SIZE-SELECTIVE PREDATION BY INLAND SILVERSIDES ON AN EXOTIC CLADOCERAN, *DAPHNIA LUMHOLTZI*

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ABSTRACT—The helmet and large spines of zooplankton inhibit predation by small fishes. *Daphnia lumholtzi,* a long-spined, helmeted cladoceran, has recently invaded Lake Texoma (Oklahoma–Texas) and much of southeastern North America. To determine if inland silversides (*Menidia beryllina*) were size-selective predators on *D. lumholtzi,* we conducted laboratory experiments using 3 size-classes of fish (22 to 35 mm, 46 to 60 mm, and 67 to 80 mm). Inland silversides were allowed to feed for 80 min on *D. lumholtzi* of various sizes. Prey selection differed among the 3 silverside size-classes. Small inland silversides ate more small *D. lumholtzi* (total length 0.99 to 1.75 mm) than did large and medium inland silversides. Large inland silversides ate more large (2.62 to 3.44 mm) and very large (3.5 to 5.25 mm) *D. lumholtzi* than did smaller inland silversides. To examine if these trends occur in nature, we compared the lengths of *D. lumholtzi* and native *Daphnia* species (*D. parvula* and *D. galeata*) eaten by large and small inland silversides collected from Lake Texoma. As in the laboratory experiment, small inland silversides ate smaller *D. lumholtzi* than did large inland silversides. Although small inland silversides ate smaller *D. lumholtzi, D. lumholtzi* might be an important food source for young-of-the-year inland silversides, because *D. lumholtzi* reaches peak abundances during summer when native daphnid densities are low in Lake Texoma.

RESUMEN—El casco y las espinas grandes del zooplanton inhiben la depredación por peces pequeños. *Daphnia lumholtzi,* un cladócero con casco y espinas largas, ha invadido recientemente el lago Texoma (Oklahoma–Texas) y una gran parte del sudeste de Norteamérica. Para determinar si los plateaditos (*Menidia beryllina*) son depredadores tamaño-selectivos en *D. lumholtzi,* condujimos experimentos de laboratorio usando tres clases de tamaño de peces (22 a 35 milímetros, 46 a 60 milímetros, y 67 a 80 milímetros). Se permitió a los plateaditos alimentarse durante 80 minutos de *D. lumholtzi* de varios tamaños. La selección de la presa se diferenció entre las tres clases de tamaño del plateadito. Los plateaditos pequeños comieron más pequeños *D. lumholtzi* (longitud total 0.99 a 1.75 milímetros) que los plateaditos grandes y medianos. Los plateaditos grandes comieron más grandes (2.62 a 3.44 milímetros) y muy grandes (3.5 a 5.25 milímetros) *D. lumholtzi* que plateaditos más pequeños. Para examinar si estas tendencias ocurren en la naturaleza, comparamos las longitudes de *D. lumholtzi,* y las especies nativas del *Daphnia* (*D. parvula* y *D. galeata*), comidas por los plateaditos grandes y pequeños colectados en el lago Texoma. Como en el experimento de laboratorio, los plateaditos pequeños comieron *D. lumholtzi* más pequeños que los plateaditos grandes. Aunque los plateaditos pequeños comieron *D. lumholtzi* más pequeños, el *D. lumholtzi* puede ser una fuente importante de alimento para los plateaditos crías en su primer año porque el *D. lumholtzi* alcanza abundancias máximas durante el verano cuando las densidades de los dáfnidos nativos son bajas en el lago Texoma.

Daphnia lumholtzi is a spiny zooplankter that recently invaded North America (Sorenson and Sterner, 1992; Havel et al., 1995). Native to Asia, Africa, and Australia, *D. lumholtzi* was first found in Texas in 1990 (Sorenson and Sterner, 1992) and has spread quickly throughout the southeastern USA (Havel et al., 1995). *Daphnia lumholtzi* is characterized by a large helmet, a long tail spine, 2 lateral fornices extending to sharp points, and 10 prominent spines on the ventral carapace margin (Havel and Hebert, 1993). The helmet and tail spine of *D. lumholtzi* can account for over 75% of the total length of the animal.

