

# Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success

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*We investigated the effects of water temperature on the exotic cladoceran Daphnia lumholtzi in a eutrophic Kansas reservoir (USA) and under laboratory conditions. Daphnia lumholtzi demonstrated a distinct late summer appearance in the reservoir at temperatures between 26 and 31°C, which corresponded with steep declines in the densities of native Daphnia spp. Laboratory life-table experiments confirmed that D. lumholtzi performs well at elevated water temperatures. The intrinsic rate of increase (r), net reproductive rate (R<sub>0</sub>), age at first reproduction, survivorship (l<sub>x</sub>) and molting rates all demonstrate that D. lumholtzi has a high temperature optimum between 20 and 30°C. A comparison of literature-reported r-values indicates that the reproductive rate of D. lumholtzi is comparable with other Daphnia spp. between 20 and 25°C, but also implies that D. lumholtzi may out-perform some Daphnia spp. at temperatures >25°C. Collectively, these results suggest that D. lumholtzi may be taking advantage of a late summer thermal niche, and that this invader may continue to colonize lakes and reservoirs in the southern US. However, life table data also indicate that D. lumholtzi performs poorly at temperatures < 10°C, which may inhibit the range expansion of this invader into northern waters.*

## INTRODUCTION

The invasion of aquatic habitats by non-native species is a critical issue in both conservation science and aquatic ecology. Foreign invaders, including exotic fishes (Moyle and Light, 1996), molluscs (Strayer, 1999) and crustacean zooplankton such as *Bythotrephes cederstroemi* (Lehman, 1987) are increasingly threatening the integrity of both marine and freshwater ecosystems. This form of biological pollution has the potential of disturbing native environments by displacing indigenous taxa, and by altering the transfer of energy and matter within an ecosystem (Vitousek, 1986; Yan and Pawson, 1997). Despite the dramatic impacts that some invasions have caused, only a small fraction of exotic species successfully establish viable populations, and even fewer invasions result in major alterations of an ecosystem (Williamson, 1996). Why do exotic species succeed or fail when introduced into a new environment? This important question can be addressed in two ways: (i) by examining a system's susceptibility to invasion, based on its community characteristics; and (ii)

by identifying species traits of an exotic organism that will make it a successful invader. The second key issue will be the focus of this research.

Invasion success is strongly influenced by a species' ability to adapt to critical environmental variables such as salinity (Thompson, 1991), moisture (Melgoza *et al.*, 1990) and temperature (Garton *et al.*, 1990). For example, temperature commonly limits the distribution and abundance of animal species by defining ranges of tolerance. Within these ranges, temperature regulates metabolic activities and influences interspecies interactions (Hall *et al.*, 1992; Stelzer, 1998; Sanford, 1999). Thus, temperature regimes can act as significant obstacles for an invading species, and are thought by some investigators to account for a majority of failed invasions (Lodge, 1993).

Late summer conditions in temperate lakes and reservoirs offer the potential opportunity for invasion by warm water-adapted zooplankton species (Foran, 1986b). Thermal variation is an essential temporal pattern that contributes to the maintenance of species co-existence in lentic ecosystems (Hutchinson, 1961; Sommer, 1989).

However, late summer temperature extremes can potentially limit some populations because the viability and performance of most temperate crustacean zooplankton begin to decline when water temperatures exceed 25°C (Moore *et al.*, 1996). Locomotion, filtering rates, ingestion rates and assimilation rates increase with temperature but are associated with high energetic costs due to elevated respiration; survivorship is also typically sub-optimal at higher temperatures (Hall, 1964; Orcutt and Porter, 1984; Foran, 1986a; Lampert, 1987; Yurista, 1999). Ultimately, population growth rates of temperature-stressed zooplankton decline, and trophic interactions may become destabilized (Moore *et al.*, 1996; Chen and Folt, 1996; Beisner *et al.*, 1997; Petchey *et al.*, 1999).

These effects, combined with the indirect effects of elevated temperatures on phytoplankton resources and predator dynamics, contribute to the seasonal succession of zooplankton communities (Lynch, 1978; Threlkeld, 1986). For example, DeMott (DeMott, 1983) documented how late summer conditions, characterized by poor-quality food resources and higher water temperatures, led to the temporary absence of *Daphnia* in the northeastern USA. Similar conditions in a Midwestern lake facilitated the establishment of a native warm-water tolerant species, *Daphnia galeata mendotae* (Hu and Tessier, 1995). Recently, late summer appearances of the exotic *Daphnia lumholtzi* (Sars) in southern US water bodies (Havel *et al.*, 1995; Work and Gophen, 1999; East *et al.*, 1999) have raised the question of whether this new crustacean invader is taking advantage of a late summer ‘open niche’ (Elton, 1958).

