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UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

THE ECOLOGY OF THE EXOTIC CLADOCERAN ZOOPLANKTON,
DAPHNIA LUMHOLTZI (SARS), IN LAKE TEXOMA, OK-TX.

A Dissertation
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
Doctor of Philosophy

By
Kirsten Work
Norman, Oklahoma
1997

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THE ECOLOGY OF THE EXOTIC CLADOCERAN ZOOPLANKTON,
DAPHNIA LUMHOLTZI, IN LAKE TEXOMA, OK-TX.

A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

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PREFACE

The four chapters of this dissertation have been prepared in submission format. Chapter 1 has been published in *Archiv für Hydrobiologie*. The other three chapters will be submitted to *Freshwater Biology* (Chapter 2), *Hydrobiologia* (Chapter 3), and *Limnology and Oceanography* (Chapter 4).

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Abstract

Daphnia lumholtzi is exotic to North America. Its original distribution included eastern Australia, central Asia, and eastern Africa. It was first found in the US in 1991 in Texas and I first found *D. lumholtzi* in Lake Texoma in 1992. Since its initial introduction, its range has expanded to include most of the southern half of the US. The purpose of this dissertation was to determine which factors have allowed this exotic species to invade the zooplankton population of Lake Texoma. The native zooplankton include: *Daphnia galeata*, *Daphnia parvula*, *Diaphanosoma leuchtenbergianum*, *Bosmina longirostris*, *Ceriodaphnia lacustris*, *Cyclops bicuspidatus thomasi*, *Mesocyclops edax*, *Eurytemora affinis*, *Diaptomus siciloides*, and many rotifer species.

In Chapter 1, I present the initial data on the distribution and abundance of *Daphnia lumholtzi* during the summer of 1993. Lake Texoma has variable and often strong horizontal gradients in temperature, conductivity, and turbidity, and the spatial distribution of *D. lumholtzi* was heterogenous along the long axis of the reservoir. Therefore, in Chapter 2 I measured the response of *D. lumholtzi* to some of the environmental variables that exhibit the strongest gradients using culture experiments. In Chapter 3, I tested the patterns that I observed in the short pilot study and in the culture experiments with field sampling for one year. I only observed large densities of *D. lumholtzi* during the warmest part of the year when the native zooplankton populations had declined. Therefore, in Chapter 4 I evaluated how the response of *D. lumholtzi* compared with two native species, *Daphnia galeata* and *Ceriodaphnia lacustris*.

As mentioned previously, *Daphnia lumholtzi* only occurred at high abundances in mid summer. It also showed a trend of declining abundance

toward the dam, which is the least variable area of the lake with respect to many environmental measurements. Both of these trends are consistent with the ecological origins of the species. *Daphnia lumholtzi* is a subtropical species that is likely to be able to tolerate warmer temperatures than zooplankton from North America, which probably evolved in the cooler natural lakes further north. Furthermore, the spatial distribution of the species in Lake Texoma indicates that *D. lumholtzi* can tolerate high physical and chemical variability. Most of the reports of the species from its native range are from disturbed habitats, such as ephemeral and wastewater ponds and reservoirs.

**The invasion of *Daphnia lumholtzi* (Sars)
into Lake Texoma (USA)**

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With 16 figures and 1 table in the text

Abstract

The first evidence of *Daphnia lumholtzi* in Lake Texoma was found in samples taken in the fall of 1991. Samples from 1993 indicate that seasonal variability exists in abundance, horizontal distribution, and morphology. The highest and lowest abundances occurred in the warmest and coldest months, with a corresponding change in distribution. In February, 1993 *D. lumholtzi* was found only in the highly saline Red River inflow waters, whereas in the summer months the species was collected throughout the reservoir. A change in morphology also corresponds with the change in temperature; during cold months the helmet and tail spines were significantly shorter than in warm months. The warmest temperatures resulted in a zooplankton community crash, during which we noticed many individuals with deformed helmets and tail spines.

Introduction

The introduction of exotic species is a recurring phenomenon throughout the world. For an introduction to be successful the species must 1) be transported to the site, 2) reproduce on the site, and 3) disperse from the initial site of introduction. Freshwater zooplankton are particularly conducive to natural distribution within a continent by floods, adherence of resting eggs to animals, and wind-mediated movement. Anthropogenic causes of zooplankton transfer are also common, such as large scale interbasin transfer of water, small scale water transfer (e.g., bait buckets), transfer of animals carrying zooplankton (e.g., fish), and transfer of mud carrying ephippial eggs. Introduction of aquatic organisms between continents is more difficult; however, two bivalves, *Corbicula fluminea* and *Dreissena polymorpha*, and two cladocerans, *Bosmina coregoni* and *Bythotrephes cederstroemii*, were successfully introduced into the Great Lakes as a result of ballast water discharge from other continents (Havel and Hebert 1993).

Once a transfer has occurred, the establishment of a population requires favorable ecological conditions. The movement of a species to a new environment may present the species with new chemical conditions as well as a new food array, competitive arena, and/or predation regime. Although the species did not evolve in the new food environment and consequently may not be able to efficiently utilize the food source, freshwater zooplankton can feed on a wide variety of phytoplankton and bacteria (DeMott 1989). Therefore, the probability that the new zooplankton species cannot feed on the phytoplankton of most lakes is low. The prospect of new competitors and predators may be a benefit or a

hinderance depending upon the capabilities of the new species. If the species evolved under an environment of more intense competition or predation, then the species may be released from that pressure in the new environment and flourish (Orians 1986). A competitor or predator may also not be equipped to accomodate the avoidance strategies that evolved in the invading species in its previous environment.

Although the mode of transport of *Daphnia lumholtzi* to the United States is unknown, the criteria for successful introduction have been met. The species was first found in the US in a small reservoir in Texas in 1990 (SORENSEN & STERNER 1992). Since the initial discovery of the introduction, it has been found in reservoirs throughout the southeastern US (HAVEL & HERBERT 1993). We discovered the species in Lake Texoma in October, 1992. Lake Texoma is a large reservoir at the confluence of the Red and Washita Rivers at the border of Oklahoma and Texas. Examination of old samples dates the introduction back to at least 1991. *D. lumholtzi* is presently a common and permanent component of the zooplankton community of Lake Texoma.

The original range of *D. lumholtzi* includes Australia, central Asia, eastern Africa, and a small region in western Africa. Several references in the original range suggest that the species is small and only achieves low abundances in relation to the other species (KHALAF & SMIRNOV 1976, SHARMA & DATTA GUPTA 1984, MANGALO & AKBAR 1988, TIMMS 1989, KING & GREENWOOD 1992). Excluding the unhelmeted (monacha) form, *D. lumholtzi* occurred at low abundances in the African rift valley lakes, primarily in shallow areas near river inlets, and only in lakes with high conductivity (GREEN 1971). SERRUYA & POLLINGER

(1983) also report that the lakes in which *D. lumholtzi* is abundant in its original range all have high salinities, including Lake Kinneret in which it was extirpated (GOPHEN 1979). However, GREEN (1967) and SWAR & FERNANDO (1979) suggest that *D. lumholtzi* was the largest cladoceran that coexisted with fish in Lake Albert, East Africa, and Lake Phewa, Nepal, respectively. MISHRA & SAKSENA (1990) report relatively high *D. lumholtzi* abundances in a water body containing effluent from an industrial complex.

D. lumholtzi is an extremely cyclomorphic species that produces a long helmet and tail spine in addition to lateral fornices. Individuals found in the US can achieve large sizes, larger than the individuals found in the original range and larger than the pre-existing *Daphnia* species in many lakes in the US. SORENSON & STERNER (1992) measured a total body length of 1.8 mm excluding spines and of 5.6 mm with spines. Furthermore, the spines grew faster than the body, the helmet grew at a constant rate, and the tail spine faster with increasing temperature over the course of the experiments.

Although the latitude of Lake Texoma is similar to parts of the original distribution of *D. lumholtzi*, it is a man-made riverine-type reservoir on a different continent. Consequently, the Lake Texoma environment is different from the lakes in which it originally existed. The objective of our study was to study what factors affected the successful colonization of Lake Texoma by *D. lumholtzi*. Preliminary results of the horizontal distribution, seasonal patterns of abundance, and morphological changes of *D. lumholtzi* over time are presented in this paper.

Materials and methods

Qualitative sampling of zooplankton was carried out from February to May 1993 at stations 1, 2, and 3 (Fig. 1.) with 3 to 5-minute horizontal tows of an 80m, 12 cm diameter plankton net at 5-10 knots. Samples were preserved in 4% buffered formalin. Up to 50 individuals from each sample were measured for helmet height (H), helmet + head height (HH), body length (B), and tail spine length (S) (Fig. 2). On June 29 we began quantitative sampling at eight stations (Fig. 1) with a 5-liter vertical Beta Plus Bottle (Wildlife Supply Company) at 5 meter intervals (1, 3, 5, 10, 15, 20). All of the 5 L samples at a given station (2-5 depths) were combined, filtered (80 mm mesh), and preserved in buffered formalin. Each sample was subsampled three times, and all of the individuals in each subsample were sorted and counted. Vertical hauls with an 80m, 12 cm diameter plankton net were also performed to collect individuals for body measurements as described above. Gradients of temperature, dissolved oxygen, pH, and conductivity were measured with a Hydrolab H20 system. Dissolved oxygen was converted to oxygen saturation due to the differential solubility of oxygen with change in temperature using the table provided in Benson and Krause (1980).

Due to the high correlation between many of the environmental variables and between the zooplankton abundances, variation in *D. lumholtzi* abundance was tested with respect to environmental gradients and to the other zooplankton abundances using principle components analysis in NTSYS (ROHLF 1993). The relationship of *D. lumholtzi* to environmental variation was tested separately from the relationships between the zooplankton categories. The PCA was run on the correlation matrices of

date- and site-specific data of temperature, oxygen saturation, pH, and conductivity and of zooplankton genus abundances, in which the environmental measurements and the zooplankton genera were considered the characters respectively (Sneath and Sokal 1973). The data were standardized such that the mean of each character was zero and the standard deviation was 1.0.

Relationships between body length and spine lengths were assessed with simple linear regression. Variation in each of the body measurements over time was assessed using ANOVA with date as the factor. Fisher's Protected Least Significant Difference comparisons were used to determine which dates differed significantly from each other.

Results

During Feb.-May we only found *D. lumholtzi* in qualitative samples collected in the riverine, saline portion of the Red River arm of the reservoir (stations 1 and 2, Fig. 1). Although at that time we did not sample the entire reservoir, we also collected qualitative samples in the vicinity of stations 1, 2, 3, 6, 7, and site B on Fig. 1 in March and April of 1994 and confirmed that *D. lumholtzi* only occurred in the Red River arm near stations 1 and 2 at that time of the year.

When the quantitative sampling program began (June 29, 1993), *D. lumholtzi* was present throughout the reservoir, although the highest abundance occurred at station 4 (Fig. 3) in the Red River arm. Throughout early July individuals were present at virtually all stations, with the lowest abundances at stations 1, 2, and 8 and the highest abundances at the confluence of the Red and Washita Rivers (station 7). During the period of

June 29 to July 15 densities (no./L) of *D. lumholtzi* increased to 46.1% of the total zooplankton population, 82.4% of all cladocera, and 100% of all *Daphnia* at some stations (Table 1). By July 17 the annual zooplankton crash (MATTHEWS 1984) occurred and by the next sampling date we only found appreciable numbers of *D. lumholtzi* at station 1, although we collected small numbers of individuals at all stations except the Washita stations (6 and 7). By July 27 we only found small numbers scattered throughout the reservoir, although it remained a large proportion of the total cladocera and total *Daphnia* populations (Table 1).

The first three axes of the PCA explain 93.8% of the variance in the matrix of *D. lumholtzi* abundance, temperature, oxygen saturation, pH, and conductivity. The first two axes account for 86.4% of the variance and contain the highest loadings of all of the variables included in the analysis (Table 2); therefore, a scattergram of the first two axes is provided with ranges of *D. lumholtzi* abundance highlighted (Figure 4). Although low densities of *D. lumholtzi* (0-20 per liter) occurred under all the conditions experienced, moderately high (20-50 per liter) and high (50-120 per liter) densities occurred at shallow stations without strong stratification (i.e., high bottom oxygen saturation), but with lower bottom temperatures in comparison with other unstratified or weakly stratified stations.

The first three axes of the PCA of zooplankton variables explain 61.8% of the variance in zooplankton abundance. The loadings for the variables are included in Table 3. Bivariate scattergrams of the first three axes are provided with the sampling dates highlighted (Fig. 5). In both scattergrams the dates prior to the zooplankton crash exhibit very little overlap with the dates after the crash; the zooplankton community before

the crash is distinct from the community after the crash. *D. lumholtzi* is associated with the pre-crash community; in particular with calanoid copepodites and copepod nauplii. The post-crash community is characterized by a high abundance of *Bosmina* spp. and rotifers (mostly brachionids).

Regressions of helmet and tail spine lengths with body length were significant ($p = 0.0001$) for all months. ANOVA of body and spine lengths with date as a factor was significant ($p = 0.0001$). The results of the post-hoc comparisons are listed in Table 4. Mean spine lengths and mean total length increased from February to May and then decreased (Table 5). On the other hand, mean body length fluctuated throughout the period with the largest body length in February and the smallest in July. All months were significantly different from each other at $\alpha = 0.01$ for the helmet/body ratio and all comparisons were significant for the tail spine/body except April-June and May-July. The helmet/body and tail spine/body ratios increased throughout the period of measurement, with the exception of June, which had a much higher standard deviation (Fig. 6).

At the time of the annual zooplankton crash (MATTHEWS 1984), we noted that the spine to body ratios were highest and most of the *D. lumholtzi* had spines that were deformed to varying degrees. Work and Gophen (1995) reported the results of temperature experiments that evaluated the effect of high temperature (30°C) on deformity. These experiments indicated an increase in the proportion of deformed individuals and an increase in mortality at 30°C than at 22°C or the field sample. Furthermore, they observed a reduction in neonate production at 30°C relative to 22°C.

Discussion

Lake Texoma is characterized by a strong gradient in salinity. The highest conductivity values were measured in the riverine portion of the Red River arm and the lowest values in the Washita arm and at the dam (Fig. 12). The Red River is much more saline than the Washita River (USGS 1992); the low values at the dam are due to a decrease in salinity over the course of the Red River arm in addition to the influx of lower salinity water from the Washita River. The decrease in salinity prior to the addition of Washita River water is probably due to the influx of several large creeks into the Red River arm.

Although numerous factors can affect zooplankton distribution and population growth, we suggest that salinity and temperature have an interactive effect on the distribution and abundance of *D. lumholtzi* in Lake Texoma. The population was confined to areas of high salinity during the cold months of February to March. When the population approached high densities throughout the reservoir (mid-June to mid-July), the highest abundances (60-90/L) occurred at one of the lowest salinity areas at the confluence of the Red and Washita Rivers (Fig. 9). On July 22 (Fig. 9), when the population was stressed with high temperatures (Fig. 13-15), it was once again collected at highest densities at the most saline station (station 1, Fig. 1).

The results of the PCA of environmental variability suggest that during July *D. lumholtzi* preferred areas with cooler temperatures and high bottom oxygen saturation (Fig. 12). These areas occur in shallows down-reservoir of the slow water area represented by station 3. Such areas exhibit small thermal gradients with only slight oxygen depletion at the bottom.

The lower surface water temperatures below the stratified area may be the result of mixing of cold water introduced into the flow by the upward movement of internal seiches. A longer temporal consideration also indicates a strong relationship between *D. lumholtzi* and temperature; the changes in the distribution and abundance over the four month period of qualitative sampling are closely associated with increasing temperature.

The experiments reported in this study on the impact of temperature on spine deformity suggest an explanation for the association of *D. lumholtzi* with lower temperatures during the hottest part of the year. At the highest temperatures the animals experienced in the lake (30°C), the experiments suggest an increase in mortality with a reduction in neonate production and at times spine deformation. These results should be considered in light of the Afro-Asiatic origin of this species; temperatures in large water bodies in Africa and Asia are generally no higher than 28°C and seasonal variation is lower than in Lake Texoma.

The results of the PCA of zooplankton abundances indicate that *D. lumholtzi* is associated with the pre-crash community that existed prior to July 17 (Fig. 13, 14). These results are also consistent with the temperature experiments in which mortality increased at the temperatures the zooplankton experienced in mid-July. The success of *Bosmina* spp. and rotifers after the zooplankton crash may be due to their higher tolerance to high temperatures alone, or in combination with a reduction in food competition and/or predation pressure.

Our results of the temporal morphological changes in *D. lumholtzi* correspond to the results presented by SORENSON & STERNER (1992). The *D. lumholtzi* population exhibited allometric growth throughout the

period of measurement. The helmet and tail spines grew longer absolutely and relative to the body length with increasing temperature until May. We suggest that the lengthening of the spines is a result of intensified predation pressure by fish (TOLLRIAN 1994). An increase in the level of zooplankton consumption by fish from Feb. to May-June was described by MATTHEWS (). Fish predation pressure in Lake Texoma is highest during the highest reproductive period of the most common fish in the lake, *Menidia beryllina* (LIENESCH, unpubl. data). Consequently, the highest predation pressure, the highest water temperatures, the zooplankton crash, and the longest spines on *D. lumholtzi* occur at the same time. However, the long spines are probably the result of fish-induced morphological change (TOLLRIAN 1994).

Further research is required to understand the ecological advantages that *D. lumholtzi* has in Lake Texoma, and the relative impact of physicochemical gradients on the distribution of *D. lumholtzi* in relation to the effect that it may have on the other zooplankton species in Lake Texoma through food competition or differential vulnerability to fish predation. However, our preliminary study documented the successful invasion of the tropical zooplankter, *D. lumholtzi*, into Lake Texoma. Successive changes in the zooplankton community structure in relation to algal diversity and fish predation after the introduction of *D. lumholtzi* must be monitored to understand the ecological significance of the invasion of this exotic zooplankter.

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Table 1. Mean percent *Daphnia lumholtzi* of total zooplankton, cladoceran and rotifer, and total *Daphnia* abundances with standard deviations.