Some zooplankton, typically smaller species (<1 mm; e.g., rotifers), develop spines as protection against invertebrate predation (reviewed by Havel, 1987; Tollrian and Dodson, 1999). In these species, spines are usually larger in early instars, which typically incur high rates of predation by invertebrate predators (Krueger and Dodson, 1981; Tollrian, 1994), and spines are reduced in adults, which are not susceptible to invertebrate predation. Spines protect small zooplankton by decreasing the handling efficiency of invertebrate predators (Havel and Dodson, 1984) and are typically ineffective against vertebrate predators. Studies indicate that large spines (>50% total length of the zooplankter), which are found on the introduced species *Bythotrephes cederstroemi* and *D. lumholtzi* but not on any native cladocerans, can protect large zooplankton (>1 mm total length) from predation by small vertebrate planktivores (Barnhisel, 1991*a,* 1991*b*; Swaffar and O'Brien, 1996; Kolar and Wahl, 1998). It has been proposed that the invasion of *D. lumholtzi* into waters of the southern USA might have negative effects on small zooplantivorous fish if it is not a suitable prey species and displaces native zooplankton (Havel et al., 1995; Kolar et al., 1997).

In Lake Texoma, Oklahoma–Texas, adult (>50 mm standard length) inland silversides (*Menidia beryllina*) feed upon *D. lumholtzi* during summer (Lienesch and Gophen, 2001). Inland silversides are particulate-feeding zooplanktivores that are most common in the littoral zone in Lake Texoma. Native zooplankton density in Lake Texoma experiences peaks in late spring and then declines drastically by mid-summer (Matthews, 1984; Threlkeld, 1986; Work, 1997). *Daphnia lumholtzi* reaches maximum abundance as native *Daphnia* species are declining (Work and Gophen, 1995; Work, 1997) and abundance of juvenile inland silversides is increasing (Lienesch and Matthews, 2000). Due to food limitation during summer, *D. lumholtzi* was an important food source in Lake Texoma and was selected by adult inland silversides (Lienesch and Gophen, 2001). *Daphnia lumholtzi* also might be an important food source for juvenile inland silversides. Because small fish have difficulty feeding on *D. lumholtzi* (Swaffar and O'Brien, 1996; Kolar and Wahl, 1998), we were interested in the effect of fish size on prey size-selection when inland silversides feed on *D. lumholtzi*.

We conducted a laboratory experiment to determine the size selectivity of 3 size-classes of inland silversides feeding on 4 size-classes of *D. lumholtzi*. To test whether the size of daphnids eaten in Lake Texoma would agree with experimental predictions, we analyzed the size distributions of *D. lumholtzi* and native *Daphnia* in the stomachs of small and large inland silversides previously collected from Lake Texoma.

METHODS—*Laboratory Experiment*—Inland silversides were collected from the littoral zone of Lake Texoma at the University of Oklahoma Biological Station and transported to the laboratory. Fish were acclimated for at least 1 week and fed flake food supplemented with live zooplankton, including native and nonnative daphnids, from Lake Texoma.

When experiments were conducted, *D. lumholtzi* had already declined in Lake Texoma and, therefore, were collected on the day of each trial from Lake Hugo, Choctaw County, Oklahoma. *Daphnia lumholtzi* were collected by surface tows of a 0.5-m diameter ichthyoplankton net (500-μm mesh) and a 0.25-m diameter Wisconsin plankton net (353-μm mesh). Zooplankton were transported to the laboratory and used in the experiment within 5 h of collection.

Two trials were conducted: one on 25 July 1995 and the other on 27 July 1995. For each trial, 2 large (67 to 80 mm), 5 medium (46 to 60 mm), or 8 small (22 to 35 mm) inland silversides were placed into 38-L aquaria, each containing 30 L of aerated lake water. Four replicate aquaria were used for each fish size-class. Fish densities were based on the results of pilot studies to equalize the overall predation pressure (number of individuals consumed) in each tank. Fish were placed in the tanks and not fed 24 h prior to the start of each trial to standardize hunger and gut fullness.

To measure silverside predation, we compared the number of *D. lumholtzi* of 4 size-classes consumed during an 80-min feeding period. We chose to use the density of *D. lumholtzi* remaining in the tank rather than directly examining *D. lumholtzi* from the stomachs of inland silversides because damage incurred during predation (e.g., broken spines) made measuring them difficult. One-liter aliquots of zooplankton (>95% *D. lumholtzi*) were introduced into each of the 12 treatment tanks. Fish in the treatment tanks were allowed to feed for 80 min, after which a zooplankton sample was collected from each treatment tank. Each sample consisted of 3 tube samples collected by placing a 4-cm-diameter PVC tube onto a rubber stopper randomly placed on the aquarium floor after gently stirring the water (Drenner and McComas, 1980). Water from the 3 tube samples was combined, the total volume measured, and the zooplankton concentrated by filtering the sample through 80-μm mesh. Initial zooplankton density was estimated by collecting 3 samples from a fishless tank inoculated with a 1-L aliquot of zooplankton.