*Daphnia lumholtzi* is a cladoceran native to Africa, Asia and Australia. It was first detected in a Texas reservoir in 1990 (Sorenson and Sterner, 1992), and was documented soon thereafter in Stockton Lake, Missouri (Havel and Hebert, 1993). Since these initial observations, *D. lumholtzi* has invaded at least 125 lakes and reservoirs in the US from Florida to Arizona (J. Havel, S.W. Missouri State University, unpublished data). Due to its tropical and subtropical origins, *D. lumholtzi* may be pre-adapted to warm water conditions that commonly exceed 25°C (Green, 1967; Gophen, 1979; Swar and Fernando, 1979; King and Greenwood, 1992). Since these environmental temperatures approach the maximum thermal tolerances reported for most temperate crustacean zooplankton (Moore *et al.*, 1996), *D. lumholtzi* may occupy a unique thermal niche in North American lakes and reservoirs. Conversely, given that *D. lumholtzi* has evolved in regions of warmer climate, water temperature may present a major physical constraint on its ecological success as an invasive species in colder waters of North America.

We report here seasonal population trends of *D. lumholtzi* and native *Daphnia* in relation to changes in surface water temperatures in a eutrophic midwestern

reservoir. Additionally, we present results from laboratory-based life table experiments that delimit the environmental tolerances and fitness of this invader over a broad thermal gradient. We identify species traits that may be useful for predicting the invasion success and the future range expansion of *D. lumholtzi*, and compare its performance with that of other *Daphnia* species using published data.

## METHOD

### Field site and field collection

Clinton Reservoir, located 8 miles south of Lawrence, Kansas, is a multi-purpose reservoir impounded by the US Army Corps of Engineers in 1978. It has a surface area of approximately 2800 ha (maximum depth = 12 m, mean depth = 5 m). Due to its large fetch and the local climate, Clinton is a polymictic reservoir that rarely stratifies. Clinton Reservoir is moderately eutrophic [TN = 611 µg l<sup>-1</sup>; TP = 40 µg l<sup>-1</sup>; chlorophyll *a* = 15 µg l<sup>-1</sup>; Secchi depth = 1.1 m (Wang *et al.*, 1999)] and supports a small–medium body size zooplankton community consisting of *Daphnia retrocurva*, *Daphnia galeata mendotae*, *Diaphanosoma birgei*, *Ceriodaphnia reticulata*, *Bosmina longirostris*, *Cyclops* spp. and *Diatomus* spp. *Daphnia lumholtzi* was first detected in Clinton Reservoir in 1994, and seasonal populations have persisted since that time.

Zooplankton were sampled at least monthly from May 1997 through December 1997. Quantitative vertical hauls were obtained from a 10 m depth, using a 220 µm Wisconsin net, at a site located 100 m from the dam. These samples were preserved with 4% formalin and identified according to Ward and Wipple (Ward and Wipple, 1959) under a Wild dissecting microscope at 20–40× magnification.

Surface water temperatures at the sampling site were recorded at six depths (0.25, 1.5, 3.0, 6.0, 9.0 and 10.0 m) using a Horiba U-10 Water Quality Checker. Although the reservoir temporarily stratified between 6 and 9 m on 12 June, no thermocline was detected on any other sampling date. The mean difference in temperature between the 0.25 m and the 10 m depths was only 1.9 ± 0.59°C over the entire sampling period; we therefore used only the 0.25 m (surface) temperature measurements in our analyses.

### Life table measurements

Gravid *D. lumholtzi* were obtained from Clinton Reservoir in August 1997 using a Wisconsin zooplankton net, and were maintained at room temperature in batch cultures using algae-amended Whatman GF/C-filtered lake water (West Campus Pond, Lawrence, Kansas). These animals

were fed weekly with equal combinations of *Selanastrum* sp. (Carolina Biological Supply Company) and *Chlamydomonas reinhardtii* (William Dentler, University of Kansas) at a total concentration of  $10^4$  algal cells  $\text{ml}^{-1}$ . Axenic algal cultures were maintained semi-continuously in Bristol's solution. Equal volumes of *Selanastrum* and *Chlamydomonas* cultures were centrifuged, resuspended in filtered lake water and counted using a hemacytometer.

