



Predation by inland silversides on an exotic cladoceran, *Daphnia lumholtzi*, in Lake Texoma, U.S.A.

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(Received 27 December 2000, Accepted 27 July 2001)

In the early 1990s, Lake Texoma was invaded by *Daphnia lumholtzi*, a large, spiny, exotic cladoceran. From April 1994 to April 1995 *D. lumholtzi* was most abundant in the lake in mid-summer, after native zooplankton declined in early June. Inland silversides *Menidia beryllina* selectively preyed on *D. lumholtzi* but appeared to prefer the large native zooplankton when they were present. *Daphnia lumholtzi* was an important prey item for silversides during summer when large native zooplankton was scarce. The invasion of *D. lumholtzi* into Lake Texoma may benefit some zooplanktivorous fishes by increasing foraging opportunities during a time of low prey availability.

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Key words: selectivity; introduced species; zooplankton; fish; planktivory; *Menidia beryllina*.

INTRODUCTION

North America has been invaded by many non-native aquatic plants and animals (Mooney & Drake, 1986; Mills *et al.*, 1994). Although many organisms, such as plants and fishes, are intentionally introduced, others are imported accidentally and their arrival often goes unnoticed (Welcomme, 1986; Mills *et al.*, 1994). Invertebrate introductions have usually occurred unintentionally, but may alter the ecosystem (Lasenby *et al.*, 1986; Mills *et al.*, 1994; Ram & McMahon, 1996). For example, the zebra mussel *Dreissena polymorpha* Pallis, which was first found in the Great Lakes in the late 1980s, is expected to have severe impacts on native mussels (Williams *et al.*, 1993; Schloesser *et al.*, 1996). Invading species not only affect competitors and prey, but also predators. How invading species influence higher trophic levels has received much less attention than effects on lower trophic levels.

Daphnia lumholtzi (Sars) is a zooplankton species that is rapidly invading North American waters (Havel *et al.*, 1995). *Daphnia lumholtzi* (Anomopoda, Daphniidae; Dodson & Frey, 1991) is a large cladoceran native from northeast Africa to southern Asia, and Australia (Benzie, 1988; Havel & Hebert, 1993). First identified in North America from Fairfield Lake, Texas, in 1991 (Sorenson & Sterner, 1992), *D. lumholtzi* is now found from Arizona to Florida and has been reported as far north as Chicago (J. Havel, pers. comm.).

Daphnia lumholtzi is a relatively large cladoceran with an elongate helmet, large tail spine, a pair of lateral fornices from the base of the helmet, and

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prominent denticles along the posterior edge of the carapace and along the tail spine (Sars, 1885). In Lake Texoma, Oklahoma–Texas, its length, including the spine and helmet, can exceed 5 mm although body length is usually <1.5 mm (Work, 1997). The helmet and spines exhibit cyclomorphosis (Sorenson & Sterner, 1992), are induced by the presence of fishes (Tollrian, 1994), and inhibit fish predation (Swaffar & O'Brien, 1996; Kolar & Wahl, 1998).

Daphnia lumholtzi was first collected from Lake Texoma in 1991 (Work & Gophen, 1995). It can reach high densities ($>100\text{ l}^{-1}$) during the summer, when it is a major component of the zooplankton community. Native zooplankton decline in abundance in early summer (Matthews, 1984; Dirnberger & Threlkeld, 1986; Threlkeld, 1986) and remain low until the end of the summer when water temperatures decrease. As densities of native zooplankton decline, *D. lumholtzi* attains its maximum density (Work & Gophen, 1995, 1999a) and, therefore, may be an important food source for zooplanktivorous fishes during this period.

The inland silverside *Menidia beryllina* (Cope) is native to the Mississippi drainage and was introduced into Lake Texoma in 1953 (Dowell & Riggs, 1958). It is a size-selective, particulate feeding zooplanktivore (McComas & Drenner, 1982). It is a size-selective, particulate feeding zooplanktivore (McComas & Drenner, 1982) and has an annual life cycle (Saunders, 1959). Inland silversides are most abundant in the littoral zone of Lake Texoma, where they feed primarily on zooplankton and dipterans (Saunders, 1959; Elston & Bachen, 1976). Unlike inland silversides in Clear Lake, California, which migrate to the pelagic zone at dawn and dusk (Wurstbaugh & Li, 1985), silversides in Lake Texoma are abundant in nearshore areas throughout the day and are less abundant at night (Matthews, 1986; C. Hubbs, pers. obs.). Zooplanktivory by inland silversides in Lake Texoma was investigated to determine whether *D. lumholtzi* would be eaten and whether it would be selectively preyed upon relative to other zooplankton.

