlum	0.503 (0.008)	–0.420 (0.026)	0.351 (0.067)	–0.045 (0.828)	0.544 (0.003)	0.470 (0.011)
Dmen	–0.604 (<0.001)	0.140 (0.477)	–0.645 (<0.001)	–0.227 (0.245)	–0.588 (0.001)	–0.139 (0.480)
Dret	–0.513 (0.006)	0.105 (0.595)	–0.409 (0.030)	–0.077 (0.697)	–0.445 (0.018)	–0.278 (0.152)
Dpar	–0.454 (0.018)	0.043 (0.828)	–0.522 (0.004)	–0.442 (0.018)	–0.598 (0.001)	–0.244 (0.210)
Site 4 (n = 26)						
Temperature	–	0.202 (0.343)	0.384 (0.064)	0.302 (0.152)	0.740 (<0.001)	0.356 (0.088)
Dlum	0.438 (0.029)	–0.278 (0.170)	0.461 (0.018)	0.239 (0.240)	0.527 (0.006)	0.422 (0.032)
Dmen	–0.190 (0.363)	0.321 (0.101)	–0.403 (0.041)	–0.013 (0.949)	–0.377 (0.058)	–0.160 (0.434)
Dret	0.086 (0.681)	0.268 (0.186)	0.126 (0.540)	0.121 (0.555)	0.062 (0.762)	0.000 (0.999)
Dpar	–0.671 (<0.001)	0.068 (0.740)	–0.459 (0.018)	–0.182 (0.372)	–0.726 (<0.001)	–0.194 (0.341)

* Bonferroni probability levels for each of k comparisons based on $[1 - (1 - \alpha)^{1/k}]$ (SOKAL & ROHLF 1995); temperature vs. *Daphnia* 0.0127, temperature vs. algae 0.0102, algae vs. *Daphnia* 0.0026.

Daphnia species tended to have negative correlations with temperature at site 2 (Table 3). Peak abundance of *D. lumholtzi* at both sites tended to coincide with the peak abundance of cyanobacteria, whereas the three native *Daphnia* species were depressed at this time (Figs 1–3). This concordance in dynamics is reflected by the positive correlation between abundance of *D. lumholtzi* and cyanobacteria and negative correlations for native *Daphnia* (Table 3).

Discussion

The rapid invasion of reservoirs in the south-central United States by *Daphnia lumholtzi* indicates that this tropical exotic is highly successful in colonizing the dominant lentic habitats in the region. The current study documents distribution and dynamics of *Daphnia* in south-central reservoirs and allows an exploration of the factors that influence its success in reservoir environments. The broad survey reveals that *D. lumholtzi* is widespread in the region, where it is most prevalent in the south, and that it coexists with a variety of native *Daphnia* species. The greatest overlap in distribution is with *D. parvula*, a species that is common in the southern United States (HEBERT 1995). Detailed study of Stockton Lake indicates that the population dynamics of *D. lumholtzi* and native *Daphnia* tend to be complementary, in that periods of maximum abundance for *D. lumholtzi* and native *Daphnia* usually occurred during different times, and population growth rates of *D. lumholtzi* and the species with which it overlaps the most (*D. retrocurva*) tended to be negatively correlated.

These dynamics are strongly associated with increased temperature and cyanobacteria during summer and are discussed in more detail below.

The brief summer peaks of *D. lumholtzi* observed in the current study are consistent with an earlier study from Stockton Lake (HAVEL et al. 1995) and with other studies from the region (WORK & GOPHEN 1995, KOLAR et al. 1997, YURISTA et al. 2000). In contrast, *D. lumholtzi* in the deep south (Florida) tends to be more perennial, with populations appearing in spring as well as summer (EAST et al. 1999, HAVENS et al. 2000). These southern populations may thus have more opportunity to overlap with native *Daphnia*. In its native range, *D. lumholtzi* has a broad distribution, concentrated in tropical and subtropical regions of Africa, Australia, and Asia, where the species is generally widespread but not abundant (BENZIE 1988). In the tropics, *D. lumholtzi* is perennial or limited to the non-monsoonal seasons (GREEN 1971, SWAR & FERNANDO 1979) and shows short periods of abundance in mild subtropical climates (TIMMS 1973, GEDDES 1984, HAWKINS 1988). The evolution of *D. lumholtzi* in the tropics (BENZIE 1988) may pre-adapt this species for developing populations during hot summer conditions, such as observed in the current study. In this native range, reservoirs and river floodplains are the dominant lentic habitats (SERRUYA & POLLINGER 1983).