Daphnia lumholtzi in each sample were counted and total length (from the tip of the helmet to the tip of the tail spine) of 50 individuals measured. From these data, the densities of 4 size-classes of *D. lumholtzi* (small, 0.99 to 1.75 mm; medium, 1.80 to 2.57 mm; large, 2.62 to 3.44 mm; and very large, 3.5 to 5.25 mm) in each tank were estimated. Initial *D. lumholtzi* density was 153/L in the 25 July trial and 218/L in the 27 July trial. For each size-class, the number of *D. lumholtzi* eaten (individuals/L) was estimated by subtracting the density of *D. lumholtzi* remaining in each tank from the initial density estimate. Tanks in which inland silversides did not feed (i.e., <10% of the *D. lumholtzi* consumed) were omitted from the analysis. Using this arbitrary criterion, 2 tanks, each containing large fish, were omitted from the analysis.

To test for differences in size-selective predation among fish size treatments, a two-way ANOVA (factors are fish size and day of experiment) was performed for each silverside size-class. Based on the results of the ANOVA, Scheffe's Multiple Comparison Procedure was performed to examine treatment effects on each *D. lumholtzi* size-class.

Field Data—To examine whether inland silversides feed on different sizes of *D. lumholtzi* and native *Daphnia* (*D. galeata* and *D. parvula*) in Lake Texoma, we analyzed diets of 10 large and 10 small inland silversides from 2 dates. The samples were collected as part of a field study on the diet of inland silversides (Lienesch and Gophen, 2001) and were selected because of the dominance of either *D. lumholtzi* or native *Daphnia* in the zooplankton community and silverside diet on each date. Detailed sampling descriptions are in Lienesch and Gophen (2001). Briefly, fish were collected from Lake Texoma with a 7.6-m by 1.5-m bag seine (3-mm mesh) and preserved in 15% formalin. The sizes of native species of *Daphnia* consumed were examined for inland silversides collected on 17 June 1994, when they dominated the inland silverside diet. The sizes of *D. lumholtzi* consumed were examined on 30 June 1994, when *D. lumholtzi* dominated the silverside diet. Because spines of most ingested *Daphnia* (including native species and *D. lumholtzi*) had been broken, total length could not be determined. We measured body length of native *Daphnia* species from the top of the head to the base of the tail spine. For this analysis, measurements of *D. lumholtzi* were taken from the base of the helmet to the base of the tail spine.

Size-frequency distributions of *D. lumholtzi* consumed by large and small inland silversides on 30 June were compared by Kolmogorov-Smirnov analysis (Sokal and Rohlf, 1981). Size-frequency distributions of native species of *Daphnia* consumed by large and small inland silversides on 17 June were likewise compared by Kolmogorov-Smirnov analysis. Size categories used in the laboratory experiment (total length) were transformed to body length to allow for direct comparisons with *Daphnia* (natives and *D. lumholtzi*) eaten by inland silversides in Lake Texoma. To determine the relationship between total length and body length of *D. lumholtzi* used in the experiments, we performed regression analysis (Sokal and Rohlf, 1981) on 100 randomly chosen individuals. The regression equation for body length on total length for *D. lumholtzi* used in the experiment (body size = 0.0897 + 0.2709 × total length; r^2 = 0.9320) was used to determine the range of body sizes included in each size-class. The ranges of body lengths were 0.35 to 0.56 mm, 0.57 to 0.79 mm, 0.8 to 1.02 mm, and 1.03 to 1.5 mm for the small, medium, large, and very large size-classes, respectively. The size-frequency distribution of *D. lumholtzi* and native *Daphnia* preyed upon by large and small fish (collected on 30 and 17 June 1994) was compared graphically.

RESULTS—*Laboratory Experiment*—Although the number of fish in each aquarium differed across the 3 fish-size treatments, the number of *D. lumholtzi* (all size-classes combined) eaten did not differ among treatments (ANOVA, $F_{2,16}$ = 0.069, P = 0.9831). This test was performed to ensure that tanks with a given size-class of inland silversides did not have higher overall predation than the other treatments. The trial term (Day) was included in the model because the beginning total densities of *D. lumholtzi* differed on the 2 days. Predation rate did vary between the 2 trials (ANOVA, $F_{1,16}$ = 17.72, P < 0.0001) but no significant interaction occurred between Day and Fish Size (ANOVA, $F_{2,16}$ = 0.305, P = 0.7342). This indicated that number of prey offered and number of prey consumed in each trial did not affect the overall pattern of predation by the 3 sizes of fish.