MATERIALS AND METHODS

STUDY SITE

Lake Texoma is a hypolimnetic-release flood control reservoir of the Red and Washita Rivers with a surface area of 360 km² (36 000 ha) on the Texas–Oklahoma border. At normal pool level (188 m above mean sea level), the reservoir has 933 km of shoreline, a storage capacity of 3.36 km³, and a shoreline development index of 13.9 (Vaughn, 1979). The average depth is 9.3 m and the maximum depth is 34 m (Vaughn, 1979). Lake Texoma is monomictic, eutrophic and has high conductivity. The littoral zone is typically gently sloping with soft mud to hard mud–sand substratum (Matthews *et al.*, 1992). Because it is used for flood control, the reservoir can experience high fluctuations in water level (>5 m).

Three sampling sites were selected on the Red River arm of Lake Texoma. Sites were characterized by a sandy substratum and extensive, moderate sloping beaches, which would allow sampling regardless of water level. The upper site was located 5 km west of the University of Oklahoma Biological Station. The beach at the biological station was the middle site. The upper and middle sites were on the northern shore, exposed to prevailing southerly winds, and adjacent to the main channel of the reservoir. The lower site, 7 km south-east of the biological station, was on the north-eastern shore of an island and faced a shallow (3 m maximum depth at normal pool level) basin. Because *D. lumholtzi* is found throughout the reservoir during the summer (Work & Gophen, 1995, 1999a), four additional sites were sampled (two in the Washita River arm and two in the

main basin of the reservoir) on two dates. These additional samples were used to determine if silverside selectivity in the Red River arm was representative of the whole reservoir.

SAMPLING

Fish and zooplankton were collected between 1200 and 1700 hours every 2 weeks during 28 April–31 August 1994, and monthly thereafter until 20 April 1995. Fish were collected from the littoral zone with a 9×1.5 m, 3 mm mesh bag seine. Capture depth was *c.* 1 m and never >1.5 m. Three 20 m seine hauls were taken at each site, and if necessary, additional hauls were taken until at least 10 adult inland silversides (≥ 50 mm standard length, L_S) were captured. After being fixed in 15% formalin for at least 1 week, fish were transferred to 50% isopropyl alcohol. In the laboratory, silversides were measured (L_S) to the nearest mm and weighed to the nearest 0.01 g. A zooplankton sample was taken immediately offshore of the seining site with a 1 l LeMotte water sampler at a depth of 1 m after the fish were collected. The sample was filtered (80 μ m mesh) and preserved in 5% sucrose formalin.

The stomach contents of 10 adult inland silversides from each sample were examined using a dissecting microscope. The silverside mean L_S per sampling date ($n=30$) ranged from 57 to 76 mm. L_S was lowest during the late summer after 1 year old fish had died and young-of-the-year (YOY) silversides were attaining adult size (>50 mm). The stomach was defined as the section of the gut anterior to the first turn. All dipteran larvae, terrestrial insects, larval fishes and amphipods were sorted and counted. A subsample of at least 10% of total volume was examined for zooplankton composition. Zooplankton were sorted according to the following categories: copepodite and adult cyclopoid copepods, copepodite and adult calanoid copepods, copepod nauplii, *D. lumholtzi*, other *Daphnia* spp. (*D. galeata* Birge and *D. parvula* Fordyce), *Bosmina longirostris* Müller, *Ceriodaphnia lacustris* Birge, *Diaphanosoma leuchtenbergianum* Fischer, rotifers, and ostracods. The availability of zooplankton in the environment was determined from the zooplankton samples. Zooplankton were identified and counted using the same categories as in the stomach content analysis.

The linear index of food selection (L) (Strauss, 1979) was calculated for the larger taxa of zooplankton (*D. lumholtzi*, copepods, other *Daphnia* spp., other cladocera). L is a normally distributed statistic that is less sensitive than many common selectivity indices to the presence of rare taxa and can be compared among sites with different prey abundances (Strauss, 1979). Smaller zooplankton (rotifers, copepod nauplii, ostracods) were not included in this analysis because they accounted for a small proportion of the overall gut content yet a large proportion of the zooplankton assemblage. Insect data were not included because they were not sampled in the environment. Student's t -tests were used to compare mean L for taxa in each sample ($n=10$) to the expected value ($L=0$) if the silversides were not feeding selectively. When L is significantly different from 0, the prey item is being positively selected ($L>0$) or is being avoided ($L<0$). When L is 0, either the prey item is being eaten in the same proportion that it is found in the prey assemblage or is present in neither diet nor environment.