Prior to initiating the life table experiments, we attempted to acclimate *D. lumholtzi* by growing animals in subcultures for multiple generations (Orcutt and Porter, 1984; Claska and Gilbert, 1998) at each of six temperatures (5, 10, 15, 20, 25 and 30°C). However, after three weeks, *D. lumholtzi* produced no eggs at either 5 or 10°C. Subsequently, we cultured a large population of *D. lumholtzi* for two generations at 25°C, and then randomly chose six groups of 15 individuals from the first clutch of the F2 generation as our experimental organisms. These individuals were transferred into 70 ml tissue culture flasks containing GF/C-filtered lake water and equal combinations of *Selanastrum* sp. and *Chlamydomonas reinhardtii* at a total algal concentration of  $10^4$  algal cells  $\text{ml}^{-1}$ . The experimental organisms were then re-acclimated in tissue culture flasks at their respective experimental treatment temperatures. Measurements indicated that it took between 75 and 110 min for lake water in the tissue culture flasks to reach the new target temperature. Pilot studies also indicated that neonates of *D. lumholtzi* did not experience mortality as a direct result of being transferred from 25°C to their respective treatment temperatures.

Two successive sets of 21-day life table experiments were conducted with these animals in environmental chambers maintained on a 16:8 h light–dark cycle, during which time we measured the life history parameters of *D. lumholtzi* grown at 5, 10, 15, 20, 25 and 30°C. At each daily transfer, we recorded survivorship, fecundity, and whether each organism had molted within the previous 24 h. We then used Euler's method to calculate the intrinsic rate of increase,  $r$  ( $\text{day}^{-1}$ ):

$$1 = \sum e^{-rx} l(x) b(x) \quad (1)$$

where  $b(x)$  is the number of neonates born to an individual female for a specific day ( $x$ ), and  $l(x)$  is the proportion of the original cohort surviving to the next day (Gotelli, 1998). Estimates of variance for the intrinsic rate of increase at each temperature treatment were generated using jack-knife methods according to Meyer *et al.* (Meyer *et al.*, 1986). From our measurements, we also determined net reproductive rate ( $R_0$ , total offspring per 21 days per female), mean clutch size, age at first reproduction and molting rate (number of molts shed per day). The relationships between temperature and the life history

traits above were analyzed using linear regression for replicated samples (Draper and Smith, 1998). Our data met assumptions of normality and equal variance, and there was no lack of fit for the models we employed. A non-parametric Kaplan–Meier analysis was performed to test for differences in survivorship among the six temperature treatments (SAS Institute Incorporated, 1995).

## RESULTS

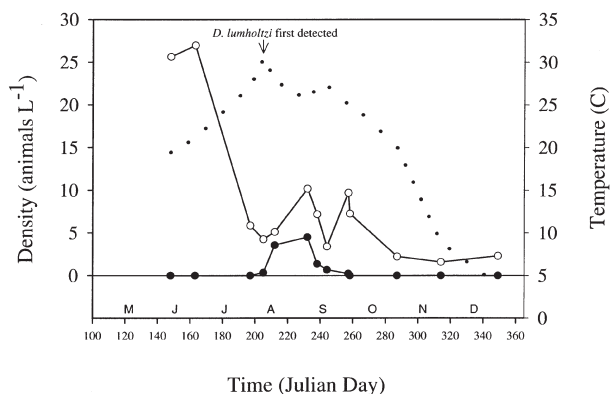
### Seasonal dynamics of temperature and *Daphnia* in Clinton Reservoir

The abundance of *D. galeata mendotae* comprised 25 and 29% of the native *Daphnia* on the May and June sampling dates, respectively. The abundance of *D. retrocurva* constituted the remaining portion of the native *Daphnia* in May and June, and was the only native *Daphnia* species present after the June sampling date. We thus grouped *D. galeata mendotae* and *D. retrocurva* together in this study, and refer to this assemblage as 'native *Daphnia*'. *Daphnia lumholtzi* was detected in the Clinton Reservoir water column only from 24 July–15 September, 1997, when surface water temperatures ranged between 25.0 and 31.0°C. *Daphnia lumholtzi* had a mean density of  $1.8 \pm 0.74$  animals  $\text{l}^{-1}$  in the reservoir water during this period.