<u>Date</u>	<u>total population</u>	<u>cladocera and rotifers</u>	<u>all <i>Daphnia</i></u>
June 29	4.8 +/- 2.14	26.7 +/- 17.76	54.2 +/- 27.60
July 9/10	17.1 +/- 9.59	65.9 +/- 33.97	92.6 +/- 9.91
July 15	18.4 +/- 12.07	67.8 +/- 15.76	96.8 +/- 1.88
July 22	5.1 +/- 5.42	30.1 +/- 29.53	81.7 +/- 25.91
July 27	0.6 +/- 0.64	8.5 +/- 13.78	66.5 +/- 43.08

Table 2. Loadings of environmental variables on principal components I, II, III.

Measurement	Axis I	Axis II	Axis III
Surface temperature	0.831	-0.532	-0.006
Bottom temperature	0.383	-0.871	0.277
Surface oxygen saturation	0.846	-0.176	-0.413
Bottom oxygen saturation	-0.974	0.106	0.199
Surface conductivity	0.845	0.452	0.269
Bottom conductivity	0.848	0.445	0.267
Surface pH	0.986	0.022	0.122
Bottom pH	0.961	0.043	0.242

Table 3. Loadings of zooplankton variables on principle components I, II, and III.

<u>Measurement</u>	<u>Axis I</u>	<u>Axis II</u>	<u>Axis III</u>
<u>Daphnia lumholtzi</u>	0.636	-0.574	0.275
<u>Daphnia</u> spp.	-0.225	0.469	-0.514
<u>Bosmina</u> spp.	-0.625	-0.569	-0.093
Other cladocera	-0.025	0.186	-0.758
Adult calanoid copepods	0.305	0.259	0.203
Juvenile calanoid copepods	0.827	-0.225	-0.105
Adult cyclopoid copepods	-0.347	0.666	0.140
Juvenile cyclopoid copepods	0.169	0.462	-0.547
Copepod nauplii	0.630	0.495	0.196
Rotifers	-0.858	-0.080	0.109

Table 4. Summary of regression statistics for helmet vs. body length and tail spine vs. body length.

Month	Variables	R ²	P-values for intercept	X	X ²
February	H + H vs. B	0.739	0.0025	0.0016	0.0008
	S vs. B	0.703	0.0005	0.4431	<0.0001
April	H + H vs. B	0.901	0.1868	<0.0001	0.0015
	S vs. B	0.847	0.1291	<0.0001	0.0109
May	H + H vs. B	0.400	0.3203	0.0180	0.0711
	S vs. B	0.593	0.0648	0.0012	0.0144
June	H + H vs. B	0.696	0.1873	<0.0001	0.3709
	S vs. B	0.686	0.9674	<0.0001	0.9003
July	H + H vs. B	0.395	0.0004	<0.0001	<0.0001
	S vs. B	0.678	<0.0001	<0.0001	<0.0001

Table 5. Change in the mean spine, body, and total lengths (mm) of *Daphnia lumholtzi*, with standard deviations.

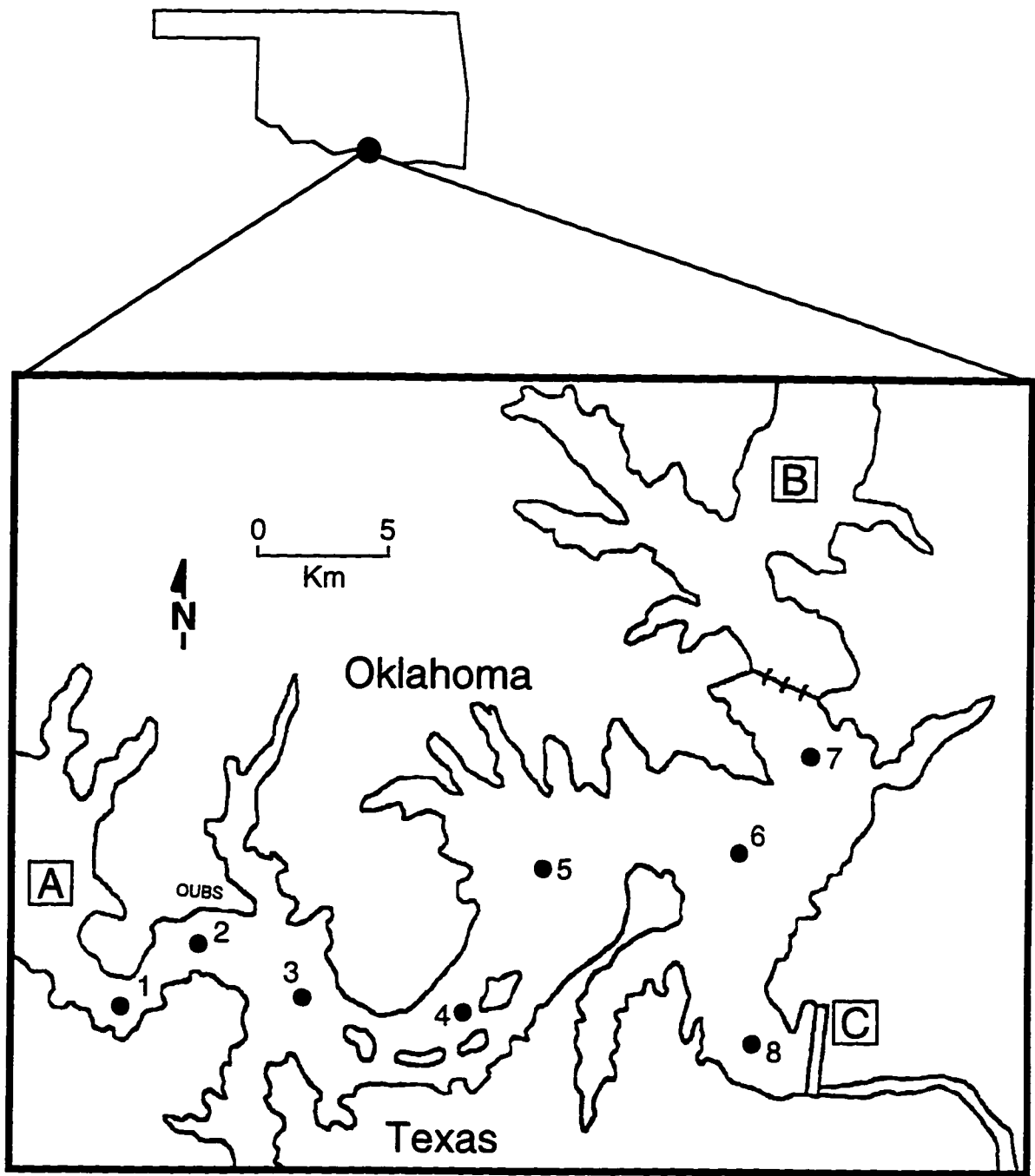
<u>Month</u>	<u>N</u>	<u>Helmet</u>	<u>Body</u>	<u>Spine</u>	<u>Total</u>
February	216	0.16 +/- 0.11	0.76 +/- 0.26	0.68 +/- 0.32	2.05 +/- 0.81
April	65	0.26 +/- 0.12	0.55 +/- 0.24	0.67 +/- 0.29	1.83 +/- 0.75
May	35	0.43 +/- 0.16	0.72 +/- 0.18	1.01 +/- 0.29	2.60 +/- 0.64
June	290	0.26 +/- 0.10	0.68 +/- 0.20	0.84 +/- 0.29	2.17 +/- 0.64
July	50	0.40 +/- 0.09	0.50 +/- 0.11	0.75 +/- 0.16	1.94 +/- 0.35

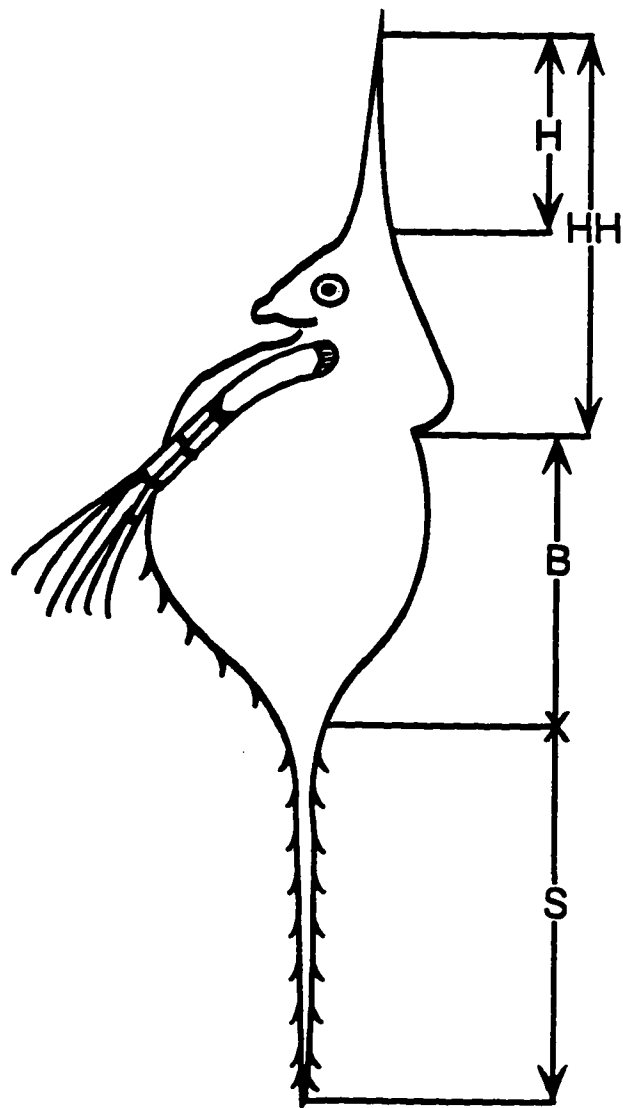
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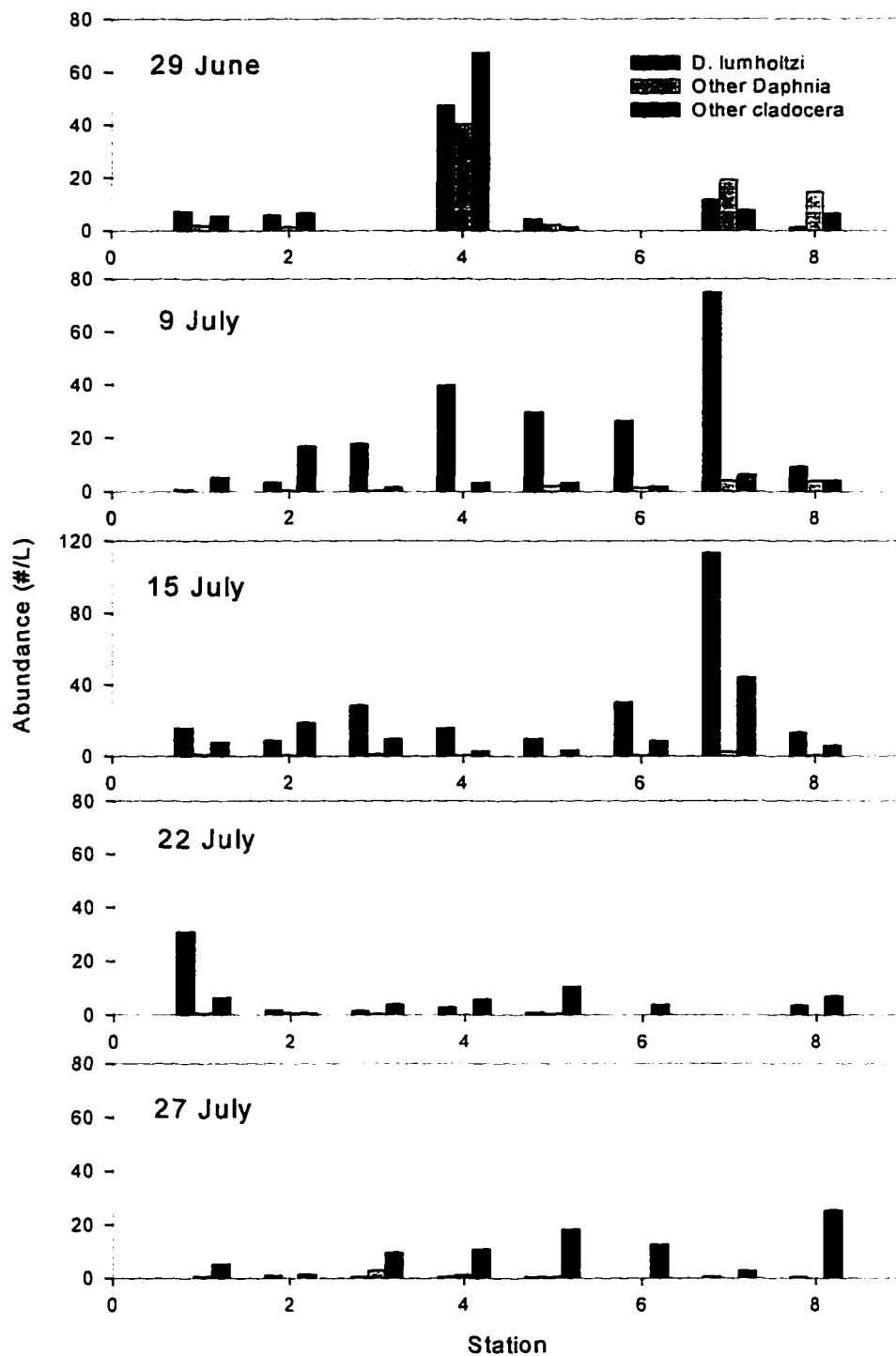
- Figure 1. Map of sampling stations on Lake Texoma. The 8 stations are represented by black dots. A = Red River, B = Washita River, C = Denison Dam, OUBS = University of Oklahoma Biological Station. Average salinity for station 1-3: 1760 $\mu\text{moh/cm}$, stations 4-5: 1320 $\mu\text{moh/cm}$, and stations 6-8: 1100 $\mu\text{moh/cm}$.
- Figure 2. Measurements taken on *Daphnia lumholtzi*. H = helmet length, HH = helmet + head length, B = body length, S = tail spine length.
- Figure 3. The horizontal distribution of *Daphnia lumholtzi* in Lake Texoma for 29 June through 27 July. Dark bars = adults, hatched bars = juveniles.
- Figure 4. Scattergram of the first two axes of the PCA of the environmental matrix. Triangles = 0-20 *D. lumholtzi*/liter, circles = 20-50 *D. lumholtzi*/liter, squares = 50-120 *D. lumholtzi*/liter.
- Figure 5. Scattergram of the first two axes of the PCA of the zooplankton matrix. All samples for a given date are outlined with polygons (top). Scattergram of the first and third axes of the PCA of the zooplankton matrix. All samples for a given

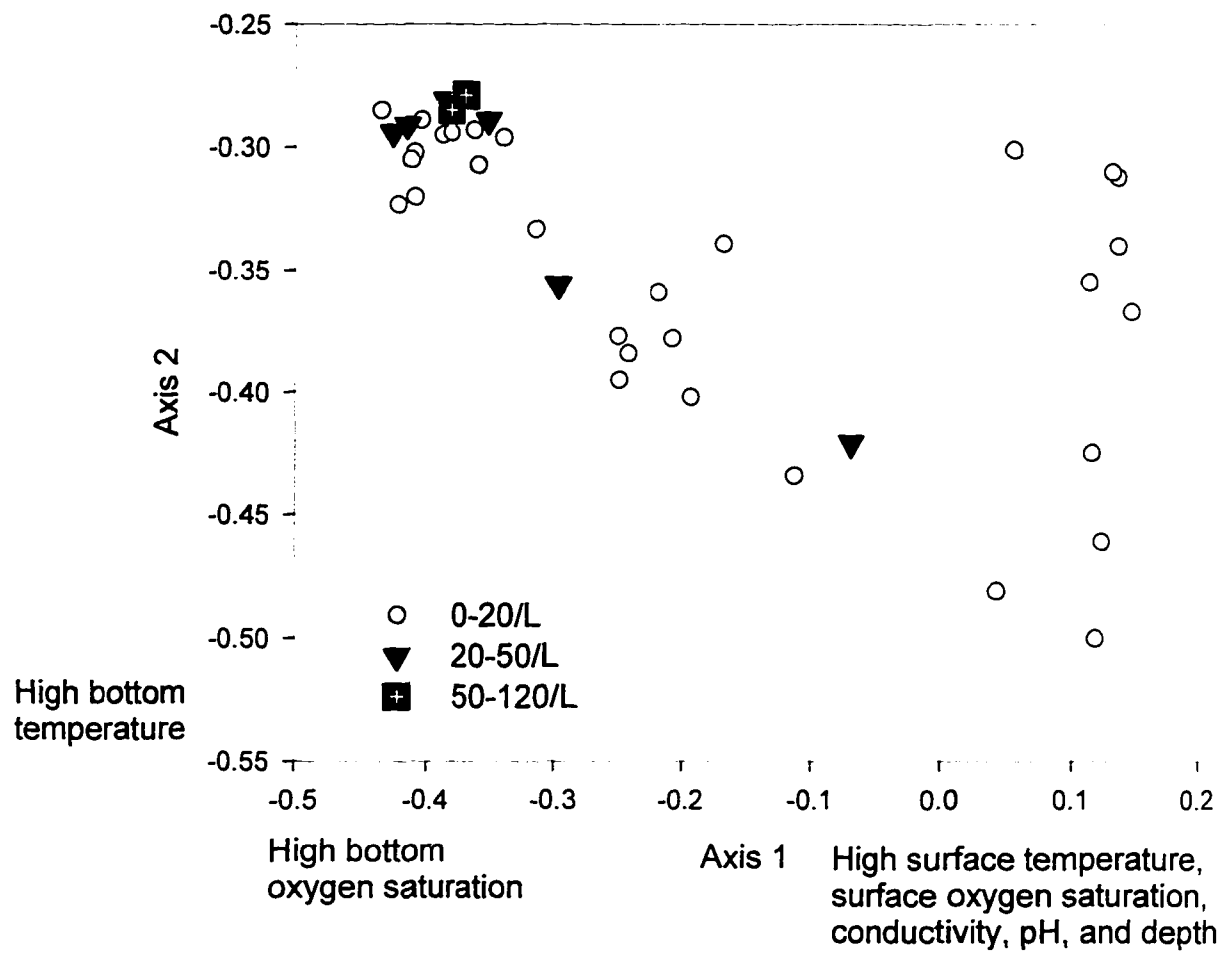
date are outlined with polygons (bottom). The zooplankton crash occurred on approximately 12 July.