RESULTS

Daphnia lumholtzi was the most abundant in the zooplankton assemblage in late June and then declined in abundance through July (Fig. 1). In early June, the density of native zooplankton (copepods and other *Daphnia* spp.) decreased in abundance as *D. lumholtzi* became more abundant. Abundance of zooplankton was low from July to September with the exception of occasional high density of *Diaphanosoma* (grouped with other cladocerans in Fig. 1) and small cyclopoid copepods. Calanoid copepods and the other species of *Daphnia* became more abundant in the autumn and persisted until spring (Fig. 1).

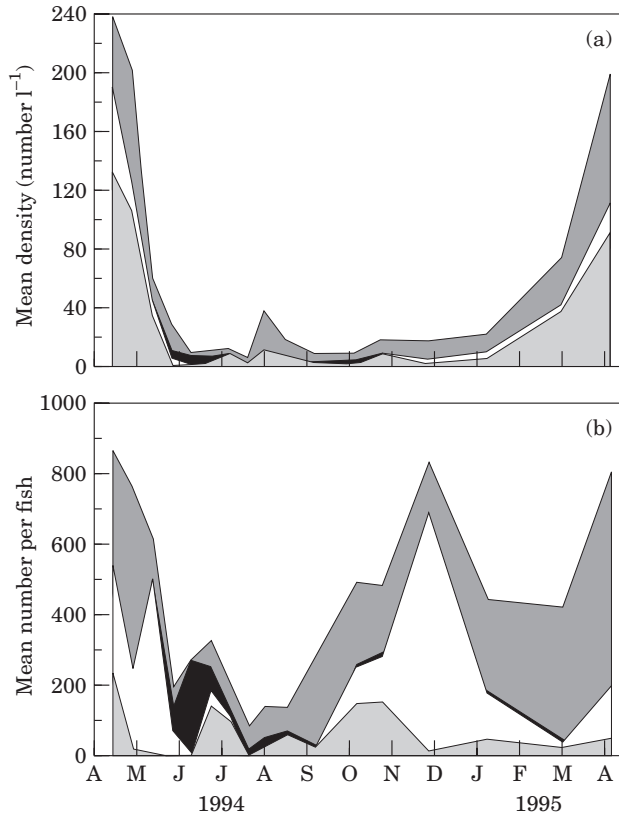


FIG. 1. (a) Mean density of cladoceran and copepod zooplankton at three sample sites combined on each sampling date. (b) Mean number of cladoceran and copepod zooplankton in the stomachs of adult *Menidia beryllina* at three sample sites ($n=30$) on each date. ■, Copepods; ■, *D. lumholtzi*; □, other *Daphnia*; □, other cladocerans.

Over the course of the study, *D. lumholtzi* accounted for 10% of the silverside diet in Lake Texoma (Table I; Fig. 1). The prey most frequently eaten by silversides were the other species of *Daphnia* (23% by number) followed by cyclopoid copepods (22%), calanoid copepods (17%). *Daphnia lumholtzi* was the major food source for silversides during the summer (Fig. 1; Table I). When the analysis was limited to samples taken from June to August, *D. lumholtzi* was the most frequently eaten food item (24%) followed by cyclopoid copepods (20%) and *Diaphanosoma* (13%). Calanoid copepods and other species of *Daphnia* combined accounted for 13% of the food items during June to August (Table I).

Silversides selectively fed on *D. lumholtzi* ($L>0$) at the upper site on 6 of the 10 sampling dates in the summer of 1994 (Fig. 2). *Daphnia lumholtzi* was positively selected at the middle site on one date and was negatively selected (i.e. avoided; $L<0$) on one date at the lower site. The other species of *Daphnia* were selected on six of 10 sampling dates at the lower site and on three of 10 sampling dates at the middle site. Silversides at the upper site selected other *Daphnia* spp. on one date and avoided them in July, when *D. lumholtzi* was abundant and native *Daphnia* spp. were scarce. Copepods were selected by silversides in April and

TABLE I. Mean number per fish and per cent occurrence of prey items in the stomachs of inland silversides, *Menidia beryllina*, from Lake Texoma. Silversides were collected from three sites on 17 dates ($n=510$ silversides) in the year-round samples. Summer samples were collected on seven dates from June to August ($n=210$ silversides)