The appearance of *D. lumholtzi* in 1997 corresponded with a decline in the density of native *Daphnia*, and also coincided with the highest water temperature (31°C) recorded during the 8 month sampling period (Figure 1). On 12 June (day 163), the total density of native *Daphnia* was 27  $\text{l}^{-1}$ . Six weeks later on 16 July (day 197), native *Daphnia* populations had decreased by 78% to only 6  $\text{l}^{-1}$ . *Daphnia lumholtzi* was first detected one week following the native *Daphnia* crash (July 24). Native *Daphnia* densities remained low while *D. lumholtzi* was present in the water column, but native *Daphnia* densities were always greater than *D. lumholtzi* densities. *Daphnia lumholtzi* never comprised more than 5% of the total zooplankton abundance or biomass on any sampling date.

### Life history characteristics of *Daphnia lumholtzi*

The apparent preference of *D. lumholtzi* for warmer temperatures in Clinton Reservoir (Figure 1) is consistent with the life history characteristics summarized in Table I. The intrinsic rate of increase ( $r$ ) for laboratory-cultured *D. lumholtzi* exhibited a unimodal response over the temperature gradient in our experiments (Figure 2a). No offspring were produced at either 5 or 10°C, and 15°C was the lowest temperature at which *D. lumholtzi* exhibited a positive intrinsic rate of increase ( $r = 0.213 \pm 0.0005$   $\text{day}^{-1}$ ). Population growth rate increased curvilinearly



**Fig. 1.** Densities of *Daphnia lumholtzi* and native *Daphnia* spp. in relation to surface water temperatures in Clinton Reservoir, Kansas 1997. (....Temperature (°C), ● *Daphnia lumholtzi*, ○ native *Daphnia* spp.).

with temperature up to 25°C ( $r_{\max} = 0.364 \pm 0.0013$  day<sup>-1</sup>), and then declined at 30°C ( $r = 0.306 \pm 0.0013$  day<sup>-1</sup>). A quadratic model provided an excellent fit to these data:

$$r = -0.73 + 0.0915 T - 0.0019 T^2 \quad (2)$$

where T is the experimental water temperature ( $P < 0.0001$ ,  $R^2 = 0.99$ ,  $n = 5$ ). This empirical model predicts that *D.lumholtzi* should have a positive net growth rate between 11 and 38°C, with optimal performance at 24°C.

Positive values for net reproductive rate ( $R_0$ ) also occurred between 15 and 30°C in our treatments (Figure 2b). As with the intrinsic rate of increase, net reproduction was unimodally distributed, with the highest offspring output occurring in the 20°C treatment. The quadratic model:

$$R_0 = -120.65 + 115.21 T - 0.363 T^2 \quad (3)$$

( $P < 0.0001$ ,  $R^2 = 0.62$ ,  $n = 55$ ) predicts positive net reproduction between 11 and 31°C, with maximum fecundity occurring at 21°C.

Age at first reproduction in the *D. lumholtzi* cultures declined asymptotically between 15 and 30°C, and could be described as:

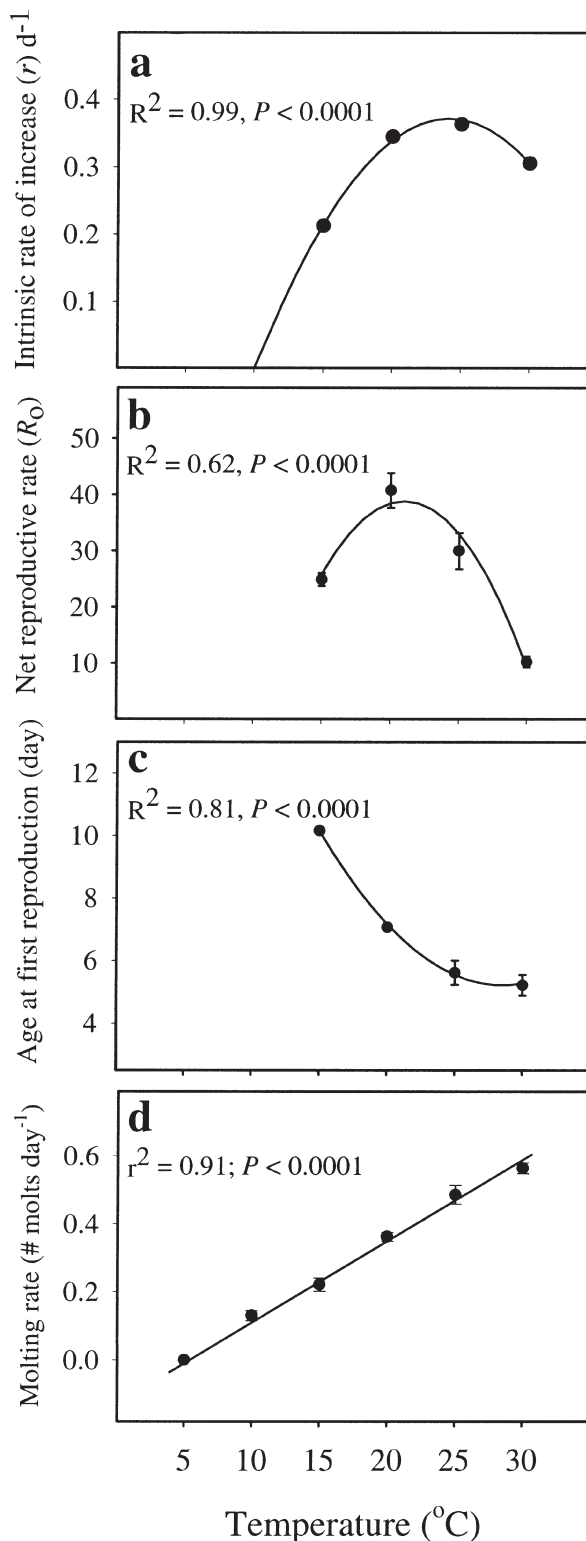
$$\text{Age} = 27.14 - 1.54 T + 0.027 T^2 \quad (4)$$