There were significant differences in the number of small, large, and very large *D. lumholtzi* eaten in each fish treatment (Table 1). Although there were differences between trials for the consumption of the 3 largest *D. lumholtzi* size-classes, the interaction terms were not significant for any of the *D. lumholtzi* size-classes. Small inland silversides ate more small

TABLE 1—Results from analysis of variance tests on the number of *Daphnia lumholtzi* of each size class eaten during 80-min of feeding by inland silversides (*Menidia beryllina*) of 3 size-classes. Mean number of *D. lumholtzi* in each size-class (individuals/L) eaten by each fish size-class are presented in Fig. 1.

D. lumholtzi size-class	Factor	*df*	*F*-value	*P*-value
Small	Fish size	2	16.33	0.0001
	Day	1	0.435	0.5187
	Fish size × day	2	0.574	0.5747
Medium	Fish size	2	0.744	0.4911
	Day	1	38.06	0.0001
	Fish size × day	2	0.087	0.9168
Large	Fish size	2	6.799	0.0073
	Day	1	5.887	0.0274
	Fish size × day	2	0.325	0.7270
Very large	Fish size	2	5.030	0.0202
	Day	1	34.18	0.0001
	Fish size × day	2	0.408	0.6719

D. lumholtzi than the large or medium-sized inland silversides (Fig. 1). Large inland silversides ate more large *D. lumholtzi* than small inland silversides and ate more very large *D. lumholtzi* than the medium-sized inland silversides. There was no difference in the number of medium *D. lumholtzi* consumed by the small, medium, and large inland silversides (Fig. 1).

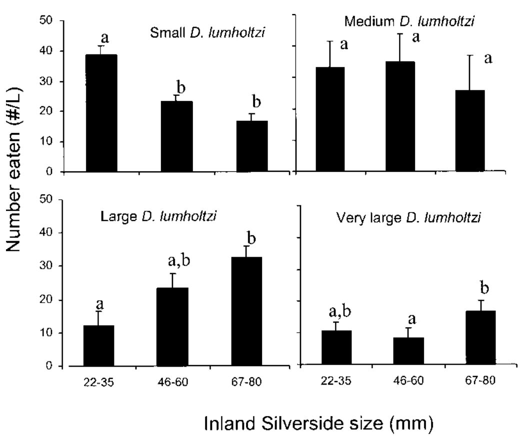

FIG. 1—Mean number/L of *Daphnia lumholtzi* (+1 *SE*) of 4 size-classes eaten in tanks containing small (22 to 35 mm), medium (46 to 60 mm), or large (67 to 80 mm) *Menidia beryllina*. Ranges of *D. lumholtzi* total lengths were 0.99 to 1.75 mm, 1.80 to 2.57 mm, 2.62 to 3.44 mm, and 3.50 to 5.25 mm for the small, medium, large, and very large size-classes, respectively. Fish-size treatments with the same letter did not differ (Sheffe's multiple comparison procedure).

Field Data—The size distributions of *D. lumholtzi* selected by large and small inland silversides were significantly different (Kolmogorov-Smirnov, $\chi^2 = 259.3$, $P < 0.0001$). We measured 332 *D. lumholtzi* from the pooled stomachs of large inland silversides ($n = 10$) and 318 *D. lumholtzi* from the pooled stomachs of small inland silversides ($n = 10$). Although there was a difference in the body sizes of *D. lumholtzi* selected by the 2 size-classes of fish, they both fed on a similar size range of animals. Small inland silversides fed on more small *D. lumholtzi* than did large inland silversides (Fig. 2). Both fish size-classes fed about equally on the medium *D. lumholtzi,* and the large inland silversides fed most heavily on the large *D. lumholtzi*. Neither size-class of fish fed heavily on very large *D. lumholtzi,* but this might have been an artifact of low abundance in the environment.

We measured 282 and 238 native *Daphnia* from the large ($n = 10$) and small ($n = 10$) inland silversides, respectively. The size distributions of native *Daphnia* selected by the 2 sizes of inland silversides were significantly different (Kolmogorov-Smirnov, $\chi^2 = 128.5$, $P < 0.0001$) (Fig. 2). Small inland silversides preyed most heavily on the medium-sized native *Daphnia,* but also consumed some individuals of the large and very large size-classes (Fig. 2).