Taxa	Year-round samples		Summer samples	
	Number per fish	%	Number per fish	%
Cyclopoid copepods	97.8	22	52.4	20
Calanoid copepods	104.7	18	10.6	4
<i>Daphnia lumholtzi</i>	26.9	10	61.3	24
Other <i>Daphnia</i> spp.	142.3	23	22.4	9
<i>Bosmina</i> sp.	42.4	6	15.4	6
<i>Ceriodaphnia</i> sp.	4.6	<1	0.5	<1
<i>Diaphanosoma</i> sp.	17.7	5	34.5	13
Ostracods	0.7	<1	1.4	<1
Nauplii	14.9	5	26.2	10
Rotifers	19.5	7	30.6	12
Dipteran Larvae	3.3	<1	2.3	<1
Terrestrial Insects	2.3	<1	1.6	<1
Insect Eggs	0.4	<1	0.1	<1
Fish	0.1	<1	0.1	<1
Fish Eggs	0.8	<1	0.5	<1
Total	478.7		260.1	

May, when large calanoid copepods were abundant, and either not selectively preyed upon or avoided in 18 of 21 samples throughout the rest of the summer, when small cyclopoid copepods dominated the assemblage and zooplanktivory by silversides was low. Other cladocera (*Diaphanosoma*, *Ceriodaphnia* and *Bosmina*) were not selected or avoided throughout the summer, even though *Diaphanosoma* was a major component of silverside diet during mid summer (Fig. 1; Table I). Although only extensive sampling was carried out in the upper Red River arm of Lake Texoma, silversides at the four supplementary sites had food item selectivities similar to those recorded at the routine sites (Fig. 2).

DISCUSSION

When *D. lumholtzi* was first found in North America, there was concern that it might have negative effects on planktivorous fishes. By competing with native *Daphnia*, *D. lumholtzi* could reduce the availability of native *Daphnia* as a food source for planktivorous fishes. If *D. lumholtzi* is less vulnerable to predation due to the helmet and tail spine, the foraging efficiency of planktivorous fishes, especially larval fishes, might be reduced (Havel *et al.*, 1995; Swaffar & O'Brien, 1996). Kolar & Wahl (1998) hypothesized that *D. lumholtzi* may be particularly harmful to fishes that spawn in early summer, such as sunfish. Because larval and juvenile sunfishes occur throughout the summer, they will probably overlap with high abundance of *D. lumholtzi* and may experience reduced growth as a result.