( $P < 0.0001$ ,  $R^2 = 0.81$ ,  $n = 55$ ). The age at first reproduction decreased from  $10.2 \pm 0.10$  days at 15°C to  $5.2 \pm 0.33$  days at 30°C (Figure 2c).

The molting rate for *D. lumholtzi* increased linearly over the experimental temperature gradient (Figure 2d):

$$\text{Molting Rate} = 0.109 + 0.023 T \quad (5a)$$

( $P < 0.0001$ ,  $r^2 = 0.91$ ,  $n = 72$ ). This response is consistent



**Fig. 2.** Life history responses of *Daphnia lumholtzi* grown at different temperatures under laboratory conditions: **a** = intrinsic rate of increase ( $r$ ); **b** = net reproductive rate ( $R_0$ ); **c** = age at first reproduction; **d** = molting rate.

Table I: Life history characteristics of *Daphnia lumholtzi* obtained from laboratory life table experiments

Treatment temperature (°C)	Intrinsic rate of increase ( <i>r</i> ) day <sup>-1</sup>	Net reproductive rate ( <i>R</i> <sub>0</sub> )	Mean clutch size	Age at first reproduction (days)	Survivorship (days)	Molting rate (days)
5	0 (N/A)	0 (N/A)	0 (N/A)	0 (N/A)	4.1 ± 0.41 <i>n</i> = 15	0 (N/A)
10	0 (N/A)	0 (N/A)	0 (N/A)	0 (N/A)	18.9 ± 1.40 <i>n</i> = 15	0.130 ± 0.0149 <i>n</i> = 14
15	0.213 ± 0.0005 <i>n</i> = 30	24.9 ± 1.15 <i>n</i> = 13	8.2 ± 0.61 <i>n</i> = 38	10.2 ± 0.10 <i>n</i> = 13	19.1 ± 1.33 <i>n</i> = 15	0.221 ± 0.0194 <i>n</i> = 15
20	0.345 ± 0.0005 <i>n</i> = 30	41.1 ± 3.09 <i>n</i> = 15	9.3 ± 0.38 <i>n</i> = 68	7.1 ± 0.07 <i>n</i> = 15	20.0 ± 0.68 <i>n</i> = 15	0.362 ± 0.0130 <i>n</i> = 15
25	0.364 ± 0.0013 <i>n</i> = 30	20.0 ± 3.22 <i>n</i> = 13	7.5 ± 0.44 <i>n</i> = 52	5.6 ± 0.39 <i>n</i> = 13	13.9 ± 1.73 <i>n</i> = 15	0.486 ± 0.0276 <i>n</i> = 13
30	0.306 ± 0.0013 <i>n</i> = 30	10.3 ± 1.00 <i>n</i> = 14	4.24 ± 0.33 <i>n</i> = 34	5.2 ± 0.33 <i>n</i> = 14	12.5 ± 0.63 <i>n</i> = 15	0.564 ± 0.0158 <i>n</i> = 15

Values represent means ± SEM, *n* = sample size.

with the Vant’ Hoff function (Hochachka and Somero, 1984):

$$Q_{10} = (V_1/V_2)^{(T_1-T_2)} \quad (5b)$$

where *V*<sub>1</sub> is the developmental rate (day<sup>-1</sup>) at temperature *T*<sub>1</sub>, and *V*<sub>2</sub> is the developmental rate (day<sup>-1</sup>) at temperature *T*<sub>2</sub>. The Vant’ Hoff function was applied to the molting rates of *D. lumholtzi* over three 10°C temperature increments (10 and 20°C; 15 and 25°C; 20 and 30°C). Molting rates for *D. lumholtzi* agreed well with the predictions of the Vant’ Hoff function, with an average *Q*<sub>10</sub> value of 2.18 between 10 and 30°C.