Small inland silversides selected the smaller-bodied individuals when feeding on *D. lumholtzi*

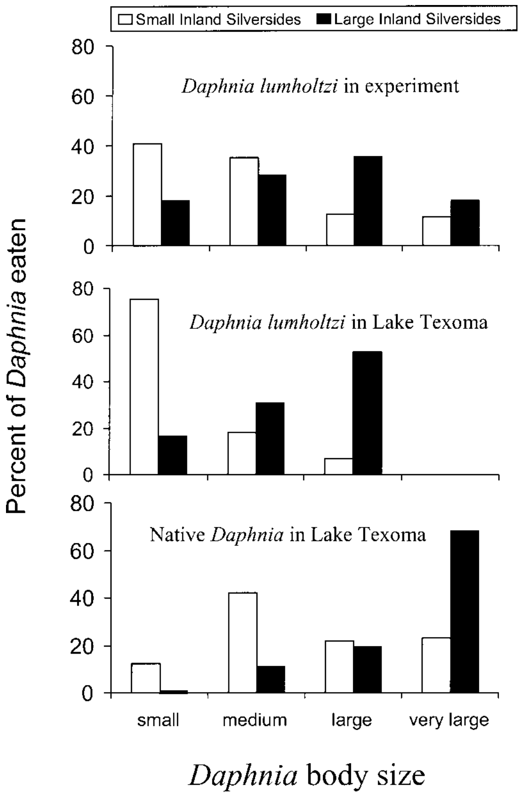

FIG. 2—Percentage of small, medium, large, and very large *Daphnia* eaten by small and large inland silversides (*Menidia beryllina*) in laboratory feeding trials and in Lake Texoma, Oklahoma and Texas. Because diets of medium-sized inland silversides were not examined from Lake Texoma, data from medium inland silversides in the laboratory experiment are not shown. Size categories used in laboratory experiment (total length) were transformed to body length to allow for direct comparisons with *Daphnia* selected by inland silversides in Lake Texoma. The ranges of body lengths were 0.35 to 0.56 mm, 0.57 to 0.79 mm, 0.8 to 1.02 mm, and 1.03 to 1.5 mm for the small, medium, large, and very large size-classes, respectively. The 2 native species of *Daphnia* in Lake Texoma were *D. galeata* and *D. parvula*.

or the native *Daphnia* (Fig. 2). The distribution of selected body sizes was skewed toward smaller sizes more for *D. lumholtzi* than for the native *Daphnia*. Seventy-five percent of the *D. lumholtzi* selected by small inland silversides had a body size 0.35 to 0.52 mm (which corresponds to the small size category after correction for body length: total length relationship). When feeding on the native *Daphnia,* 45% of the prey selected by small inland silversides had a body size larger than 0.76 mm (large and very large size categories). Only 6.5% of the *D. lumholtzi* consumed by small inland silversides were larger than 0.76 mm, even though large *D. lumholtzi* were present in the environment. We know large *D. lumholtzi* were available in the environment because large inland silversides were feeding on them. Over 50% of the *D. lumholtzi* eaten by large inland silversides were larger than 0.76 mm (Fig. 2).

DISCUSSION—Particulate feeding zooplanktivorous fish, such as inland silversides, detect, attack, and consume individual zooplankton. They typically feed upon the largest zooplankton available (Werner and Hall, 1974), or zooplankton that appear largest (O'Brien et al., 1976). Laboratory and field studies (Drenner and McComas, 1980; Lienesch and Gophen, 2001) have shown that large inland silversides feed selectively on larger species of zooplankton, including *D. lumholtzi.* This study showed that large inland silversides also feed selectively on the larger individuals within a species. Our results were similar to those of Lemke et al. (2003), who examined size-selectivity of 7 species of fish feeding on *D. lumholtzi* in Illinois and found a general trend of increasing selectivity in larger fish, although 2 species (freshwater drum, *Aplodinotus grunniens,* and emerald shiner, *Notropis atherinoides*) showed negative selection for *D. lumholtzi* regardless of fish size. Although large inland silversides fed most heavily on large *D. lumholtzi* in our experiments, small inland silversides selected the smaller size classes. Both the experimental and field parts of this study showed that small inland silversides are capable of feeding on large *Daphnia* (*D. lumholtzi* and native species), yet small fish fed more on the smaller size-class than did large fish. This pattern also has been found for small fish feeding on native, non-spiny species of *Daphnia* and is likely a result of reduced handling efficiency for large prey (Hansen and Wahl, 1981; Mills et al., 1984; Bence and Murdoch, 1986; Parrish and Margraf, 1991).