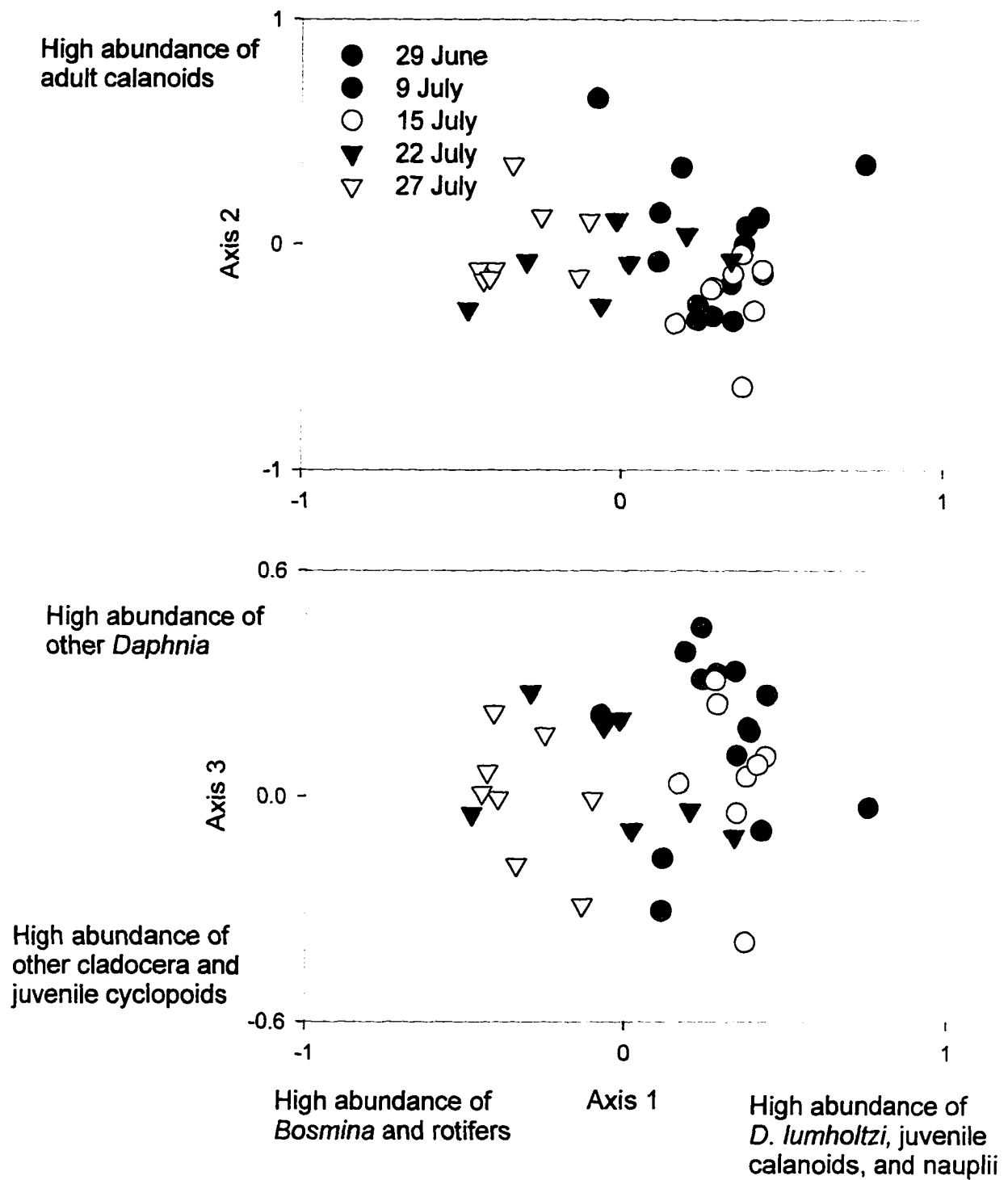
Figure 6. Changes in the helmet + head to body ratio (HH/B) and the tail spine to body ratio (S/B) over the course of the study period. Sample size is given next to each point.

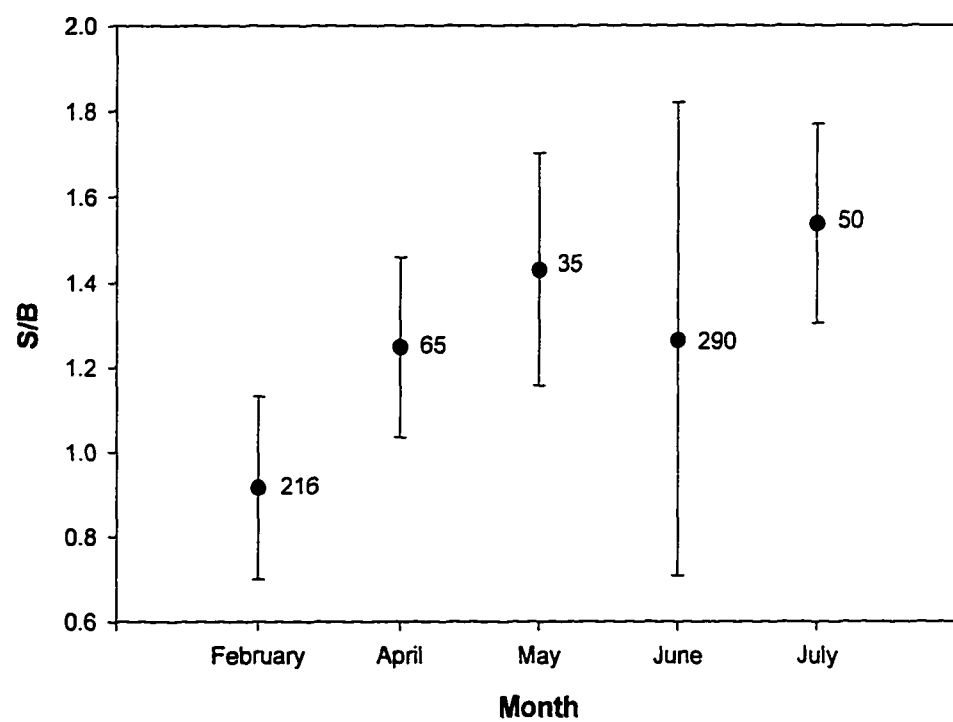
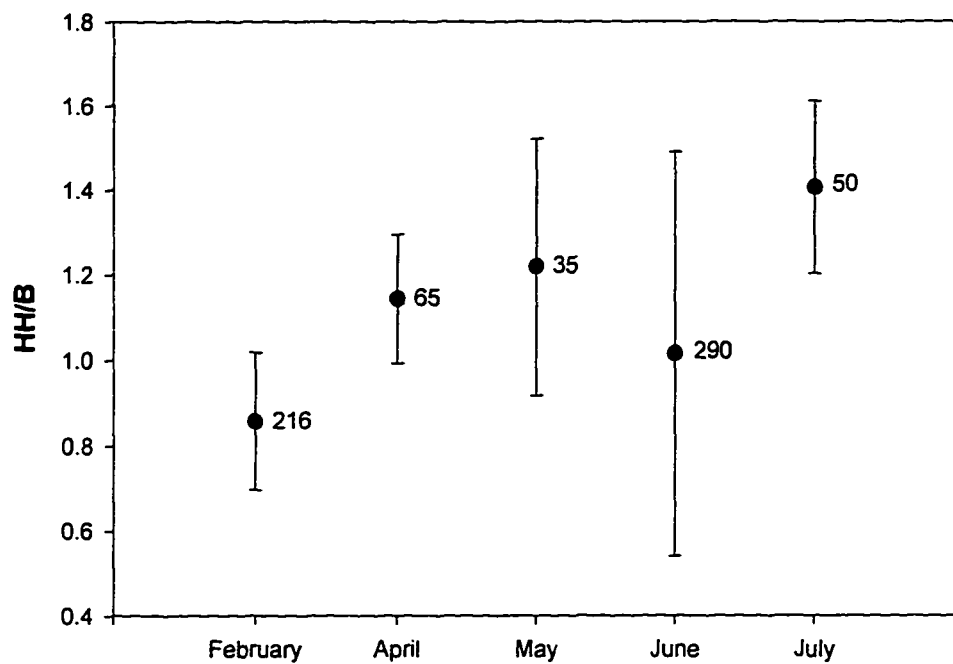












Experimental analysis of factors that affect the
abundance of a reservoir invader, Daphnia lumholtzi (Sars)

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Running Head: Analysis of a Reservoir Invader

SUMMARY. 1. *Daphnia lumholtzi* (Sars) is an exotic species which is rapidly spreading throughout reservoirs in the southern United States. Reservoirs typically have strong spatial and temporal gradients in biotic and abiotic factors, such as food availability, temperature, conductivity, and turbidity.

2. We experimentally examined the response of *D. lumholtzi* birth rate, molting rate, and survival to extremes of food concentration, temperature, conductivity, and turbidity.

3. Increases in temperature (15-29°C) and decreases in turbidity (0-6.7 µg/l) significantly increased birth rates and molting rates, whereas food concentration only affected birth rates and conductivity had no effect. Survival was significantly affected only by temperature and conductivity.

4. *Daphnia lumholtzi* can tolerate extremely warm conditions (28-30 °C) while other cladoceran populations disappear at such temperatures. Therefore, *D. lumholtzi* may exploit underutilized resources and enhance populations during a period in mid-summer when few other cladocera are present to be potential competitors.

Introduction

The issue of invasions of exotic species by intent or by accident and of range expansions of local species has been growing as ecosystems become increasingly disturbed biologically and physically. However, the factors that allow exotic species to invade and the effects of the invasions are often difficult to predict (Williamson & Fitter, 1996). Moyle & Light (1996) suggest that the suitability of abiotic factors predetermine the success of an invasion regardless of the biotic interactions in the new habitat. Numerous other papers cite the influence of biological capabilities of exotic species on invasion success, such as high dispersal and reproduction rates, good competitive abilities, and predation resistance (Schoenherr, 1981; Taylor, Courtenay, & McCann, 1984; Evans, 1988; Garton & Berg, 1990; Lehman, 1991; Mackie, 1991; Tippie, Deacon, & Ho, 1991). Because unfavorable abiotic conditions preclude a successful invasion, a consideration of the conditions in both the native and the new habitats is a requisite first step to answering the question of why a species is able to invade an ecosystem.

Daphnia lumholtzi (Sars) is exotic to North America, although the mode of introduction is unknown. The native range of Daphnia lumholtzi includes Australia, southeast Asia, and Africa. Most records in its native range are from reservoirs, rivers, ephemeral lakes, or other systems with moderate to high disturbance (Khalaf & Smirnof, 1976; Bricker, Wongrat, & Gannon, 1978; Duncan, 1984; Geddes, 1984; Mangalo & Akbar, 1988; Timms, 1989; Mishra & Saksena, 1990; King & Greenwood, 1992), although it does occur in some natural lakes (Green, 1967; Timms, 1973; Swar & Fernando, 1979). Daphnia lumholtzi was first collected in North America in 1990 from a small lake in Texas (Sorenson & Sterner, 1992).

Since the initial discovery of the species on this continent, it has been found as far east as Florida, west to Arizona, and north to Illinois (J. Havel, pers. comm.). Most reports in the US are from reservoirs or rivers (J. Havel, pers. comm.).

We first found *Daphnia lumholtzi* in Lake Texoma in 1992, although the species was present in a few plankton net tows conducted by a limnology class in 1991. Lake Texoma is a large, bottom release reservoir built at the confluence of the Red and Washita rivers on the border of Oklahoma and Texas. The Red River is approximately twice as saline as the Washita (Table 1) when it reaches the reservoir and it provides the majority of the flow. Much of the surrounding watershed of both rivers is farmed, thus both rivers carry a high suspended sediment load (Table 1). As a result, Lake Texoma has strong horizontal gradients in conductivity and turbidity in addition to the gradients in temperature, oxygen, etc. that occur in most reservoirs. All of these gradients may be altered further during spring floods (Matthews, 1984; Dimberger & Threlkeld, 1986; Threlkeld, 1986a), which can change flow into the lake from a normal flow of 30-140 m³/s to 4500 m³/s during a flood (USGS, 1996).

A preliminary study of the distribution and abundance of *Daphnia lumholtzi* in Lake Texoma (Work & Gophen, 1995) suggested that it occurred at low densities in late winter, primarily in the more riverine areas, and at high densities throughout the lake in the summer. This pattern suggested a correlation between temperature and *D. lumholtzi* production and a temporally variable relationship between the strong physical and chemical gradients of Lake Texoma and *D. lumholtzi* distribution. *Daphnia lumholtzi* also persisted later into the summer than did other daphnids in Lake Texoma (*Daphnia galeata*, *Daphnia parvula*) and attained densities up

to 120/L at high temperatures (28-30°C). Most pelagic zooplankton in North America are not adapted to the high flow or high temperatures found in reservoirs of the southern portion of the US. Therefore, a species that was introduced from a riverine or otherwise highly disturbed environment may be predisposed to an environment like Lake Texoma.

Our objectives in this study were to determine how reservoir-type conditions might favor the invasion of exotic species into an otherwise pelagic zooplankton community. Therefore, this study was designed to test how variability in food availability and abiotic conditions affects the survival, growth, and reproduction of Daphnia lumholtzi. We examined temperature, turbidity and conductivity because of their strong relationship with D. lumholtzi production in the preliminary study (Work & Gophen, 1995). These factors are also some of the most variable abiotic factors in the lake; the surface temperature in Lake Texoma varies from 7-30 °C, the silt laden flood waters can change the water transparency from a secchi depth of 110 cm to 5 cm overnight (Matthews 1984, Work, 1997), and the Red River is much more saline than the Washita River (Table 1). We hypothesized that D. lumholtzi production would be higher under conditions like those found in the riverine areas of the reservoir, such as high food level, temperature, and conductivity and moderate turbidity.

Methods

Food availability experiments were conducted in summer 1994 and the other experiments were conducted in spring 1995. Daphnia lumholtzi were collected with 5 minute tows of a larval fish net (1/2 meter, 500 µm) and a 353 µm plankton net in the Red River arm of the lake offshore from the University of Oklahoma Biological Station (Fig. 1). They were brought

to the laboratory and separated into three treatments, each with 25 animals. Each animal was cultured alone in a 5 ml flat-bottomed vial. Water in the vials was changed every other day with fresh lake water filtered through 3.0 μm filter paper. Animals were fed Scenedesmus sp. after each change of water at a density of 540 cells/ml for all individuals except those in the low and high food treatments in the food availability experiment (Table 2). As the water was changed every other day, the Daphnia were examined under a dissecting microscope for eggs, offspring, ephippia, and molts. Any offspring, ephippia, or molts that were present in the vial were counted and removed. Each experiment lasted 4 weeks, which was approximately the life span of D. lumholtzi in the laboratory.

Each experiment included low, medium, and high treatments for the factor being tested (Table 2). The ranges of food concentrations were based on preliminary studies that determined the food concentrations too low to sustain reproduction and so high that algal respiration at night reduced oxygen levels down to the point of death for D. lumholtzi. Ranges for the temperature experiment were taken from the field data to represent temperatures that sustain reasonable growth of D. lumholtzi in the lake. Due to a reduction in the population in the lake, we performed the temperature experiment with 2-3 day old neonates that were produced in the laboratory by individuals taken from the lake. The animals in the three treatments were incubated in an environmentally-controlled room (15°C), at room temperature (22°C), or in a dry bath (29°C, DB66125, Thermolyne).

To test for the effects of conductivity, we incubated animals in Washita River water (1060-1110 $\mu\text{mhos/cm}$) for the low treatment, in Red River water (1280-1450 $\mu\text{mhos/cm}$) for the high treatment, and in a mixture of Washita and Red River waters for the intermediate treatment (Table 2).

Although the factors that differ most between the two rivers are turbidity and conductivity, filtered water from the two rivers may differ chemically in respects other than conductivity (Table 1). Therefore, we tested the relative ability of D. lumholtzi to survive and reproduce in Washita River water and Red River water. Finally, for the turbidity experiment, we added to each vial 1 ml of a suspension made from natural Red River clay (Table 2).

For each experiment we calculated the birth rate and molting rate as the mean number of offspring and molts produced per day. Although molting rate is not always directly correlated with growth in size, molting rate should approximate the amount of energy allocated to growth (Thorp and Covich, 1991). We analyzed the effect of each factor on birth rate, molting rate and survival separately with a one-way analysis of variance. Post-hoc comparisons were calculated with Fisher's protected least significant difference test (Toothaker, 1991).

Results

Results presented in Fig. 2 indicate that increases in food concentration had a positive effect on Daphnia lumholtzi production. Birth rate increased significantly and linearly with food concentration, although molting rate and survival were not significantly related to Scenedesmus density (Fig. 2). Very few ephippia were produced in all treatments.

Increases in temperature increased Daphnia lumholtzi growth and reproduction, but decreased survival. The highest temperature resulted in the fastest sexual maturation of D. lumholtzi (26 days vs. 18 or 13 days), as indicated by the presence of a brood pouch. Temperature also significantly affected birth rate including ephippia production (Fig. 2), which exceeded egg production. Although animals in the two highest temperature

treatments produced more offspring than those in the lowest treatment, only the intermediate temperature differed significantly from the low treatment ($p = 0.0070$). In contrast to the birth rate, molting rate increased linearly with temperature and survival decreased linearly with temperature (Fig. 2).

Conductivity significantly affected only ephippia production and survival. Birth rate was low and not related significantly to conductivity (Fig. 2). However, ephippia production was related significantly ($p = 0.0030$) to conductivity with the Washita-Red mixture treatment significantly higher ($p = 0.0007$) than the Washita treatment alone. Conductivity did not affect molting rate significantly, although it did affect survival (Fig. 2). Animals in the Washita-Red treatment had significantly higher survival ($p = 0.0044$) than the Washita treatment (Fig. 2).

Clay turbidity significantly affected only birth rate and molting rate (Fig. 2). For both measurements the low and high turbidity treatments were significantly lower than the treatment without clay ($p = 0.0008$). Although survival increased with clay concentration, the pattern was not significant (Fig. 2).

Discussion

Daphnia lumholtzi has most of the theoretical traits of a successful colonizer. One of the characteristics most beneficial to a potential invader is the ability to use human movement to cross geographic barriers (Ehrlich, 1986). D. lumholtzi adults and ephippia can be transported undetected in water carried in bait buckets, fish transfers, and any other water transfers in addition to possible natural passive transport of ephippia by wind, birds, mammals, etc (Thorp and Covich, 1991). The ability to reproduce quickly

and frequently in the new habitat also increases the likelihood that a species will be a successful invader (Stauffer, 1984). The ability of Daphnia to reproduce parthenogenically not only ensures that they can reproduce quickly, but also may reduce the size of the propagule required for successful colonization. The relative ease of movement also increases the probability that a colonization event would occur more than once and reduces the probability of extinction after colonization (MacArthur & Wilson, 1967).