Survivorship (*l*<sub>x</sub>) of *D. lumholtzi* was highest between 10 and 20°C; at these temperatures, 80% or more of the original organisms were still alive on day 21. Survivorship was significantly lower for animals grown at 25 and 30°C. In the 5°C treatment, *D. lumholtzi* survival was the lowest and all animals died by day 7 (Figure 3).

## DISCUSSION

Seasonal thermal variation has long been recognized as a significant factor contributing to the co-existence of plankton species in lakes and reservoirs (Hutchinson, 1961; Sommer, 1989). In a direct sense, zooplankton respond to temperature according to the species’ tolerances and optima. However, indirectly, temperature influences species interactions (e.g. competition and predation), which can lead to seasonal species turnover (Lynch, 1978; Threlkeld, 1986; Hu and Tessier, 1995). It

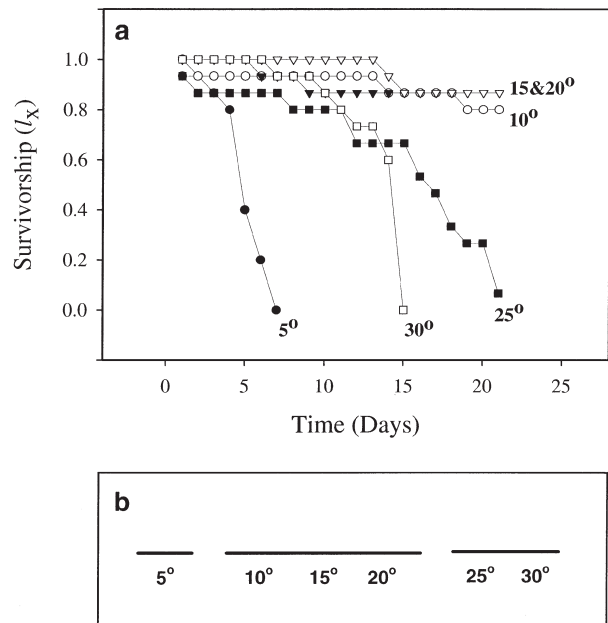


Fig. 3. Survivorship (*l*<sub>x</sub>) of *Daphnia lumholtzi* grown at different temperatures under laboratory conditions: **a** = percent survivorship of individuals over the experimental time; **b** = results from a non-parametric Kaplan-Meier survival analysis. Separation of solid lines denotes statistical differences among treatments.

is during these seasonal transitions that plankton invasion success may be promoted by reversals in competitive ability for resources, and by native species’ intolerance of late summer temperature extremes. Population- and

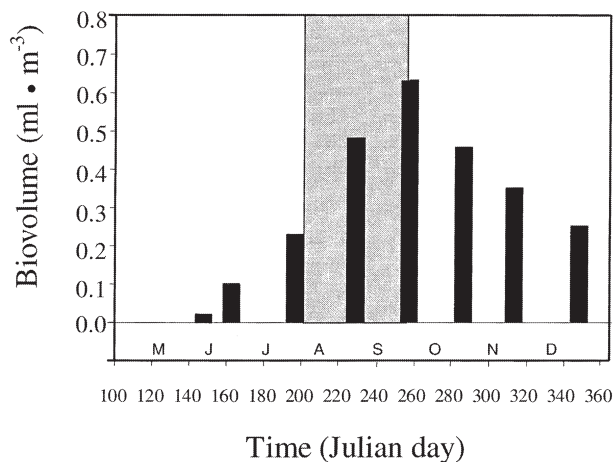
community-level information may provide clues about community assembly at these critical times, and help to identify potential temporal opportunities for biological invasions.