Previous laboratory studies have shown that planktivorous fish have difficulty feeding on *D. lumholtzi. Daphnia lumholtzi* incurs longer handling times than non-spiny native *Daphnia,* and smaller fish have longer handling times than larger conspecifics (Swaffar and O'Brien, 1996; Kolar and Wahl, 1998). In addition, planktivorous fish also exhibit a higher rejection rate when eating *D. lumholtzi* than when feeding on native *Daphnia* (Swaffar and O'Brien, 1996; Kolar and Wahl, 1998). Although we did not measure handling time in our experiment, our results were consistent with what would be expected if feeding efficiency is negatively related to prey size and positively related to predator size. Handling time for a large predator would be minimal for large and small prey; therefore, the predator will selectively feed on the larger prey. A small predator feeding on large prey will have longer handling times than when feeding on small prey and, therefore, would be expected to feed selectively on the smaller, more easily handled, prey.

Spines are common in North American species of zooplankton but they are most pronounced in smaller individuals. Dodson (1974) hypothesized that these spines protect small zooplankters from invertebrate predation. Spines are less pronounced in larger individuals because spines have an energetic cost to the individual, larger individuals are already protected from invertebrate predation by their larger size, and the spines are ineffective against most vertebrate predators. *Daphnia lumholtzi* has larger spines than any native *Daphnia* in North America (Sorenson and Sterner, 1992), the spines are longest during summer (Work and Gophen, 1995), and they are inducible by high temperatures and fish kairomones (Tollrian, 1994; Yurista, 2000; Dzialowski et al., 2003). Unlike the spines of native *Daphnia,* the spines of *D. lumholtzi* seem to function in protection of the animal from fish predation.

Although its spines might inhibit fish predation, the appearance of *D. lumholtzi* in the zooplankton community during mid-summer might make it beneficial for some zooplanktivorous fishes. In Lake Texoma, *D. lumholtzi* is abundant in mid-summer while native zooplankton, especially large-bodied zooplankton, are scarce (Work and Gophen, 1995, 1999*a*). At the same time, inland silversides are spawning, juvenile fish are abundant (Lienesch, 1997), and predation on *D. lumholtzi* by adult inland silversides is most intense (Lienesch and Gophen, 2001). Even though the energetic value of *D. lumholtzi* might be lower than that of a native *Daphnia* of similar body size (either due to differences in handling time or possible nutritional differences), *D. lumholtzi* occurs when the other large zooplankton in the lake are scarce, and therefore, *D. lumholtzi* might be the best available prey during summer. We propose that *D. lumholtzi* might have a beneficial effect on planktivorous fish in lakes and reservoirs that have depauperate zooplankton assemblages during the summer. Further research is needed to ascertain whether planktivorous fish in areas with *D. lumholtzi* have increased growth compared to planktivorous fish in areas without *D. lumholtzi.*

Daphnia lumholtzi could still have a negative effect on fish if it is competing with native *Daphnia.* Work and Gophen (1999*a,* 1999*b*) concluded that in Lake Texoma, *D. lumholtzi* does not compete with native *Daphnia,* which decline in early summer, a pattern of abundance present in Lake Texoma prior to invasion of *D. lumholtzi* (Matthews, 1984; Threlkeld, 1986). Studies of competition between *D. lumholtzi* and native *Daphnia* in other systems concur that *Daphnia lumholtzi* is a weak competitor and is most likely found in abundance during mid-summer as a result of its ability to tolerate high temperatures and reduced competition from other species, rather than displacement of native *Daphnia* (Lennon et al., 2003; Pattinson et al., 2003).

Although this study, and that of Lemke et al. (2003), showed that *D. lumholtzi* was eaten by some juvenile and adult zooplanktivorous fishes and, therefore, might be beneficial, the full ramifications of its introduction on aquatic ecosystems are not fully known. More information on the nutritional value of *D. lumholtzi,* interactions with native zooplankton, and effects on ecosystem functioning (e.g., nutrient cycling, primary productivity) are needed before we can conclude what effect it has on native fishes. Even in the absence of direct competition with native daphnids, *D. lumholtzi* could have negative effects on spring zooplankton assemblages by altering the composition of zooplankton over-wintering (Kolar et al., 1997). As with all introduced species, the spread of *D. lumholtzi* should be discouraged.

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