Characteristics that allow a species to take advantage of underutilized resources, or that enhance its competitive ability or resistance to local predators also may increase the probability of successful invasion. Although there is debate over whether local populations can be saturated and vacant niches can exist (Herbold & Moyle, 1986; Cornell & Lawton, 1992), numerous studies have suggested that the success or failure of an invader is related to its ability to outcompete native species or to exploit underutilized niches. For example, Shoenherr (1981), Moyle (1986), Tippie et al. (1991), and Douglas, Marsh, and Minckley (1994) attribute the replacement of native desert fish in the western US by exotic species to the greater competitive ability, predation on juvenile stages, and high reproductive rates of the exotics. Ogutu-Ohwayo (1990) and Lowe-McConnell (1993) suggest that the successful introduction of an exotic tilapia (Oreochromis niloticus) in Lake Victoria is due to a greater competitive ability of the exotic than the native Oreochromis and to a resistance of the exotic to predation from the exotic Nile perch (Lates niloticus).

There is currently no experimental documentation of competition between Daphnia lumholtzi and the cladoceran species native to the US.

However, D. lumholtzi becomes most abundant after the native cladocerans crash, which occurs in summers when lake surface temperatures reach 28-30 °C (Matthews, 1984; Threlkeld, 1986b; Work & Gophen, 1995; Work, 1997). Although the present experiments indicate that D. lumholtzi survival was lower at these high temperatures, its growth and reproduction rates were higher than at low temperatures. Therefore, D. lumholtzi is physiologically able to utilize resources in late June or early July that the other species of cladocera in Lake Texoma cannot. Furthermore, reservoirs in the southern US are typically warmer than the natural lakes in which the native cladocera evolved (Hrbacek, 1987). Therefore, D. lumholtzi may take advantage of an underexploited niche in reservoirs.

The ability of Daphnia lumholtzi populations to withstand local predation pressure has not yet been evaluated. However, D. lumholtzi has extremely long head and tail spines (Sorenson & Sterner, 1992), much longer than native species. Long spines have been shown to provide a refuge from both invertebrate and vertebrate predators for other cladocerans (Swift & Fedorenko, 1975; O'Brien, Kettle, & Riessen, 1979; O'Brien et al., 1980; Krueger & Dodson, 1981; Havel & Dodson, 1984; Havel, 1985; Pijanowska, 1990; Parejko, 1991). This refuge may be enhanced by the induction of longer spines (cyclomorphosis) in the presence of predators or extracts of predators (Krueger & Dodson, 1981; Havel, 1985; Parejko, 1991). Tollrian (1994) was able to induce spine lengthening in D. lumholtzi with fish extracts, although only one fish species was tested. The ability of D. lumholtzi to undergo cyclomorphosis to produce more extreme spines than native cladocera may provide D. lumholtzi with an advantage in US reservoirs, which contain predators that are native to the extreme morphology of D. lumholtzi. Therefore, we predict that zooplanktivorous

fish and invertebrate predators in Lake Texoma will prey more heavily on native cladocera.

Characteristics of the new habitat also affect the probability of successful colonization. Similarity to the native habitat, and a high degree of disturbance (Orians, 1986) and patchiness (Stauffer, 1984) may enhance colonization success. Lake Texoma has these characteristics. Many of the systems from which Daphnia lumholtzi was recorded in the native range are riverine or disturbed (Khalaf & Smirnof, 1976; Bricker et al., 1978; Duncan, 1984; Geddes, 1984; Mangalo & Akbar, 1988; Timms, 1989; Mishra & Saksena, 1990; King & Greenwood, 1992). A reservoir is by definition a disturbed, semi-riverine habitat that may be susceptible to invasion (Moyle, 1986) because it was constructed from rivers rather than formed geologically.

A reservoir also has strong horizontal gradients that create at least large scale patchiness. In Lake Texoma the strongest abiotic gradients are conductivity and turbidity. Daphnia lumholtzi was able to survive, grow, and reproduce in all treatments in each experiment, but the response varied with the extremes of the treatments. In contrast, high temperature, conductivity, and turbidity may negatively affect North American daphnids that evolved in natural lakes without large inputs of warm, saline, turbid river water. Clay turbidity in particular can affect zooplankton production by flocculating with phytoplankton (Avnimelech & Troeger, 1982) and by reducing feeding rates, particularly for daphnids (McCabe & O'Brien, 1983; Threlkeld, 1986a; Hart, 1987; Hart, 1988).

Although survival of Daphnia lumholtzi was reduced at the highest temperature used in these experiments, the reduction in survival may be alleviated by the increase in growth and birth rates. We initially attempted

to use 30 °C as the warmest treatment, but all of the animals died within a week. Our inability to incubate D. lumholtzi at 30 °C may indicate that above 29 °C the mortality exceeds the effect of increased growth and productivity. High conductivity did not have an inhibitory effect either in these experiments; birth rate, growth rate, and survival were highest in the water from areas with moderate to high conductivity. Finally, although turbidity reduced the birth and molting rates, survival appeared to be enhanced by addition of low or high concentrations of clay. Therefore, D. lumholtzi appears to be relatively well adapted to these reservoir-type conditions that are likely to be stressful for the native daphnids, and may take advantage of an underutilized temporal niche in mid summer.

The conditions examined in this study often change simultaneously. Therefore, future research should examine how combinations of these potentially stressful factors affect Daphnia lumholtzi production. This study only examined the effects of abiotic factors and food availability on growth and reproduction; future research should examine the effect of the presence of competitors on production.

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Table 1. Selected water quality data for the Red and Washita Rivers taken from USGS (1996). Data for the Red River were collected from a station at 33°N and 97°W and are averaged over 12 months. Data for the Washita River were collected from a station at 34°N and 96°W and are averaged for 5 months; the data were taken at regular intervals throughout the year. Lake Texoma is at 34°N and longitude 97°W.

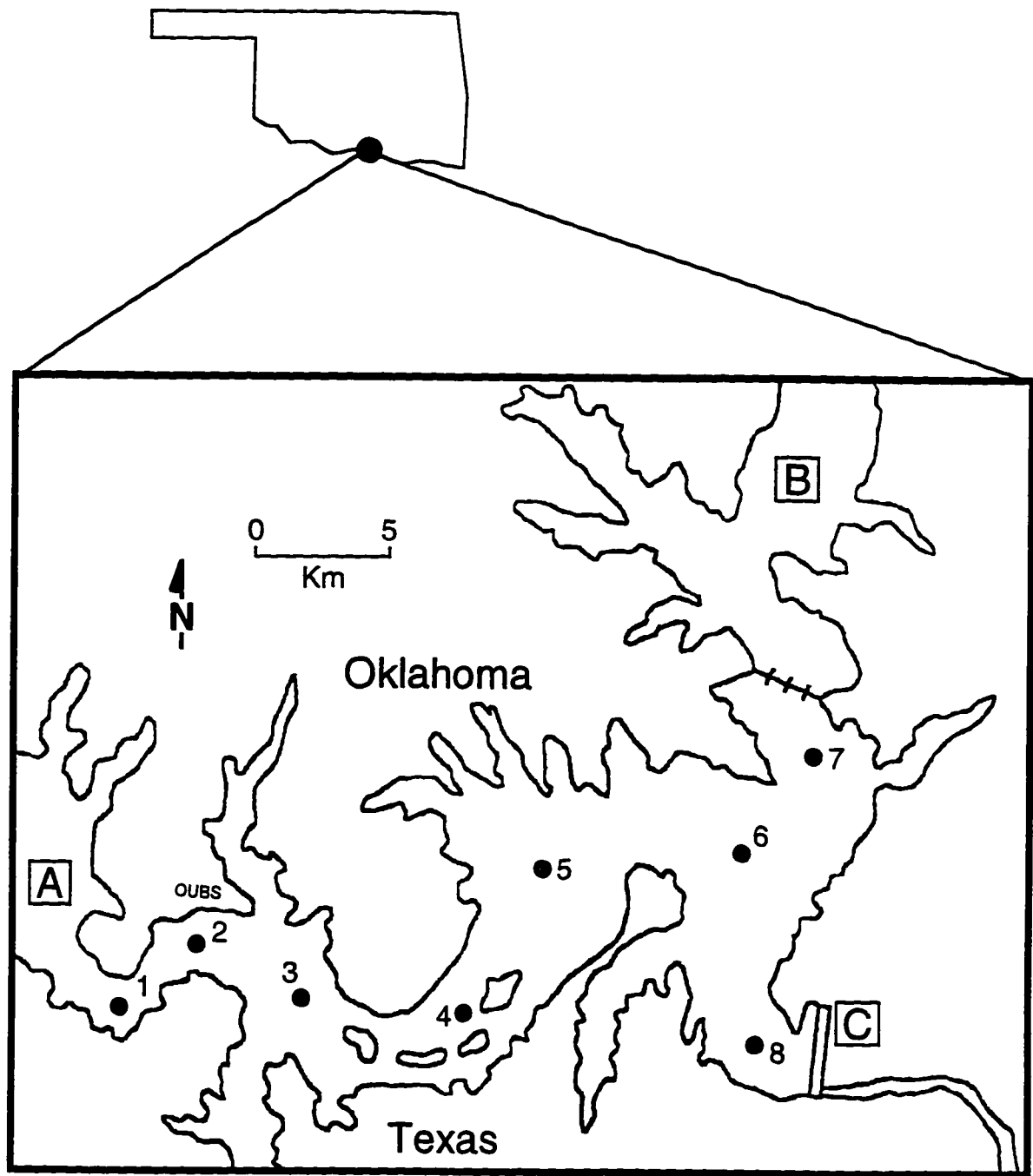
<u>Factor</u>	<u>Red River</u>	<u>Washita River</u>
Discharge (m ³ /sec)	610	160
Conductance (us/cm)	2220	949
pH	8.0	8.2
Temperature (C)	20	21
Turbidity (NTU)	262	635
Dissolved oxygen (mg/l)	8.1	8.3
Calcium (mg/l)	112	101
Magnesium (mg/l)	37	37
Sodium (mg/l)	295	45
Potassium (mg/l)	6.1	4.5
Sulfate (mg/l)	285	265
Chloride (mg/l)	461	45
Fluoride (mg/l)	0.27	0.38
Silica (mg/l)	7.6	8.7
Dissolved solids (mg/l)	1279	612

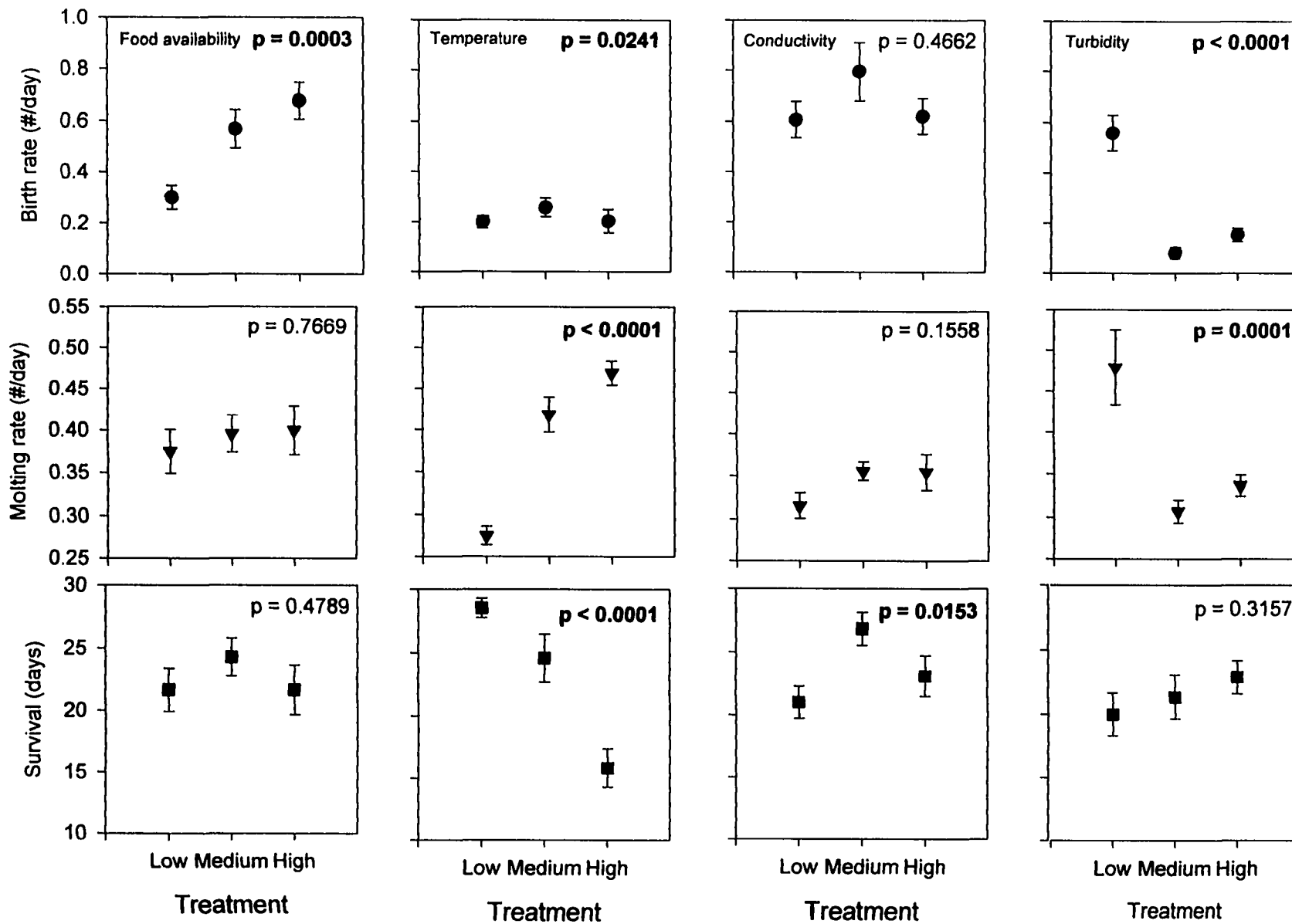
Table 2. Treatment levels for the four experiments, which tested the effects of food concentration, temperature, conductivity, and turbidity on Daphnia lumholtzi production.

<u>Experiment</u>	<u>Low</u>	<u>Medium</u>	<u>High</u>
Food concentration (cells/ml)	210	540	1070
Temperature (°C)	15	22	29
Conductivity (µmhos/cm)	1100	1250	1400
Turbidity (µg(dw)/l)	0	3.3	6.7

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- Fig. 1. Map of Lake Texoma indicating historical zooplankton sampling stations with numbered dots. Zooplankton were collected in the vicinity of station 3. A = Red River arm, B = Washita River arm, C = Denison Dam, and the hatched bar is a train bridge.
- Fig. 2. The effects of the four experimental parameters on aspects of Daphnia lumholtzi birth rate, molting rate, and survival during the course of a 4 week culture experiment. Each graph includes the mean, standard error and p-values in the corner of the graph.





**A multivariate analysis of the abundance and distribution of
the exotic cladoceran, Daphnia lumholtzi (Sars),
in Lake Texoma, OK-TX, USA**

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Key words: exotic species, zooplankton, life table, reservoir

Abstract

Daphnia lumholtzi is a recent addition to the zooplankton species pool of the southern US. It invaded the US from its original distribution of Africa, southern Asia, and Australia in the late 1980's. We examined the factors that affected the distribution and abundance of the D. lumholtzi in a large southern plains reservoir throughout one year. We measured zooplankton and phytoplankton abundances and vertical profiles of environmental variables over the large horizontal gradients in Lake Texoma. Daphnia lumholtzi was most abundant in the most riverine portions of the lake and during the warmest part of the year. The pattern of variation in distribution and abundance did not correspond to the spatio-temporal patterns for most of the other resident zooplankton taxa, nor did it correspond to changes in the phytoplankton community. We conclude that the ability of D. lumholtzi to withstand disturbed conditions and the physiological effects of temperature on reproduction and survival have a strong influence on the distribution and abundance of D. lumholtzi in Lake Texoma. Furthermore, because D. lumholtzi became abundant only in the summer, after many of the other taxa had experienced an annual decline, we suggest that it has little potential for impact on the other members of the zooplankton community.

Introduction

The rate of species invasions, particularly for taxa of diminutive body size, is increasing as intercontinental movement of people, goods, and services increases and as ecosystems become more disturbed. Movement of microorganisms and many insects potentially can occur in any transfer of nonsterile material. Once an exotic organism has reached an ecosystem, disturbance may increase the invasibility of the system by lessening the stability of interactions between organisms (Orians, 1986; Lodge 1993; Moyle and Light, 1996) and creating conditions under which native organisms cannot thrive (Orians, 1986). Furthermore, ecosystems that are disturbed may be more likely to be exposed to exotic species, particularly if the exotic is travelling with an intentionally introduced species (Welcomme, 1984). An ecosystem that is disturbed is likely to have more human contact than a relatively pristine ecosystem, and increased interactions with humans increase the likelihood that the ecosystem will be exposed to exotic species.

Daphnia lumholtzi is exotic to North America. Its original range consisted of eastern Australia, southcentral Asia, and eastern Africa. The species was first found in the United States in 1990 in Fairfield Lake, a small reservoir in Texas (Sorenson & Sterner, 1992). In the US, the range of the species has expanded from the unknown original site of introduction to now include most of the southeastern parts of the country, with sites as far north as Illinois and as far west as Arizona (Havel, pers. comm.). Because very few natural lakes exist in the southeastern US, most of the reports of D. lumholtzi are from reservoirs. Reservoirs typically have high variability in

physical, chemical, and biological parameters due to the strong horizontal gradients that occur in a flow-through system in addition to the classic vertical gradients of natural lakes (Wunderlich, 1971; Thorton, et al., 1990). Furthermore, many of the bodies of water from which D. lumholtzi has been reported in its native range are reservoirs, ephemeral ponds, and wastewater ponds (Khalaf & Smirnof, 1976; Bricker et al., 1978; Duncan, 1984, Geddes, 1984, Mangalo & Akbar, 1988; Timms, 1989; Mishra & Saksena, 1990; King & Greenwood, 1992).