The underlying cause of seasonal succession by *Daphnia* in warm-water reservoirs is intriguing, and likely is due to a combination of changing environmental factors stimulating development and reproduction, interactions with other species, and disturbance. We explore each of these factors in the following paragraphs. Although competition among the plankton may sometimes be important in lakes (see review in DEMOTT 1989), this process depends to a great extent on equilibrium conditions that may rarely be met in reservoirs. Reservoirs are prone to hydrologic disturbance, which affects both invasion and seasonal succession. The large watersheds relative to reservoir volume causes rapid and variable water-renewal rates and loading of nutrients and sediments (THORNTON et al. 1990). Flooding and subsequent advective washout contribute to population declines of cladocerans (THRELKELD 1986 a). Changes in water level can be quite large (flood-control reservoirs) and frequent (hydropower reservoirs). The subsequent loss of littoral vegetation removes habitat structure and increases turbidity (WETZEL 1990), and enhanced turbidity causes lower food quality for grazers (KIRK & GILBERT 1990). Finally, the extensive hydrologic connectivity among reservoirs contributes to invasion processes (HAVEL et al. 2005 a), thus increasing recruitment by immigration. Overall, these processes may act to override the long-term effects of biotic interactions on zooplankton communities in reservoirs. Nevertheless, the complementary dynamics of *Daphnia* in the current study (Fig. 3) reveal that disturbance in Stockton Lake does not overwhelm these population cycles.

Succession of *Daphnia* species may be partially explained in terms of differences among species in their tolerance of specific environmental conditions. The widespread tropical distribution of *D. lumholtzi* (BENZIE 1988) and the summer peak in its dynamics (current study) suggest that this species is well adapted to summer conditions of temperate reservoirs it has invaded. One such factor is temperature. *D. lumholtzi* may be less sensitive than native *Daphnia* to the effects of high epilimnetic temperatures typical of reservoirs in the south-central United States. This hypothesis is supported by the positive and negative correlations of *D. lumholtzi* and native *Daphnia*, respectively, with temperature in Stockton Lake (Table 3). Life table experiments indicate that *D. lumholtzi* can maintain positive growth rates from 10 to 30 °C (LENNON et al. 2001). In contrast, many temperate zooplankton are suppressed, both directly and indirectly, by temperatures above 25 °C (MOORE et al. 1996). For instance, *Daphnia magna* shows a sharp decrease in growth rates above an optimum at about 25 °C (MITCHELL et al. 2004). Such differences between species could be due to the effects of metabolic stress on the tradeoff in energy budget, resulting in a greater expenditure on respiration and less expenditure on reproduction. Sensitivity to warm temperatures also is suggested by a recent large-scale experiment on vertical migration. When the epilimnion reached 29 °C, *D. mendotae* adults avoided this stratum and remained in deeper and food-poor waters, whereas *D. lumholtzi* continued to migrate into the epilimnion (HAVEL & LAMPERT 2006). The anoxic hypolimnion common in Stockton Lake (and other reservoirs) would drive *D. mendotae* out of this refuge and hence into suboptimal thermal conditions during mid-late summer.