Field results from Clinton Reservoir indicate that *D. lumholtzi* grow well at elevated water temperatures of late summer, while native *Daphnia* populations decline. *Daphnia lumholtzi* had a distinct seasonal occurrence in the water column and was not detected until late July when surface water temperatures reached 31°C (Figure 1). The temperature on this sampling date was the highest recorded for Clinton Reservoir in 1997 and approaches the maximum observed water temperature of most lakes and reservoirs worldwide (Welch, 1952; Straškraba, 1980). The seasonal emergence of *D. lumholtzi* under these conditions indicates that its thermal optimum may exceed that of native *Daphnia*. The majority of native *Daphnia* in temperate lakes and reservoirs are not well adapted to these upper temperature extremes (Moore *et al.*, 1996); it is likely that increasing surface water temperatures from June to July affected the performance of native *Daphnia* and contributed to the concurrent steep decline in their abundance (Figure 1). Even though densities of native *Daphnia* always exceeded densities of *D. lumholtzi*, population crashes of native species during late summer most likely decreased the degree of intra-guild competition that this invader might have otherwise experienced (DeMott, 1983, 1989; Crisman *et al.*, 1995; Hu and Tessier, 1995).

The late summer successional appearance of *D. lumholtzi* cannot be attributed solely to the direct effects of temperature, however. The quality and quantity of phytoplankton influences seasonal zooplankton assembly (DeMott, 1983, 1989; Sommer *et al.*, 1989; Hu and Tessier, 1995; Pinto-Coelho, 1998). Late summer phytoplankton communities in temperate lakes and reservoirs often comprises cyanobacteria, which are generally considered a poor quality food source for zooplankton due to handling difficulties, toxins and low nutritional content (Fulton and Paerl, 1988; Gulati and DeMott, 1997; Claska and Gilbert, 1998). The phytoplankton community of Clinton Reservoir shifted towards cyanobacterial dominance beginning in mid-June, with maximum cell concentrations occurring in mid-September (Figure 4). The timing of this bloom coincided with water column TN:TP ratios below 10 by mass (Meyer, 1998) as predicted by resource-ratio theory (Smith, 1983; Smith and Bennett, 1999). Synergistic interactions between low quality food and elevated water temperatures explain late summer declines for some *Daphnia* populations (Threlkeld, 1986; Claska and Gilbert, 1998) and thus, may also be responsible in part for the observed late summer crash of native *Daphnia* in Clinton Reservoir. In contrast, *D. lumholtzi*,

along with other tropical cladocerans, may be well adapted to late summer conditions in temperate waters. Epilimnetic water temperatures in the native range of *D. lumholtzi* are 10–15°C degrees warmer than lakes in temperate latitudes; furthermore, tropical–subtropical lakes support cyanobacteria communities for extended time periods due to intrinsically low TN:TP ratios (Thornton, 1987). Therefore, eutrophic Midwestern US reservoirs in late summer may closely simulate the native conditions of *D. lumholtzi* and thus, may provide a temporal opportunity that is favorable for invasion success.

Life history traits are key biological factors that help to determine invasion success of a particular species. Life table data provided by this study indicate that at elevated temperatures, *D. lumholtzi* exhibits a high reproductive rate, short life cycle duration, early reproductive maturity and fast development rates—all of which are characteristics of an ‘ideal invader’ (Crawley, 1986; Ehrlich, 1986). Table II compares the intrinsic rate of increase ( $r$ -value) of *D. lumholtzi* with literature-reported  $r$ -values for six additional species of *Daphnia*, grown under similar conditions, at temperatures between 20 and 30°C. Based on this comparison, it appears that *D. lumholtzi* performs comparably with other *Daphnia* spp. at temperatures between 20 and 25°C, but that it may outperform some *Daphnia* spp. at temperatures >25°C. At 20°C, both *D. magna* and *D. pulex* have marginally greater  $r$ -values than *D. lumholtzi* (Smith, 1963; Arnold, 1971); however, other studies report that *D. magna* and *D. pulex* have lower  $r$ -values (Frank *et al.*, 1957; Goulden *et al.*, 1982). The  $r$ -value of *D. lumholtzi* is greater than that of both *D. galeata mendotae* and *D. pulicaria* at 20°C and at 25°C, *D. lumholtzi* has a greater  $r$ -value than



**Fig. 4.** Cyanobacteria biovolume and the seasonal occurrence of *Daphnia lumholtzi* in Clinton Reservoir, Kansas 1997. ■ = Cyanobacteria; ■ = *D. lumholtzi* > 0.