We first found Daphnia lumholtzi in Lake Texoma in 1992, although it occurred in the reservoir at least by 1991 (Work & Gophen, 1995). Lake Texoma is a large bottom release reservoir built at the confluence of the Red and Washita Rivers in 1944. The Red River provides the majority of the flow and the water entering the reservoir from the Red River has a much higher conductivity than the water from the Washita River (USGS, 1996). Although both rivers can contribute large amounts of suspended sediments during annual spring floods (Matthews, 1984; Dimberger & Threlkeld, 1986; Threlkeld, 1986a), the Washita River is more turbid (USGS, 1996). Therefore, Lake Texoma is a good example of a reservoir with strong horizontal gradients, with higher variability in the more riverine areas than in deeper, more lacustrine areas near the dam (Fig. 1, Table 1).

A short-term pilot study of the distribution and abundance of Daphnia lumholtzi in Lake Texoma was conducted in 1993 (Work & Gophen, 1995). The study included qualitative sampling of zooplankton from February to May 1993 and quantitative sampling from 29 June to 27 July 1993. Maximum densities of Daphnia

lumholtzi occurred in the most riverine area of the reservoir during the coldest and hottest period of the study. The quantitative sampling indicated that the highest densities of D. lumholtzi were associated with relatively low temperatures, surface oxygen concentration, conductivity, and pH and relatively high bottom oxygen saturation and depth. However, this study spanned only a one month period during the hottest time of the year.

The pilot study also examined the relationship of Daphnia lumholtzi to the rest of the zooplankton community. D. lumholtzi varied positively with juvenile calanoid copepods and all copepod nauplii and negatively with Bosmina and rotifers, and varied in an altogether different pattern from the rest of the zooplankton community. Overall, D. lumholtzi abundance did not overlap substantially in time with any of the other cladoceran zooplankton or most of the copepods. During the course of the pilot study, most of the zooplankton community showed a severe reduction in abundance and many of the taxa disappeared in mid summer. This pattern has been documented as an annual occurrence by Matthews (1984) and Threlkeld (1986b). We also discovered deformed D. lumholtzi individuals during the zooplankton crash, and we experimentally measured a decrease in reproduction and survival concurrent with the increase in deformity at high temperatures (Work & Gophen, 1995).

Based on the results of the pilot study and many of the reports of Daphnia lumholtzi occurrences in its native range, we tested the hypothesis that D. lumholtzi would be most abundant in the relatively lotic areas in Lake Texoma that have higher variability in many physical and chemical characteristics (Fig. 1, Table 1). We predicted

that D. lumholtzi abundance would be spatially heterogenous over the course of an entire year, with higher abundances in the more riverine areas of the lake (i.e. stations 1-3 on Fig. 1). Due to extremely high densities of D. lumholtzi immediately before the overall zooplankton crash, we also predicted that D. lumholtzi would be most abundant during the hottest portion of the year. Finally, because the native zooplankton most likely evolved in more stable northern natural lakes (Hrbacek, 1987), we predicted that D. lumholtzi would respond to the high variability of Lake Texoma in a different pattern than the native species.

Materials and Methods

We collected weekly or bimonthly samples from 13 July 1994 to 13 July 1995 from 8 stations along the length of the reservoir (Fig. 2). At each station we collected zooplankton and phytoplankton samples and measured vertical gradients in temperature, dissolved oxygen, conductivity, and redox potential with a Hydrolab H20. Water transparency was approximated with a secchi disk and discharge data was provided by the Army Corps of Engineers.

To obtain a quantitative measure of zooplankton abundance, a 5-liter Beta Plus Bottle (Wildlife Supply Company) was lowered to depths of 1, 3, 5, 10, 15, and 20 m where possible, and all depths were combined to form one integrated sample for each station. For the phytoplankton sample, 100 ml of water was removed from the integrated sample and a few drops of Lugol's solution were added. The remainder of the integrated sample was filtered through an 80 μm mesh, treated with carbonated water to reduce egg loss from

cladocerans (Havel, pers. comm.), and preserved with 4 % buffered formalin. The qualitative zooplankton sample was collected with a vertical tows of an 80 μ m, 12 cm diameter Wisconsin net.

The quantitative zooplankton samples were subsampled three times and counted to species or the most convenient taxon. The Daphnia lumholtzi population only exhibited a significant increase during mid summer (8 June-13 July), so we calculated birth rates, death rates, and population rate of increase from egg numbers and development times (Work, 1997) for this period. Phytoplankton were identified with a compound microscope and a Sedwick-Rafter counting chamber. Individuals were grouped using the categories of Threlkeld (1986): filamentous cyanophytes, colonial cyanophytes, chlorophytes, diatoms, and dinoflagellates. All of the zooplankton variables were correlated with the phytoplankton variables using Spearman rank correlation. A logistic regression was calculated to determine whether phytoplankton abundance is related to the presence or absence of D. lumholtzi in the population.

Because many of the environmental measurements were correlated and we did not have complete species turnover, we used principal components analysis (PCA) to examine the relationship between Daphnia lumholtzi abundance, environmental factors, and other zooplankton abundances. PCA creates new orthogonal variables (axes) from the original matrix of variables, which represent the combination of variables that correlated (loaded) highly with that axis. We performed a PCA on two matrices of data from station 1, which had the highest abundances of D. lumholtzi. The first analysis used the environmental variables, including the phytoplankton

categories, as the matrix and the second analysis used the zooplankton species, including D. lumholtzi, as the matrix. After performing each PCA, we correlated the abundance of D. lumholtzi of each sample to the sample score on the PCA axes and overlaid the abundance of D. lumholtzi for each sample.

However, PCA is not predictive, so we also performed a discriminant analysis to predict the conditions under which Daphnia lumholtzi would occur. Although discriminant analysis uses presence/absence data and we collected abundance data, the abundance was low or zero in the majority of the samples and we considered that little information was lost. To perform the analysis, we randomly selected half of the samples (148) to create the model. We evaluated the model with the other half of the data by the proportion of the samples the model would categorize accurately.

Results

The spatial distribution of Daphnia lumholtzi in Lake Texoma was not uniform in terms of mean annual abundance or for any given sampling date. The abundance of D. lumholtzi decreased from the most riverine stations toward the dam (Fig. 2 and 3) with the exception of station 4, which is very shallow (3-6 m). All copepod nauplii and rotifers showed a similar pattern (Fig. 4) and were least abundant near the dam. In contrast, adult copepods were more abundant in the more lacustrine areas of the reservoir and cladocera other than D. lumholtzi exhibited no pattern along the axis of the reservoir (Fig. 5).

The temporal abundance of Daphnia lumholtzi also lacked uniformity (Fig. 6). Daphnia lumholtzi was absent from the samples at the onset of the sampling program (13 July) and first appeared in the samples in August. The population maintained a low abundance (0.1-1.5/l) throughout the fall and spring, but disappeared during the winter (Fig. 6). The only period of large increase occurred in mid summer when the abundance reached up to 36/l at some stations and dates. In contrast, the other cladocera and adult copepods were present throughout the year with peaks of abundance in fall and early spring (Fig. 6). Both groups, with the exception of Diaphanosoma and adult cyclopoids, declined in mid summer when the D. lumholtzi population was most abundant.

The pattern of the abundance of the phytoplankton categories corresponds to a decrease in abundance during the winter and an increase again in the spring (Fig. 8). Of all of the phytoplankton variables, Daphnia lumholtzi was only correlated with filamentous cyanophyte abundance (Table 2). The other two Daphnia species and adult calanoids were not correlated with any phytoplankton variables. The rest of the zooplankton taxa were correlated with some combination of phytoplankton variables, but in no obvious pattern (Table 2). The logistic regression indicated that phytoplankton abundance was not a significant predictor of the presence or absence of *D. lumholtzi* ($n = 36$, $p = 0.134$).

The first three axes of the PCA using the environmental measurements as the variables accounted for 75.0 % of the variability in the original matrix. The first axis was primarily influenced by temperature, dissolved oxygen on the bottom, secchi depth, and

phytoplankton abundance (Table 3). Surface dissolved oxygen, conductivity, pH, and discharge were most highly correlated with the second axis (Table 3). Daphnia lumholtzi abundance was correlated with the first axis ($r = -0.361$, $p = 0.04$) and not correlated with axis 2 ($r = -0.167$, $p = 0.36$) nor axis 3 ($r = 0.058$, $p > 0.50$). The highest densities of D. lumholtzi occurred in samples from dates that had high temperature, secchi depth, discharge, and phytoplankton abundance and low dissolved oxygen, conductivity, and pH (Fig. 9).

The first three axes of the PCA of the patterns of the zooplankton species abundances accounted for 75.4 % of the variability. Daphnia lumholtzi abundance was most highly correlated with axis 3 ($r = 0.523$, $p = p < 0.001$) and axis 2 ($r = 0.386$, $p = 0.01$) and not correlated with axis 1 ($r = 0.037$, $p > 0.50$). The first axis predominantly consisted of copepodites, adult calanoid copepods, and other cladocera except Diaphanosoma (Table 4). Adult cyclopoid copepods and Diaphanosoma were most highly correlated with axis 2, whereas copepod nauplii and rotifers were most highly correlated with axis 3 (Table 4). In other words, large numbers of D. lumholtzi occurred primarily in samples that contained low abundances of or lacked all groups except adult cyclopoids, Diaphanosoma, nauplii, and rotifers (Fig. 10). Therefore, the patterns exhibited by most copepods and other cladocera differed from those that describe D. lumholtzi, Diaphanosoma, copepod nauplii, and rotifers.

The discriminant analysis supported the results of the principal components analysis of the environmental variables. We derived a significant model by including station, temperature, dissolved oxygen, pH, and conductivity in the analysis, although conductivity

was not significant (Table 5). We correctly classified 98 out of 136 samples (72 %) using this model. Of the five significant variables, temperature was the most important predictor of the presence or absence of Daphnia lumholtzi (Table 5). Therefore, we examined the population demographics to determine whether this pattern was reflected in the birth and death rates during the period of greatest increase and decline (8 June-13 July). Previous laboratory experiments (Work, 1997) indicated that birth rates for D. lumholtzi increase up to 29 °C, above which the animals die before reproducing. In the field, the birth rates, death rates, and population rate of increase all increased until late June, after which they all declined (Fig. 11). Only the death rate increased again and exceeded the birth rate by the end of the sampling period.

Discussion

As predicted, Daphnia lumholtzi was most abundant in the Red River arm of the reservoir, which is the most riverine portion with the highest variability of the stations we sampled. Although the other cladocera and adult copepods and copepodites could also survive in the riverine portion of the lake, the pattern of declining abundance toward the dam for D. lumholtzi indicates that it is better adapted to the level of disturbance encountered in Red River arm of Lake Texoma than to the relatively lacustrine area near the dam. In terms of the temporal distribution of D. lumholtzi, it only became abundant in late June and early July after most of the other zooplankton populations were already declining in abundance. Furthermore, the PCA indicated that D. lumholtzi varied in a different pattern than

most of the other species, which suggests that the factors that drive a population increase in D. lumholtzi are different than those that drive most of the other species. As a result, there was little temporal overlap between D. lumholtzi and most of the other zooplankton species in Lake Texoma.

The lack of correlation between Daphnia lumholtzi and the food resources suggests that food limitation is not a likely cause of the low abundance or lack of D. lumholtzi during the cooler months of the year. Threlkeld (1986b) also examined the relationship between zooplankton species abundances in Lake Texoma and the same phytoplankton categories used in this study. He found a correlation between the disappearance of Daphnia galeata, Daphnia parvula, and Ceriodaphnia in mid July and a large increase in filamentous cyanophytes. Although we did not observe a complete disappearance of either D. galeata or D. parvula in mid July, we also did not find the high densities of filamentous cyanophytes that Threlkeld (1986b) observed in 1981 (1,000 vs. 20,000 cell/ml). Therefore, the potential for interference by the filamentous bluegreens with the feeding process of cladoceran zooplankton in 1994-95 was lower than in 1981.

The demographics of Daphnia lumholtzi for June and July 1995 suggest that the reduction in the population in mid July is the result of both a decrease in the birth rate and an increase in the death rate. This pattern, in combination with the trends in phytoplankton abundance and the temperature experiments of the pilot study (Work & Gophen, 1995), suggests that there is a negative physiological effect of extremely high temperatures on the reproduction and

survival of D. lumholtzi. However, an increase in filamentous cyanophytes to densities as high as seen in Threlkeld (1986b) may exacerbate the effect of temperature. The persistence of D. lumholtzi further into the warm period than most of the native species indicates that it may be able to withstand high temperatures better than the native species. Taylor & Mahoney (1988) and Leeper & Taylor (1995) measured zooplankton abundance in nuclear reactor cooling ponds and found that most of the zooplankton other than Diaphanosoma, Moina, rotifers, and some cyclopoids were eliminated from water warmer than 30°C. The surface temperatures of Lake Texoma exceed this temperature in mid July (29-31°C) and water at 5 m can reach this temperature (27-30°C). Therefore, the zooplankton community in mid July may be structured by a combination of temperature tolerances and interference of filamentous cyanophytes with zooplankton food collection, with the possibility of other biological effects such as predation by invertebrate and vertebrate predators that we did not measure.

These conclusions are supported by the probable ecological origins of these organisms. The southern US contained very few natural lakes before the construction of dams in the early part of this century, whereas the northern part of the country contains many lakes and many of the same zooplankton species. Therefore, the zooplankton that are in southern reservoirs probably evolved in the cooler northern lakes (Hrbacek, 1987) and have since invaded southern reservoirs. These southern reservoirs can reach higher temperatures due to the warmer climate and to the origin of their flow from relatively shallow, warm rivers. Daphnia lumholtzi, however,

originated in subtropical lakes in Africa, Asia, and Australia, many of which can exceed 30°C annually (Serruya and Pollinger, 1983).

Therefore, D. lumholtzi is likely to be better adapted to the warm temperatures that occur in Lake Texoma in the middle of the summer.

These conclusions are consistent with much of the theory of biological invasions. One of the primary predictors of the potential of an organism to invade an ecosystem is similarity to the native habitat (Moyle and Light, 1996). An organism that is invading an ecosystem similar to its native system may be considered to be somewhat preadapted to the habitat and does not have to rely on physiological plasticity to survive in the new habitat. As mentioned previously, D. lumholtzi originated in subtropical lakes that reach high midsummer temperatures and many of the reports are from disturbed ecosystems, such as ephemeral and wastewater ponds and reservoirs.

Furthermore, (Orians, 1986) has suggested that a disturbed system is more vulnerable to invasion than a relatively stable one. Because Lake Texoma is a reservoir in the southern plains, it experiences more disturbance than a typical natural lake (Table 1, Wunderlich, 1971, Thorton, et al., 1990). As a result, Lake Texoma may be particularly vulnerable to invasion.

Although Daphnia lumholtzi has established a population in Lake Texoma that has persisted for at least 6 years, the minimal temporal overlap between D. lumholtzi and most of the native species suggests that it will have only a minor impact on the zooplankton community. However, because it has persisted longer into the summer than most of the native species, it may have an impact on the phytoplankton community or it may provide a new food resource for

invertebrate and vertebrate predators. The impact of D. lumholtzi on the zooplankton, phytoplankton, and fish communities will also depend upon its abundance. During the pilot study, we recorded densities up to 120/L (Work & Gophen, 1995), whereas in this study the D. lumholtzi population only achieved a maximum density of 36/L. Comparisons of years of contrasting abundance may allow us to assess the impact of D. lumholtzi on the ecosystems in which it has invaded.

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Table 1. Mean annual standard deviations of temperature, dissolved oxygen, and conductivity in the most riverine (Red River arm) and the most lacustrine (dam) stations taken from the 36 sampling dates.

<u>Variable</u>	<u>Red River arm</u>	<u>Dam</u>
Temperature (°C)		
Surface	7.17	6.80
Bottom	6.94	4.88
Dissolved oxygen (mg/L)		
Surface	1.75	1.43
Bottom	2.97	3.99
Conductivity (µmho/cm)		
Surface	0.025	0.013
Bottom	0.041	0.015

Table 2. Spearman rank correlations (r) of zooplankton taxa with filamentous and colonial cyanophytes, chlorophytes, diatoms, and dinoflagellates for 36 samples at station 1. Correlations that are significant at $p = 0.05$ are boldface, whereas correlations that are significant after a Bonferroni correction are highlighted with an *.

<u>Zooplankton</u>	<u>Filament.</u>	<u>Colonial</u>	<u>Greens</u>	<u>Diatoms</u>	<u>Dinoflagellates</u>
<u>Daphnia lumholtzi</u>	0.33	0.30	0.30	0.32	0.19
<u>Daphnia galeata</u>	0.19	0.00	0.02	-0.08	0.12
<u>Daphnia parvula</u>	-0.05	-0.21	-0.21	-0.20	-0.06
<u>Bosmina</u>	-0.15	-0.40	-0.38	-0.47	-0.25
<u>Diaphanosoma</u>	0.37	0.64*	0.63*	0.71*	0.45
<u>Ceriodaphnia</u>	0.42	0.34	0.10	0.17	0.45
All rotifers	-0.35	-0.24	0.01	-0.14	-0.30
Adult cyclopoids	0.32	0.40	0.38	0.36	0.28
Juvenile cyclopoids	0.20	0.07	0.05	0.03	0.15
Adult calanoids	0.13	-0.07	-0.21	-0.19	0.17
Juvenile calanoids	-0.19	-0.42	-0.50	-0.56*	-0.28
All copepod nauplii	-0.20	-0.26	-0.07	-0.37	-0.24

Table 3. Loadings for the PCA of environmental variables for 36 samples taken from station 1. Significant loadings are highlighted with an * based on a table-wide Bonferroni correction for significance of $p < 0.004$. Highest loadings are highlighted with boldface type for each variable. Units for the measurements are: dissolved oxygen (mg/L), temperature (°C), conductivity (µhmo/cm), secchi depth (cm), discharge (acre-ft), and phytoplankton abundance (no./ml).

Factor	Axis 1	Axis 2	Axis 3
Eigenvalue	4.79	3.47	1.49
% of variance	46.81	26.70	11.50
Surface dissolved O ₂	0.122	0.830*	-0.353
Bottom dissolved O ₂	0.819*	0.432	-0.028
Temperature	-0.902*	-0.311	-0.139
Conductivity	-0.009	0.693*	-0.082
pH	0.214	0.807*	-0.482*
Redox potential	0.106	0.267	0.866*
Secchi depth	-0.704*	0.364	-0.181
Discharge	0.063	-0.777*	-0.470*
Filamentous bluegreens	-0.899*	0.171	0.054
Colonial bluegreens	-0.742*	0.541*	0.024
Greens	-0.472*	-0.415	-0.255
Diatoms	-0.612*	0.103	0.059
Dinoflagellates	-0.899*	0.232	0.186

Table 4. Loadings for the PCA of zooplankton variables (no./L) for 36 samples taken from station 1. Significant correlations are highlighted with an * based on a table-wide Bonferroni correction for significance of $p < 0.004$. Highest loadings are highlighted for each variable.