Daphnia lumholtzi may be capable of expanding its thermal niche. This species can maintain positive growth at temperatures as cool as 10 °C (LENNON et al. 2001), and in-situ enclosure experiments revealed that *D. lumholtzi* can grow to high densities in late spring (JOHNSON & HAVEL 2001). During the current study of Stockton Lake, surface water temperatures exceeded 10 °C by April and 20 °C by June, but *D. lumholtzi* did not appear in the water column until later in the summer. If *D. lumholtzi* were abundant during early summer in Stockton Lake, then this species would overlap further with the native *Daphnia* species. The small winter populations of *D. lumholtzi* detected in the current study (Fig. 3) and in another reservoir in the region (Bull Shoals Lake, Missouri-Arkansas; J. HAVEL, pers. obs.) suggest some temporal expansion by this tropical species. The recent appearance of populations in the Great Lakes (Lake Erie, MUZINIC 2000) and Lake Pepin (a natural lake in the upper Mississippi River (BURDIS & HIRSCH 2005) indicates favorable conditions for *D. lumholtzi* in northern lakes as well. It is not clear why *D. lumholtzi* populations do not develop earlier (in spring) in south-central reservoirs while other *Daphnia* are abundant. Perhaps the specific cues for hatching resting eggs

(SCHWARTZ & HEBERT 1987) are not yet present. Alternatively, biotic interactions may slow population growth rate until summer.

Changes in algal food resources also may contribute to seasonal succession of *Daphnia*. Algae composition is well known to shift seasonally (PORTER 1977, Fig. 2), and the summer dominance of cyanobacteria in eutrophic lakes can inhibit zooplankton feeding and growth (DEMOTT 1989). It is well known that zooplankton differ among higher taxa (e. g., copepods vs. cladocerans, *Bosmina* vs. *Daphnia*) in their ability to discriminate against cyanobacteria (RICHMAN & DODSON 1983, DEMOTT 1989). The commonness of *D. lumholtzi* in eutrophic lakes (MAGADZA 1994, HAVEL et al. 2005 b) and in large rivers (THORP et al. 1994) suggests that this species is well adapted to persist in low-food-quality environments. Indeed, the current study from Stockton Lake reveals a strong positive association between the abundance of *D. lumholtzi* and the concentration of cyanobacteria (Table 3). Native *Daphnia* species tended to show the reverse pattern. Consistent with this trend, diet analysis of native and exotic *Daphnia* caged in a eutrophic lake indicates that, although they acquire a similar food composition, *D. lumholtzi* consumes more food than native *D. parvula* and *D. mendotae* when cyanobacteria are abundant in the environment (PATTINSON et al. 2003). Thus, it is possible that *D. lumholtzi* has a greater tolerance for cyanobacteria during summer conditions in reservoirs. Nevertheless, the positive correlation between temperature and cyanobacteria indicates that either factor alone or their interaction could be driving this pattern. Future experiments are necessary to determine the relative importance of temperature and cyanobacteria on the succession of native and exotic *Daphnia*.

In North American reservoirs, gizzard shad is widely stocked as a forage fish and is an important planktivore (DETMERS & STEIN 1992, DRENNER et al. 1996). This fish is also abundant in Stockton Lake (MICHALETZ 1997) and may contribute to the low summer densities of *Daphnia* observed in this lake as well as in other warm-water reservoirs. In the current study, peak summer densities of *D. lumholtzi* in Stockton Lake were much lower than the spring peak of native *Daphnia* (Fig. 3). Although *D. lumholtzi* are protected by their long spines against predation by larval and young juvenile bluegill sunfish (SWAFFAR & O'BRIEN 1996), the protection is not effective against larger bluegills (>50 mm, KOLAR & WAHL 1998), and diet analyses indicate positive selectivities by several sunfishes and white bass toward *D. lumholtzi* (LEMKE et al. 2003). Because *Daphnia* are a vital component of lake food webs and *D. lumholtzi* are abundant when native *Daphnia* are scarce, this exotic may contribute to food resources during summer conditions. This would mean that, all else being equal, we would expect fish production to go up in lakes that have been invaded by *Daphnia lumholtzi*.

In summary, the widespread invasion and population dynamics of *D. lumholtzi* in reservoirs of the south-central United States indicate they are well adapted to summer conditions in these systems. The underlying reasons for the seasonal succession between this exotic and native *Daphnia* in reservoirs may be linked to temperature and cyanobacteria, but requires careful experiments to tease out cause and effect.

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