Table II: Intrinsic rate of increase ( $r$ ) for *Daphnia* species grown under laboratory conditions at temperatures  $>20^{\circ}\text{C}$ 

Temperature	Species	$r$ ( $\text{day}^{-1}$ )	Study	Food concentration (cells $\text{m}^{-3}$ )	Body size (mm)	Food type
20°C	<i>D. magna</i>	0.44	Smith (1963)	$10^6$	2.0–5.0	<i>Chlorella et al.</i>
	<i>D. pulex</i>	0.37	Arnold (1971)	$6 \cdot 10^4$	1.1–3.5	Ankistrodesmus
	<i>D. lumholtzi</i>	0.345	This study	$10^4$	0.8–1.9	<i>Chlamydomonas</i> , <i>Selenastrum</i>
	<i>D. pullicaria</i>	0.33	Frank (1952)	$1.5 \cdot 10^6$	1.4–3.2	<i>Chlorococcum</i>
	<i>D. magna</i>	0.316	Goulden <i>et al.</i> (1982)	$10^4$	2.0–5.0	<i>Chlamydomonas</i> , Ankistrodesmus
	<i>D. pulex</i>	0.29	Frank <i>et al.</i> (1957)	$10^7$	1.1–3.5	<i>Chlamydomonas</i>
	<i>D. galeata mendotae</i>	0.286	Goulden <i>et al.</i> (1982)	$10^4$	1.2–2.8	<i>Chlamydomonas</i> , Ankistrodesmus
	<i>D. galeata mendotae</i>	0.22	Hall (1964)	$1.6 \cdot 10^4$	1.2–2.8	<i>Chlorella et al.</i>
	<i>D. laevis</i>	0.246	Foran (1986a)	$10^4$	1.1–1.8	<i>Chlamydomonas</i>
	<i>D. magna</i>	0.082	Foran (1986a)	$10^4$	2.0–5.0	<i>Chlamydomonas</i>
21°C	<i>D. lumholtzi</i>	0.364	This study	$10^4$	0.8–1.9	<i>Chlamydomonas</i> , <i>Selenastrum</i>
	<i>D. galeata mendotae</i>	0.36	Hall (1964)	$1.6 \cdot 10^4$	1.2–2.8	<i>Chlorella et al.</i>
	<i>D. parvula</i>	0.347	Pace (1980)	$10^4$	1.1–1.4	natural seston
	<i>D. parvula</i>	0.32	Orcutt and Porter (1986)	$10^4$	1.1–1.4	<i>Chlamydomonas</i>
25°C	<i>D. laevis</i>	0.307	Foran (1986a)	$10^4$	1.1–1.8	<i>Chlamydomonas</i>
	<i>D. magna</i>	0.138	Foran (1986a)	$10^4$	2.0–5.0	<i>Chlamydomonas</i>
30°C	<i>D. lumholtzi</i>	0.306	This study	$10^4$	0.8–1.9	<i>Chlamydomonas</i> , <i>Selenastrum</i>

both *D. galeata mendotae* and *D. parvula*. Life table studies conducted at temperatures >30°C for other temperate zone *Daphnia* are severely lacking, but survival and reproduction for *Daphnia* typically declines at temperatures >25°C (Moore *et al.*, 1996). *Daphnia lumholtzi* is a relatively small-bodied daphnid and has a high *r*-value at 20°C and at 25°C relative to most of the *Daphnia* species listed in Table II. This evidence qualitatively agrees with suggestions (i) that invasion success may decrease with body size (Lawton and Brown, 1986) and (ii) that successful invaders often have high reproductive rates.

While high temperatures may contribute to the invasion success of *D. lumholtzi*, low temperatures decrease its performance and may contribute to failed invasions in colder water bodies. Low temperatures significantly affected the life history characteristics of *D. lumholtzi* and may account for its absence in Clinton Reservoir during cooler water temperatures less than 25°C. *Daphnia lumholtzi* has low fecundity and survivorship at temperatures below 10°C (Table I), which may influence this invader's seasonality and its temporal opportunity for range expansion. In contrast, the native cladoceran *D. retrocurva* was able to maintain population densities of at least 1.5 animals l<sup>-1</sup> in Clinton Reservoir at temperatures as low as 4.0°C.

Field and laboratory results from this study demonstrate that invasive clones of *D. lumholtzi* have a high temperature optimum. These data support both historical studies (Green, 1967; Gophen, 1979; Swar and Fernando, 1979) and current invasion trends (Work and Gophen, 1995, 1999; Stoeckel *et al.*, 1996; East *et al.*, 1999). These data suggest that this invader should be a very successful colonizer of warm water lakes and reservoirs in the southern US, but our life table data suggest that the sensitivity of *D. lumholtzi* to lower water temperatures below 10°C may inhibit or impede the expansion of this exotic cladoceran into northern waters.

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