Factor	Axis 1	Axis 2	Axis 3
Eigenvalue	4.41	2.04	1.40
% of variance	46.7	17.0	11.7
<u>Daphnia lumholtzi</u>	0.037	0.386	0.523*
<u>Daphnia galeata</u>	-0.849*	0.177	0.059
<u>Daphnia parvula</u>	-0.782*	-0.030	0.035
<u>Bosmina</u>	-0.757*	-0.377	-0.007
<u>Diaphanosoma</u>	-0.082	0.831*	-0.005
<u>Ceriodaphnia</u>	-0.570*	0.170	-0.403
Rotifers	0.237	-0.264	0.740*
Adult cyclopoids	-0.402	0.694*	0.253
Juvenile cyclopoids	-0.788*	0.262	0.142
Adult calanoids	-0.846*	-0.068	-0.095
Juvenile calanoids	-0.696*	-0.553*	0.024
Nauplii	-0.359	-0.269	0.565*

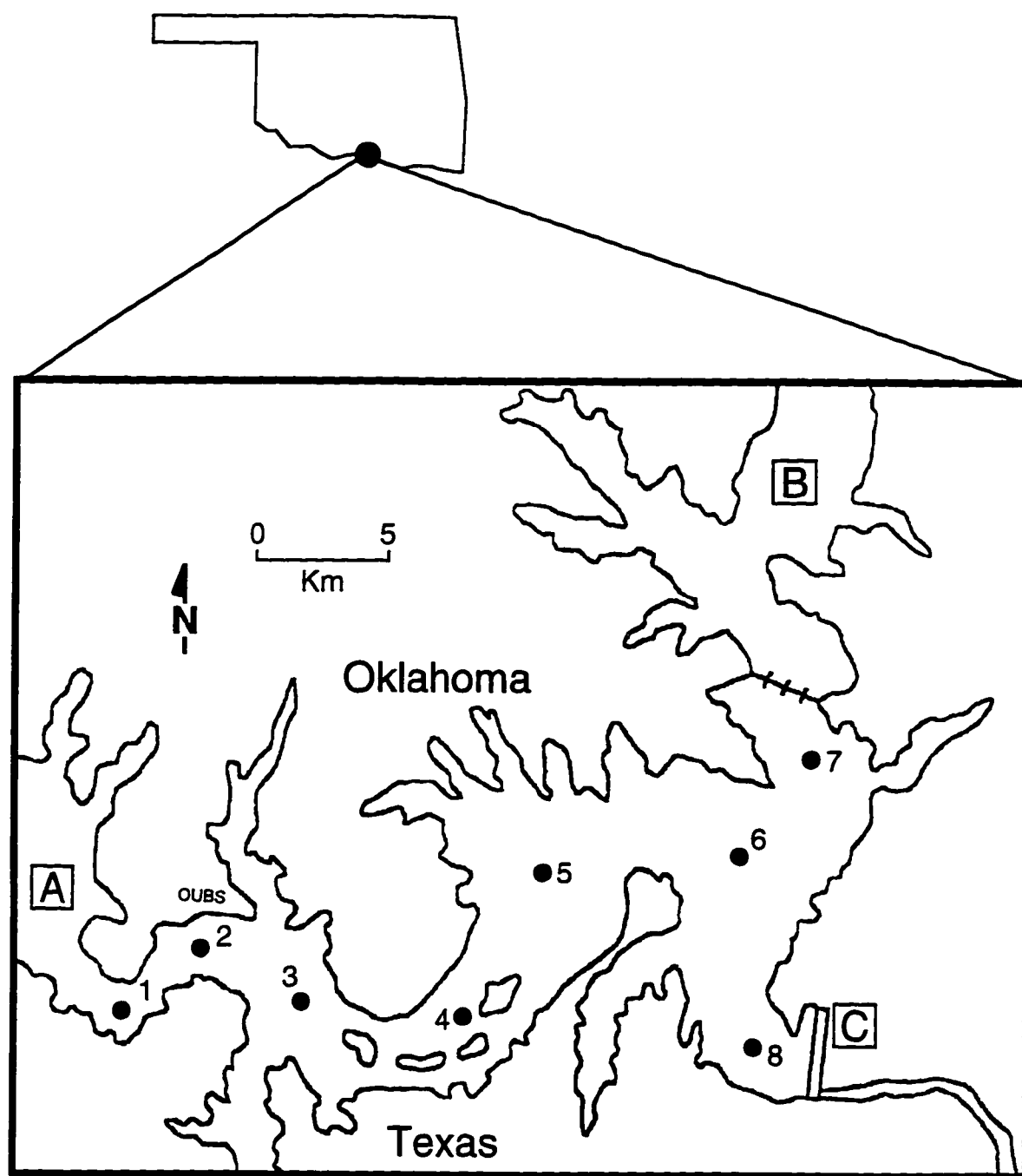
Table 5. Discriminant analysis for factors that predict Daphnia lumholtzi presence or absence in the zooplankton community using 136 samples randomly selected from the total of 235 for all stations and dates.

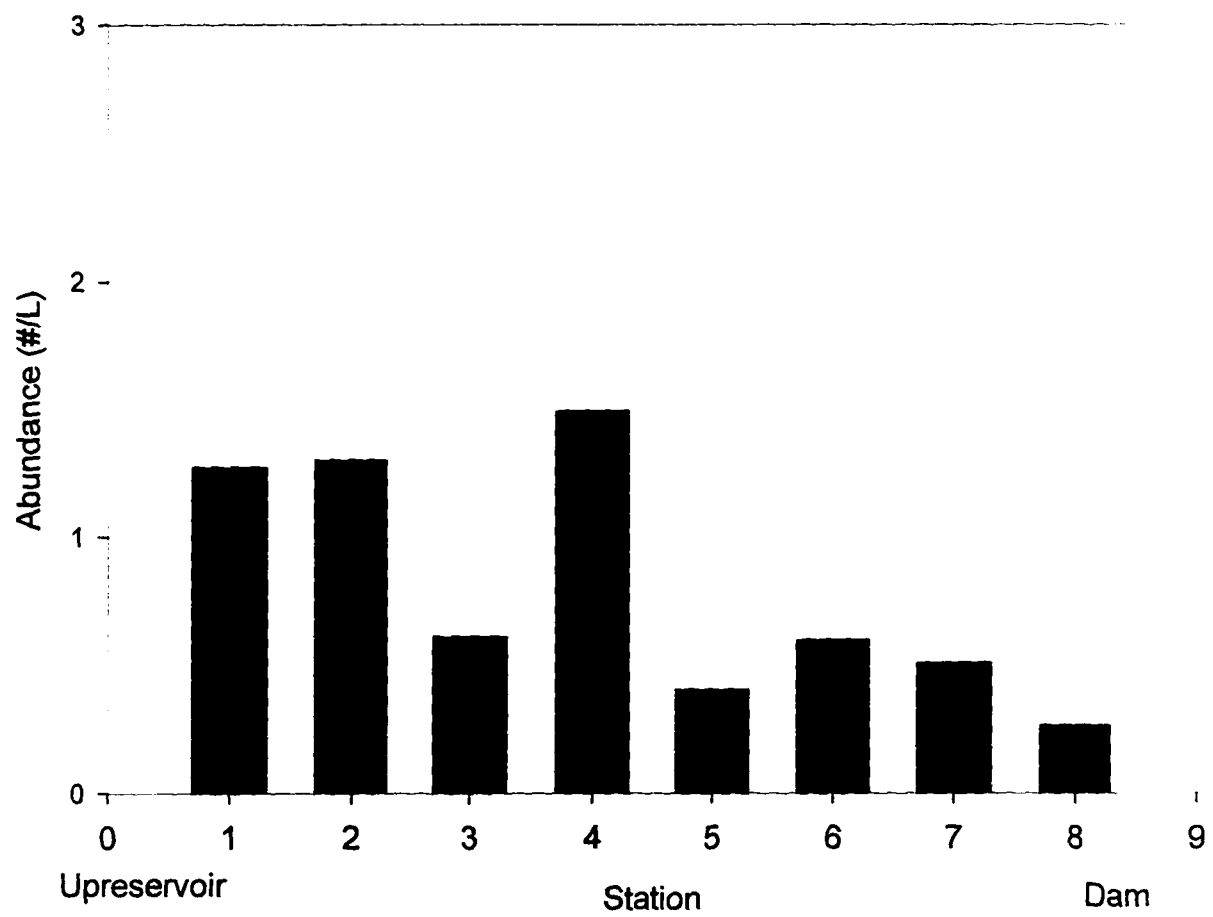
<u>Factor</u>	<u>F-ratio</u>	<u>P-value</u>	<u>Loading</u>
Surface temperature	20.45	<0.0001	0.748
Bottom dissolved O ₂	15.56	<0.0001	-0.652
Bottom pH	13.60	<0.0001	-0.610
Station	6.56	0.011	-0.423
Surface dissolved O ₂	5.19	0.024	-0.377
Bottom conductivity	3.27	0.073	0.299

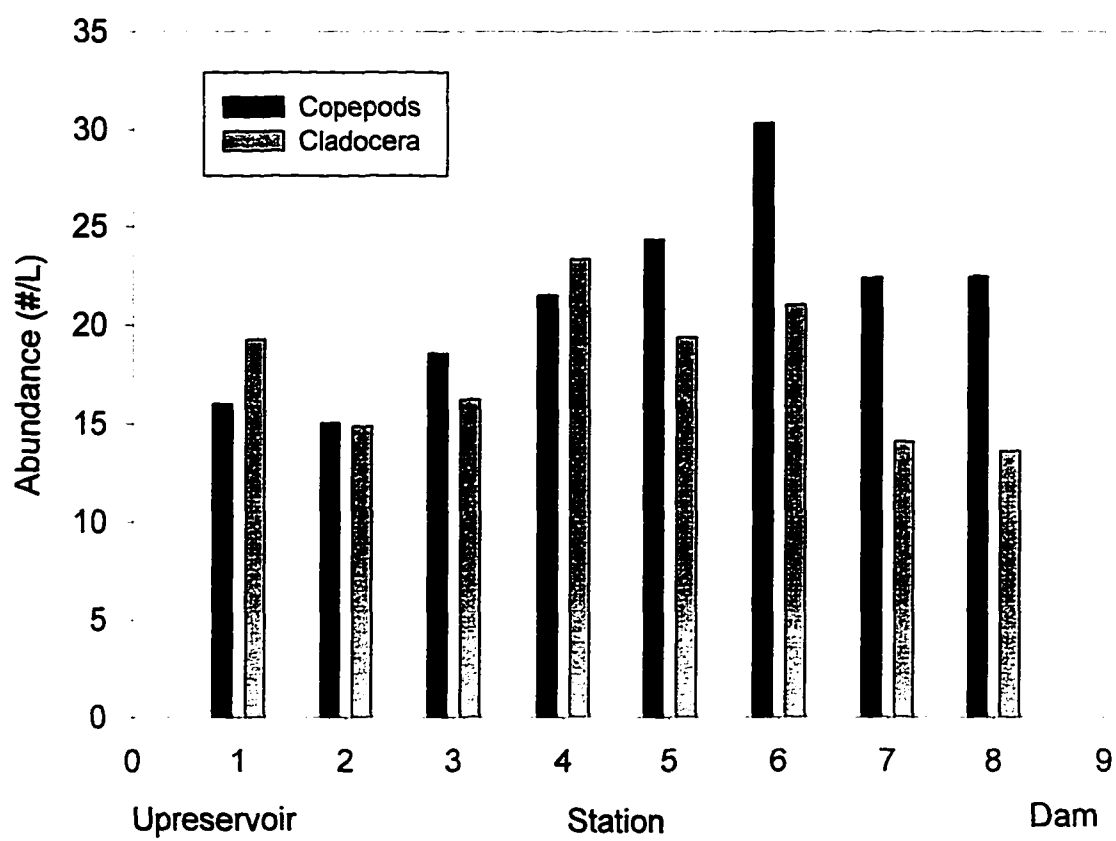
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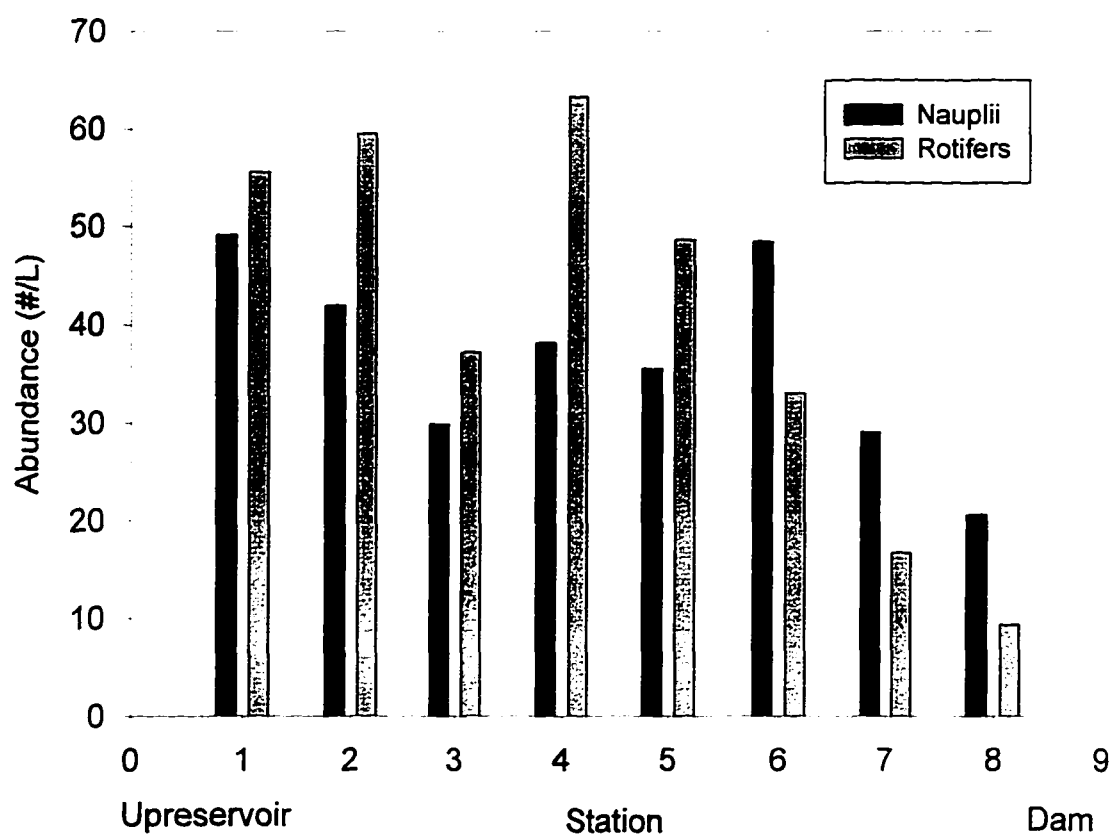
- Fig. 1. Map of Lake Texoma with sampling stations represented by dots. A - Red River arm; B - Washita River arm; C - Denison Dam. Station 1 is the most riverine station and station 8 is the most lacustrine station.
- Fig. 2. Mean annual abundance (no./L) of Daphnia lumholtzi at the 8 sampling stations in Lake Texoma. The abundance at each station was averaged for 36 sampling dates.
- Fig. 3. Mean annual abundance (no./L) of copepods and other cladocera at the 8 sampling stations in Lake Texoma. The abundance at each station was averaged for 36 sampling dates.
- Fig. 4. Mean annual abundance (no./L) of all copepod nauplii and rotifers at the 8 sampling stations in Lake Texoma. The abundance at each station was averaged for 36 sampling dates.
- Fig. 5. Mean monthly abundance (no./L) of native cladocera and Daphnia lumholtzi for all stations. The abundance for all 8 stations was averaged for each month.
- Fig. 6. Mean monthly abundance (no./L) of copepods and Daphnia lumholtzi for all stations. The abundance for all 8 stations was averaged for each month.

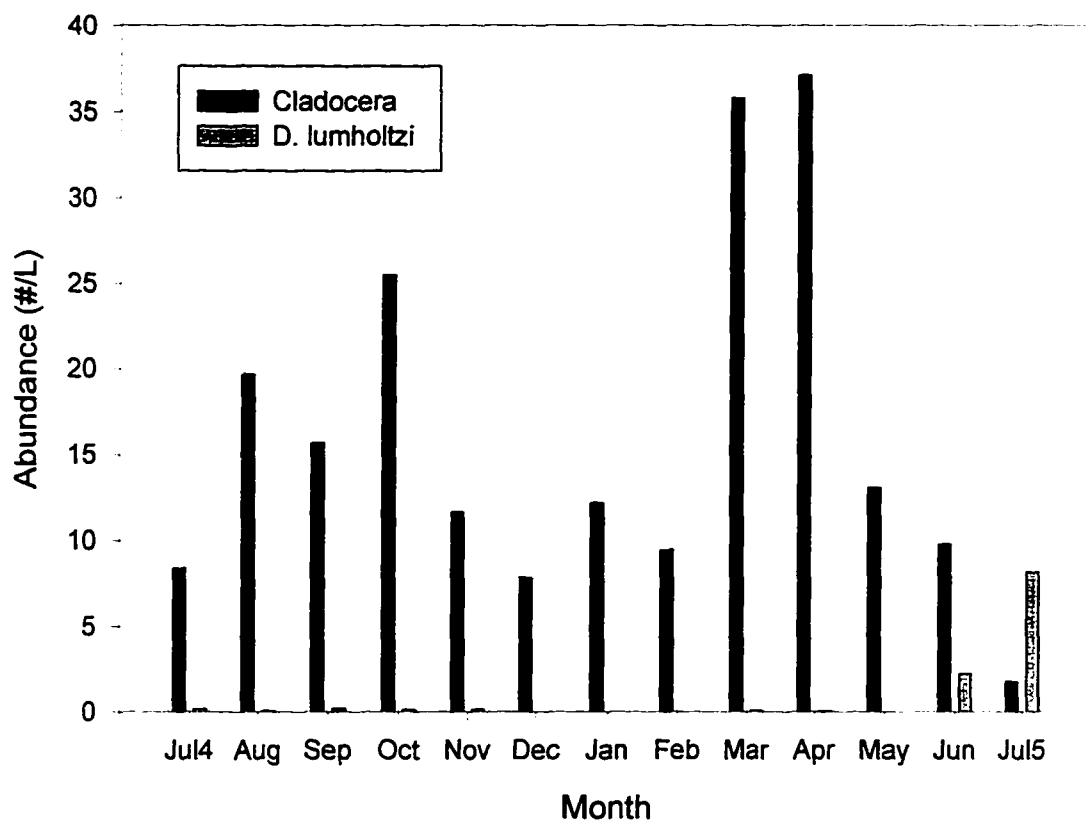
- Fig. 6. Phytoplankton abundances (no./mL) for each sampling date at station 1.
- Fig. 7. Scattergram of the first two axes of the PCA of the environmental matrix. The density of Daphnia lumholtzi was overlaid with open circling = no D. lumholtzi; squares = 0-1 D. lumholtzi/L; and triangles = 16-36 D. lumholtzi/L. Polygons distinguish three major periods during the year: late summer/fall, winter/early spring, and late spring/early summer.
- Fig. 8. Scattergram of axes 2 and 3 of the PCA of the zooplankton matrix. The density of Daphnia lumholtzi was overlaid with open circling = no D. lumholtzi; squares = 0-1 D. lumholtzi/L; and triangles = 16-36 D. lumholtzi/L. The polygon distinguishes the post-zooplankton crash community in late summer/early fall, which differed from the rest of the year.
- Fig. 9. Birth rate, death rate, and population rate of increase (ind./day) for Daphnia lumholtzi during the period when it is most abundant: 8 June to 13 July.

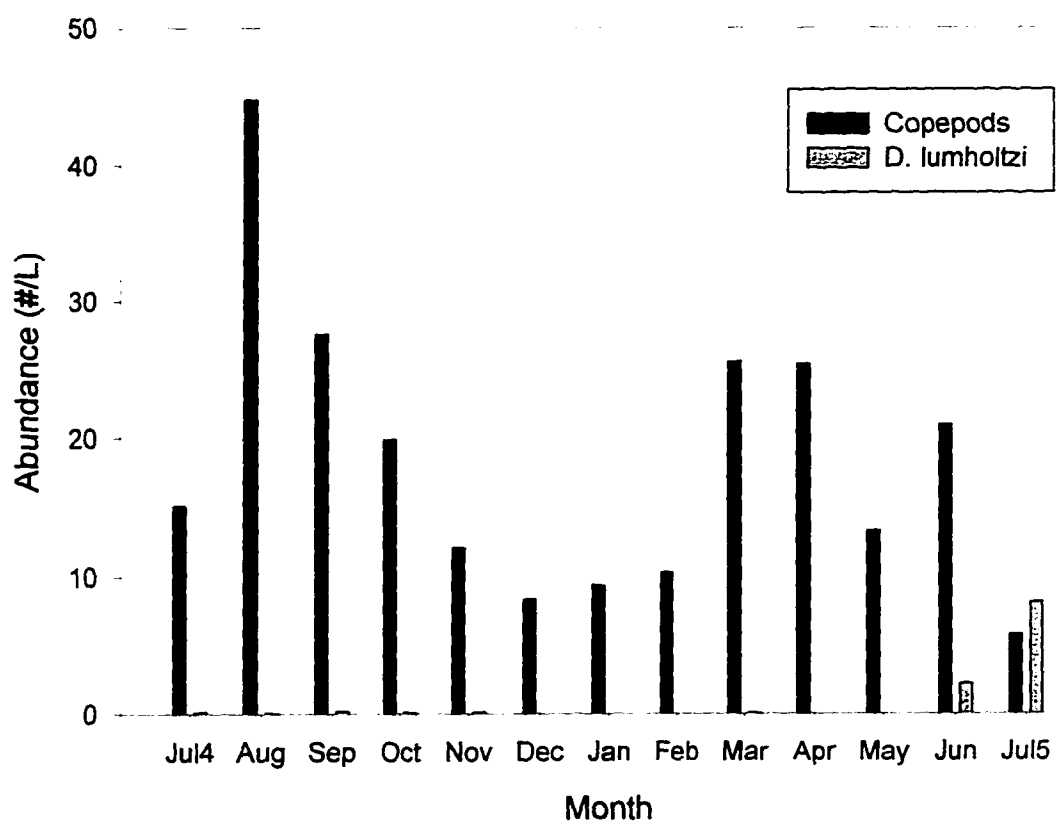


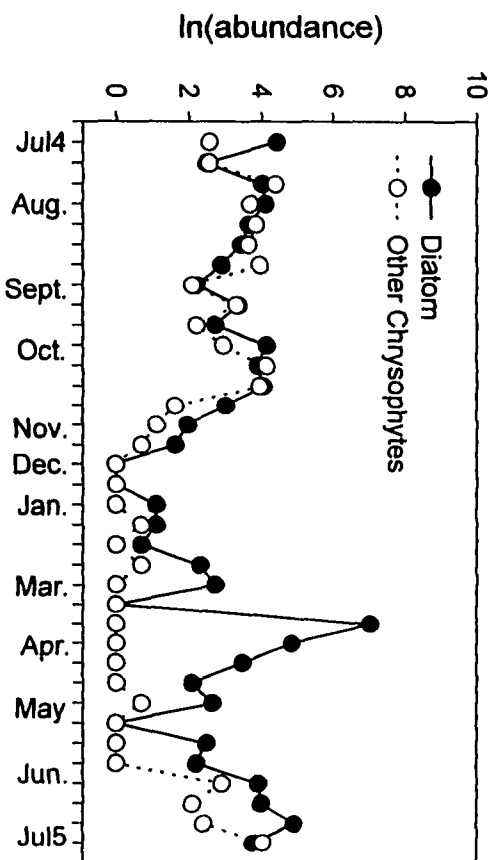
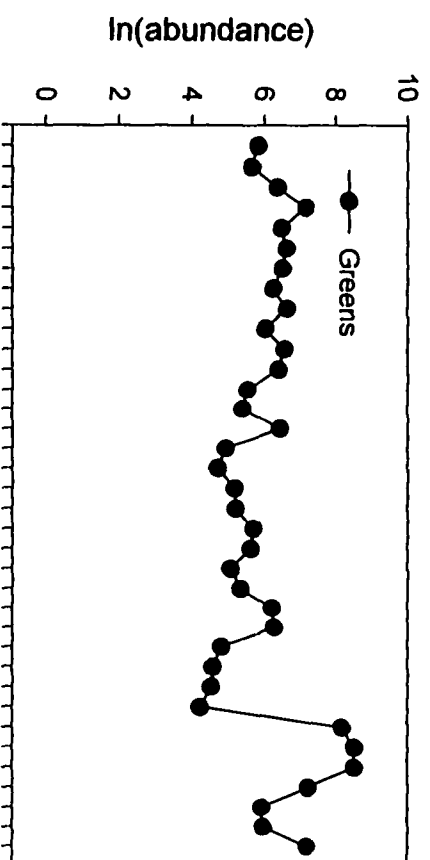
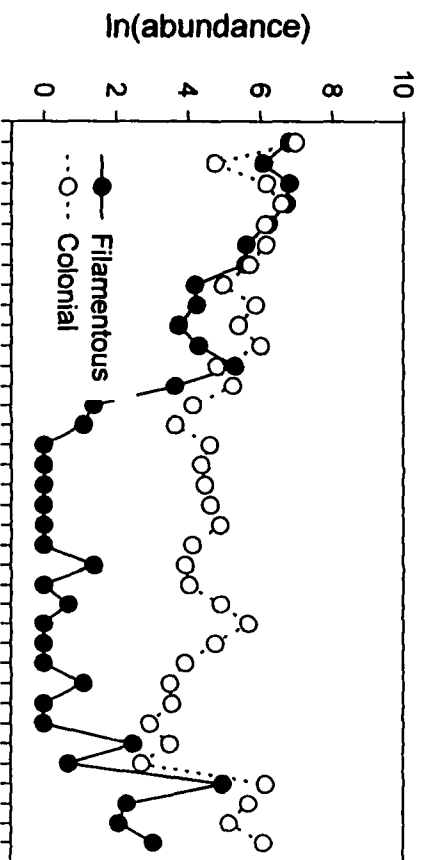


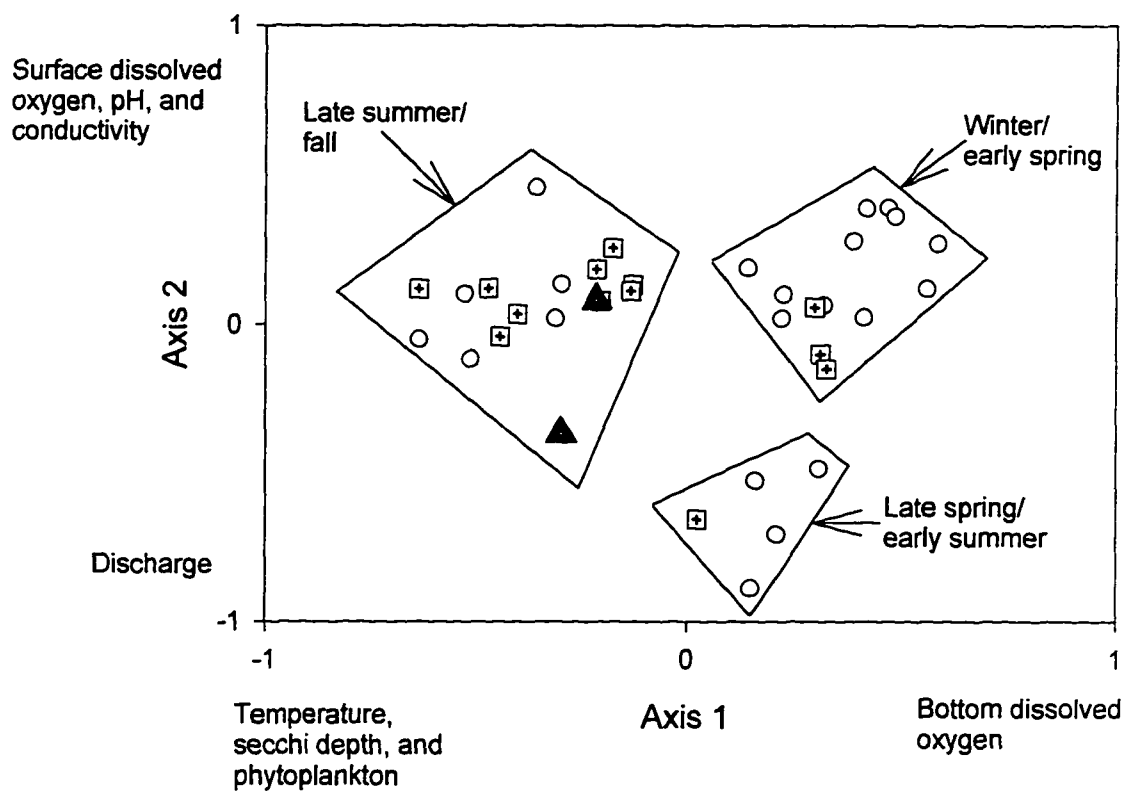


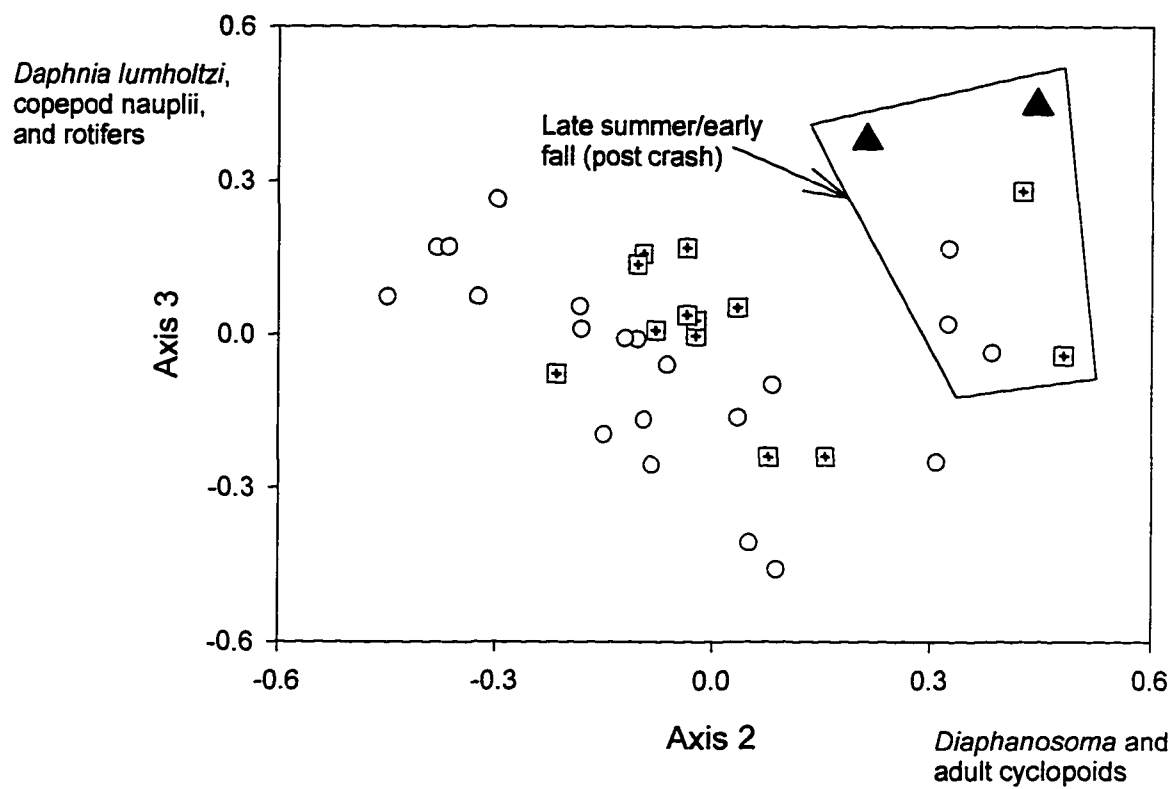


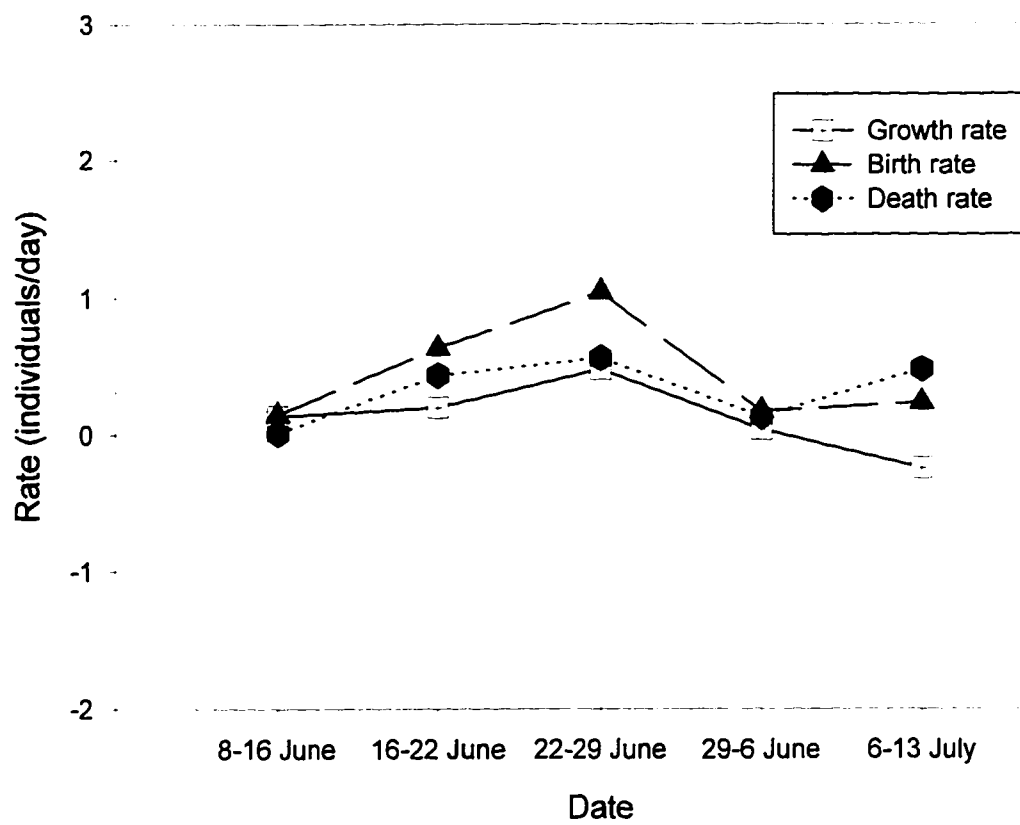












The effect of temperature on the birth rate,
molting rate, and longevity of Daphnia lumholtzi (Sars)
and two cladocerans native to Lake Texoma, OK-TX, USA

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Abstract

Daphnia lumholtzi is an exotic species that becomes seasonally abundant in Lake Texoma after most of the native zooplankton populations have declined in midsummer. We measured the effect of temperature on molting rate, birth rate, and survival of D. lumholtzi and two species with which it co-occurs in Lake Texoma. We cultured 25 individuals of each species individually at three temperatures (10, 18, and 26°C) and measured molts and offspring produced every other day. Although the molting and birth rates of Daphnia galeata were higher than D. lumholtzi, the survival of D. galeata was lower. Life table calculations indicated that total reproductive output was higher for D. lumholtzi under the experimental conditions. In addition, D. lumholtzi went through more instars and had a reproductive surge later in life than did D. galeata. Both the molting and birth rates of Ceriodaphnia were negatively affected by increasing temperature and its survival was low in all treatments. The patterns of growth and reproduction in this experiment suggest that the seasonal changes in abundance of the three species may be the result of differences in allocation of energy to growth and reproduction and in their survival at elevated temperatures.

Introduction

Daphnia lumholtzi is exotic to North America. It was first found in Fairfield Lake, Texas in 1991 (Sorenson and Sterner, 1992). Since the initial introduction of the species into the United States, the range has expanded to encompass reservoirs or rivers in most southern states from Florida to Arizona and as far north as Illinois (Havel, pers. comm.). The original range of D. lumholtzi includes eastern Africa, southeastern Asia, and eastern Australia (Havel and Herbert, 1994). Most of the water bodies from which it has been collected in its native range are either anthropomorphically disturbed or ephemeral (Khalaf and Smirnof 1976; Bricker, et al. 1978; Duncan 1984; Geddes 1984; Mangalo and Akbar 1988; Timms 1989; Mishra and Saksena 1990; King and Greenwood 1992), much like reservoirs and rivers in the southeastern United States.

Daphnia lumholtzi was first found in Lake Texoma in 1991 (Work and Gophen 1995) and it has been a significant part of the zooplankton community since its initial discovery (Work and Gophen 1995, Work 1997). Previous work on D. lumholtzi in Lake Texoma indicated that the species became abundant during midsummer when most other crustacean zooplankton were historically absent (Matthews 1984; Threlkeld 1986b; Work and Gophen 1995; Work 1997). There are several potential reasons for the reduction in the zooplankton community in midsummer, such as the physiological effects of high temperature, strong predation pressure by larval and juvenile fish produced in the spring and early summer, seasonal reduction in available food, and changes in physical and chemical factors in the lake due to spring flooding.

Daphnia lumholtzi can survive longer under the conditions that reduce the native zooplankton in midsummer. The term "native" should be

used somewhat loosely for these species because reservoirs are relatively young (Lake Texoma, 1944). These lakes are recent additions to the landscape of the southeastern US and as a result, most of these zooplankton did not occur in the majority of these areas. Therefore, these zooplankton probably did not originally speciate in the southeastern US, but in lakes further north in cooler climates (Hrbacek, 1987).

Zooplankton species differ in their temperature tolerances (Taylor and Mahoney 1988; Leeper and Taylor 1995), and Taylor and Mahoney (1988) observed that many of the crustacean zooplankton were eliminated from reservoirs receiving nuclear reactor cooling waters, leaving a community primarily composed of Diaphanosoma, Moina, and several rotifers. Although nuclear reactor cooling ponds are obviously an extreme example, D. lumholtzi evolved in subtropical areas where lakes regularly reach temperatures in the range of 25-30°C (Serruya and Pollinger 1983) and midsummer surface temperatures in Lake Texoma can reach 32°C. Therefore, we tested the hypothesis that D. lumholtzi would have higher growth and reproduction rates and better survival at elevated temperatures than species native to the southeastern US. We used two species that are common in Lake Texoma, Daphnia galeata and Ceriodaphnia lacustris, for comparison.

Methods

The animals for the experiment were collected on 17 November and the experiment ran from 25 November to 23 December, 1996. Zooplankton were collected from the Red River arm of the lake offshore from the University of Oklahoma Biological Station (Fig. 1) with 80 µm and 153 µm plankton nets towed horizontally for 5 minutes. The collections were sorted

to obtain 75 Daphnia lumholtzi, 75 Daphnia galeata, and 75 Ceriodaphnia of various sizes and ages. These 75 individuals of each species were randomly divided into 3 treatments of 25 individuals, which were maintained at temperatures of 10 °C, 18 °C, and 26 °C in environmental chambers with a 12:12 photoperiod.

Each individual was cultured separately in a flat bottomed vial containing 6 ml of filtered lake water (80 µm mesh size). Every other day each vial was examined for neonates and molts, each adult was transferred into new water, and food was added in excess (c.a. 1.0×10^6 cells/l Scenedesmus quadricauda) to each clean vial. The number of offspring and molts produced by the day of each water change, the day at which a brood pouch was first observed in immature individuals, and the number of days each individual survived the experiment were recorded. Birth rate per day was calculated as the number of offspring produced during the period (in days) in which the individual was mature. Molting rate was the number of molts produced during the period the animal was alive.

Differences between the birth rate, molting rate, and survival of the different species and the treatments were examined with one-way ANOVA (N = 25) and Fisher's PLSD for post-hoc tests. Because the animals were put into treatments directly from the field and were therefore of various ages, we calculated total population life-time reproductive output (R_t) with the following equation.

$$R_t = \text{sum (number surviving on day x) / (birth rate on day x)}$$

We also calculated the multiplication rate per instar, V_x , and the net reproductive rate, R_0 , from life tables (Krebs 1985) for those individuals that matured during the course of the experiment. The first instar used in the life table was the period between the first and second molts after the

brood chamber appeared. We followed successive instars until the death of the animal or the termination of the experiment. Therefore, the age-specific birth rate was calculated for each instar after maturity.

Results

Temperature significantly affected all three parameters examined (Table 1). For all three species birth rate increased with temperature (Fig. 2a) and both the main effects of species and temperature and the interaction term were significant. However, Daphnia lumholtzi and Daphnia galeata increased to a greater degree than did Ceriodaphnia (Fig. 2a). Although the three species had similar birth rates at 10°C, the mean birth rate for both Daphnia species was significantly higher than that for Ceriodaphnia ($p = 0.002$ and $p < 0.0001$ respectively). Daphnia galeata had the largest range in birth rates and attained the highest birth rate (Fig. 2a), although it was not significantly different from that of D. lumholtzi ($p = 0.41$). The mean birth rates for 18°C and 26°C were not significantly different ($p = 0.09$) due to a decrease for D. lumholtzi at 26 °C and a large variance in both medium and high treatments (Fig. 2a). The birth rates in the medium and high treatments were significantly greater than in the low treatment ($p < 0.0001$).

The main effects of species and temperature were also significant for molting rate, although the interaction term was not (Table 1). Molting rate increased with temperature for all species (Fig. 2b); however, molting rates for all species and treatment combinations were significantly different from each other. The mean molting rates for both 18°C and 26°C were significantly higher than for 10°C ($p < 0.0001$) and the molting rate at 26°C was significantly higher than at 18°C ($p < 0.0001$). The molting rate of Daphnia galeata was significantly higher than that for Daphnia lumholtzi (p

= 0.02), and molting rates for both species were significantly higher and increased faster than that for Ceriodaphnia ($p < 0.0001$).

In contrast to birth rate and molting rate, survival decreased with temperature. There were significant differences between species and temperatures and the interaction term was significant for survival (Table 1). Survival was lowest overall at 26°C and survival was significantly higher than 18°C and 26°C ($p < 0.0001$ and $p = 0.0002$, respectively), which were not significantly different from each other ($p = 0.24$). Individual Daphnia lumholtzi survived longer than either Daphnia galeata or Ceriodaphnia ($p < 0.0001$) in all treatments (Fig. 2c). Survival of D. galeata and Ceriodaphnia was not significantly different ($p = 0.08$), although the pattern exhibited by the two species was different (Fig. 2c). D. galeata survival was lower at 26°C, whereas Ceriodaphnia showed no significant pattern of changes in survival with temperature.

Life tables were not calculated for Ceriodaphnia because the response in birth rate, molting rate, and survival of the species to changes in temperature was very different than the response of the other two species. Total population reproductive output (R_t) for the other two species indicated that the Daphnia lumholtzi population produced more offspring than the Daphnia galeata population at all temperatures in this experiment (Table 2). The life table experiments also support this pattern; total population reproductive rate (R_0) was higher for D. lumholtzi than for D. galeata for all treatments (Tables 3). For both species, net reproductive rate was highest at 18°C, although R_0 for D. lumholtzi at 26°C was higher than R_0 for D. galeata at 18°C. Furthermore, allocation of reproductive output also differed for the two species (Tables 4 and 5). V_x for D. galeata at 26°C was low or zero after the 2nd instar, whereas D. lumholtzi had a second peak in

V_x during the 6th instar (Fig. 3). Finally, Daphnia galeata survived through more instars at lower temperatures than D. lumholtzi, but D. lumholtzi survived through more instars at 26°C.

Discussion

If growth, reproduction, and survival are examined as mean responses to temperature, Daphnia lumholtzi did not exhibit the predicted pattern of relatively higher responses than Daphnia galeata at higher temperatures. The response of both species to the increase in temperature was similar, although D. galeata actually surpassed D. lumholtzi in birth rate at the highest temperature in this experiment (26°C). The decrease in birth rate of Daphnia lumholtzi at the highest temperature in this experiment was consistent with the results of a previous experiment performed on the species alone (Work 1997), although the highest temperature in that experiment was 29°C. We chose 26°C as the highest temperature for this experiment because we were concerned that D. galeata and Ceriodaphnia would not survive at 29°C.

Several studies have noted similar patterns both for other species of cladocera and for copepods. Hebert (1978) reported a compilation of the data from several papers on the effects of temperature on Daphnia production. These data exemplified a reduction in embryonic development time, age at first reproduction, and lifespan for several species of Daphnia. Orcutt and Porter (1984) tested the effects of temperature on additional measurements of production for Daphnia parvula and looked for an interactive effect of food concentration. In addition to the general decline in the embryonic development time, age at first reproduction, and lifespan with temperature, they found that the average brood size, number of young per

reproductive female, and the net reproductive rate increased with temperature. However, five of the six measurements (all but number of young per reproductive female) were affected by an interaction between temperature and food concentration and the effect of the interaction was different for each measurement. Korpelainen (1986) also noted a decrease in lifespan and generation time and an increase in the intrinsic rate of increase for Daphnia magna.

Finally, Gophen (1976, 1978a, 1978b, 1981) measured the effect of temperature on production of a cyclopoid copepod, Mesocyclops leuckarti, although Gophen (1981) also reports measurements for selected cladocerans (Diaphanosoma brachyum, Bosmina longirostris, and Ceriodaphnia reticulata). He found that food intake, metabolism (measured by excretion), respiration (measured by oxygen consumption), specific rate of growth, % of copepod females that carry eggs, and productivity/biomass (P/B) increased with temperature from 15 to 27°C. However, the % of females that carried eggs declined past 27°C and the lowest P/B for cladocera occurred at the intermediate temperature (22°C). These reports on the effects of temperature on zooplankton production support the results of this experiment; increases in temperature generally result in increases in productivity and decreases in lifespan.

Analysis of the instar-specific responses of Daphnia lumholtzi and Daphnia galeata indicates that allocation of energy to growth and reproduction is different between the two species. Total population reproductive output was higher for D. lumholtzi at all temperatures in this experiment, including 26 °C, and midsummer temperatures can exceed 26 °C in Lake Texoma, particularly in the euphotic zone (Work and Gophen 1995). On a finer scale, Daphnia galeata cohort-specific birth rates were

lower, but at lower temperatures they went through more instars more frequently than did D. lumholtzi. On the other hand, D. lumholtzi went through more instars and had two reproductive surges at 26°C, rather than the one peak in reproductive effort early in the lifespan of D. galeata. Therefore, D. galeata had relatively more opportunities to reproduce at lower temperatures and D. lumholtzi had relatively more at higher temperatures.

This allocation of energy and reproduction reflects the pattern in the field data for Lake Texoma in 1994-95 (Work 1997); D. galeata was more abundant in colder periods and D. lumholtzi was more abundant in warmer periods. On the other hand, Ceriodaphnia became most abundant in fall and early spring, but virtually disappeared by June. This pattern in the field data also reflects the experimental data for Ceriodaphnia; both birth and molting rates were negatively affected by increasing temperature.

Regardless of the single factor effect of temperature on Daphnia lumholtzi, D. galeata, and Ceriodaphnia production, combinations of biotic and abiotic factors work together to produce the zooplankton community at any given time. Large changes in flow, conductivity, and turbidity can occur in Lake Texoma with the annual spring floods (Matthews 1984; Dirnberger and Threlkeld 1986; Threlkeld 1986a; Work and Gophen 1995), and may affect the composition of the zooplankton community in combination with the effect of temperature (Dirnberger and Threlkeld 1986; Threlkeld 1986a). Biological changes in the reservoir also may affect zooplankton community structure. The large spines of many species of Daphnia, which Daphnia lumholtzi possesses in extreme proportions, have been observed to reduce vertebrate and invertebrate predation (Swift and Fedorenko 1975; O'Brien et al. 1979; O'Brien et al. 1980; Krueger and

Dodson 1981; Havel and Dodson 1984; Havel 1985; Pijanowska 1990; Parejko 1991). None of the native species have spines as extreme as those of D. lumholtzi. Therefore, changes in the abundance of invertebrate predators, such as Chaoborus and Leptodora, may also restructure the community by favoring species/individuals that can produce long spines (Black and Hairston 1983; Pijanowska 1990). Adult D. lumholtzi may be too large for invertebrate predators to consume, or the spines may prevent handling by the invertebrate predators.

The large influx of juvenile Menidia beryllina that occurs in the spring or early summer (Gelwick and Matthews 1990) also may help to shift the zooplankton community toward domination by Daphnia lumholtzi by mid summer. Other studies have shown that most adult and some juvenile fish select large and relatively easy prey to capture, such as Daphnia species (Mills and Forney 1975; Eggers 1982). The large spines that may occur on many species of Daphnia may be induced by invertebrate predators and are proportionally largest in the juvenile stages (O'Brien et al. 1979; Dodson 1988; Pijanowska 1990; Hanazato 1991; Parejko 1991). Therefore these spines usually are considered to be antipredator devices for invertebrate predators rather than for fish (Havel and Dodson 1984; Dodson 1988; Tollrian 1990). However, Tollrian (1994) succeeded in inducing spine elongation in D. lumholtzi with fish extracts and this induction occurred in the adult stages. Therefore, the spines of D. lumholtzi may act as antipredator devices for fish rather than for invertebrate predators. Even juvenile Menidia can consume D. lumholtzi, but smaller fish prefer smaller D. lumholtzi (Lienesch 1997). Therefore, differential survival due to a large influx of Menidia in early to mid summer may augment the differential effects of temperature on reproductive rate and survival seen in this paper to

drastically alter the zooplankton community in favor of D. lumholtzi in mid summer.

The life table responses of Daphnia lumholtzi and Daphnia galeata to changes in temperature suggest that the patterns of abundance of the two populations may reflect changes in energy allocation between growth and reproduction. However, other factors, such as the physical, chemical, and biological changes mentioned above, also must interact with temperature to produce the zooplankton community in Lake Texoma in midsummer.

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Table 1. ANOVA for the effects of temperature on birth rate, molting rate, and survival of Daphnia lumholtzi, Daphnia galeata, and Ceriodaphnia. Significant p-values are highlighted and N = 25.

<u>Experiment</u>	<u>Factor</u>	<u>Df</u>	<u>F-values</u>	<u>p-values</u>
Birth rate	Species	2	9.273	0.0001
	Temperature2	4	7.107	<0.0001
	Interaction	4	5.050	0.0007
Molting rate	Species	2	36.656	<0.0001
	Temperature2	2	36.397	<0.0001
	Interaction	4	1.651	0.1626
Survival	Species	2	26.679	<0.0001
	Temperature2	1	3.643	<0.0001
	Interaction	4	3.225	0.0135

Table 2. Total population reproductive output for 28 days for Daphnia lumholtzi, Daphnia galeata, and Ceriodaphnia lacustris at 10, 18 and 26°C.

<u>Species</u>	<u>10°C</u>	<u>18°C</u>	<u>26°C</u>
<u>Daphnia lumholtzi</u>	118.6	393.1	292.4
<u>Daphnia galeata</u>	57.1	272.7	248.7
<u>Ceriodaphnia</u>	62.1	152.6	240.4

Table 3. Net reproductive rate, R_0 , for Daphnia lumholtzi, Daphnia galeata, and Ceriodaphnia lacustris at 10, 18 and 26°C.

<u>Species</u>	<u>10°C</u>	<u>18°C</u>	<u>26°C</u>
<u>Daphnia lumholtzi</u>	5.3	15.3	10.5
<u>Daphnia galeata</u>	1.5	9.1	4.1

Table 4. Life tables for *Daphnia lumholtzi*: n_x = no. alive at each instar, l_x = proportion surviving at each instar, b_x = instar-specific birth rate, V_x = instar-specific multiplication rate, R_0 = net reproductive rate.

Instar	10°C				18°C				26°C			
	n_x	l_x	b_x	V_x	n_x	l_x	b_x	V_x	n_x	l_x	b_x	V_x
1	11	1.00	2.64	2.64	9	1.00	2.55	2.55	11	1.00	1.91	1.91
2	6	0.54	4.83	2.61	9	1.00	2.78	2.78	11	1.00	2.00	2.00
3	1	0.09	0	0	9	1.00	4.00	4.00	11	1.00	1.64	1.64
4					7	0.78	4.00	3.12	9	0.82	0.67	1.49
5					6	0.67	3.00	2.01	7	0.64	1.57	1.00
6					3	0.33	2.67	0.88	7	0.64	3.14	2.01
7									6	0.54	2.17	1.17
8									5	0.45	0.60	0.27
9									2	0.18	0	0
10									2	0.18	0	0
11									2	0.18	0	0
R_0				5.25				15.34				11.49

Table 5. Life tables for *Daphnia galeata*: n_x = no. alive at each instar, l_x = proportion surviving at each instar, b_x = instar-specific birth rate, V_x = instar-specific multiplication rate, R_0 = net reproductive rate.

Instar	10°C				18°C				26°C			
	n_x	l_x	b_x	V_x	n_x	l_x	b_x	V_x	n_x	l_x	b_x	V_x
1	10	1.00	0	0	9	1.00	2.22	2.22	12	1.00	0.58	0.58
2	5	0.50	1.00	0.50	8	0.89	1.87	1.66	12	1.00	1.83	1.83
3	2	0.20	2.00	0.40	7	0.78	1.86	1.45	5	0.42	1.80	0.76
4	2	0.50	3.00	0.60	7	0.78	1.71	1.33	4	0.33	0.75	0.25
5	1	0.10	1.00	0.10	3	0.33	2.67	0.88	3	0.25	1.00	0.25
6					2	0.22	3.50	0.77	3	0.25	1.33	0.33
7					2	0.22	2.00	0.44	2	0.17	0.50	0.08
8					1	0.11	3.00	0.33	1	0.08	0	0
9									1	0.08	0	0
R_0				1.60				9.08				4.08

List of Figures

- Fig. 1. Map of Lake Texoma indicating the area of collection of animals for the experiment.
- Fig. 2. Changes in the birth rate (top), molting rate (middle), and survival (bottom) of Daphnia lumholtzi, Daphnia galeata, and Ceriodaphnia lacustris at 10, 18, and 26°C.
- Fig. 3 Differences in the cohort-specific reproductive rates of Daphnia lumholtzi (top) and Daphnia galeata (bottom) at 10, 18, and 26°C. V_x = instar-specific multiplication rate.