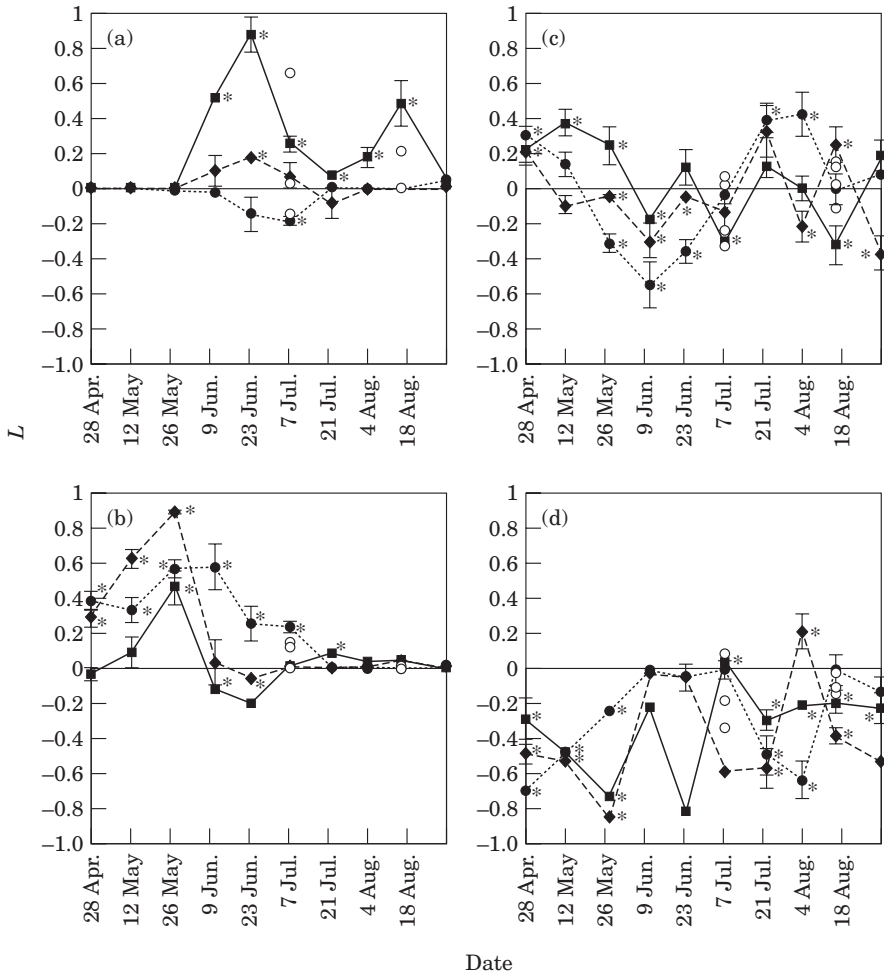


FIG. 2. Mean \pm S.E. linear index of food selection (L) for adult *Menidia beryllina* ($n=10$) at the Upper (■), Middle (◆) and Lower (●) sites in Lake Texoma during summer 1994. * differed significantly from 0. ○, mean L for silversides from the lake-wide supplementary sites that were sampled on two dates. (a) *Daphnia lumholtzi*; (b) other *Daphnia*; (c) copepods; (d) other cladocerans. Other *Daphnia* includes *D. galeata* and *D. parvula* and other cladocerans includes *Bosmina longirostris*, *Ceriodaphnia lacustris* and *Diaphanosoma leuchtenbergianum*.

Daphnia lumholtzi is usually not abundant at the same time of year as other large zooplankton and therefore, direct competition between the two groups is unlikely (Work & Gophen, 1995, 1999a; Kolar *et al.*, 1997). During the present study, *D. lumholtzi* was most abundant in June, after the native *Daphnia* abundance had declined. Work & Gophen (1995, 1999a) found similar patterns in 1993 and 1995. The decline of native zooplankton in Lake Texoma in early summer occurred prior to the introduction of *D. lumholtzi* (Matthews, 1984; Dirnburger & Threlkeld, 1986) and is probably controlled by factors such as temperature and resource availability (Threlkeld, 1986). Work & Gophen (1999b) found that *D. lumholtzi* can survive in temperatures up to 29°C and hypothesized that temperature tolerance allows *D. lumholtzi* to exploit resources

during summer, when native *Daphnia* are not present. Whereas competition with native *Daphnia* in Lake Texoma is probably minimal, *D. lumholtzi* may affect planktivorous fishes by competing with *Diaphanosoma*, the second most common silverside prey during the summer. Although *Diaphanosoma* was not selected by adult silversides, it may be important to smaller planktivorous fishes.

Laboratory studies on bluegill *Leopomis macrochirus* Rafinesque foraging indicate that *D. lumholtzi* is less vulnerable to fish predation than native species of *Daphnia* (Swaffar & O'Brien, 1996; Kolar & Wahl, 1998). Bluegill sunfish incurred longer handling time when feeding on *D. lumholtzi* than when feeding on native *Daphnia* (Swaffar & O'Brien, 1996; Kolar & Wahl, 1998). Although *D. lumholtzi* is less vulnerable to fish predation, silversides as small as 22 mm L_S can ingest adults, but select smaller individuals when available (Lienesch, 1997). The present study has shown that *D. lumholtzi* is an important food source for adult silversides in Lake Texoma during the summer, and is selected over the small native zooplankton, including *Diaphanosoma*, available at that time. Similarly, Kolar & Wahl (1998) found bluegill >50 mm selected *D. lumholtzi* over native zooplankton in Lake Springfield, Illinois. Bluegill <50 mm selected against *D. lumholtzi* and selected for native zooplankton (Kolar & Wahl, 1998). The large size of *D. lumholtzi* compared to native zooplankton available in Lake Texoma during summer may make it an attractive prey item despite the handling difficulty associated with the helmet and tail spine.

The timing of peak *D. lumholtzi* abundance is important because it occurs during the spawning season for silversides (from late March to mid-July; Mense, 1967). Silverside spawning ceases when water temperature $\sim >30^\circ\text{C}$ (Hubbs & Bailey, 1977). Silversides have an annual life-cycle and most adults die before August of their second summer. Although silverside reproduction was not measured, the presence of an additional food source at the end of the spawning season may allow adult silversides to survive later in the spawning season, thereby increasing reproductive output.

The timing of the increase of *D. lumholtzi* abundance may also be important for young of the year (YOY) silversides. Predation often is highest on the smaller size classes of juvenile silversides (Stoeckel & Heidinger, 1992; Gleason & Bengtson, 1996). Lake Texoma supports a large striped bass *Morone saxatilis* (Walbaum) fishery and juvenile striped bass were often caught in the same seine haul as silversides. Moreover, white bass *Morone chrysops* (Rafinesque) and three species of black bass (*Micropterus* spp.) also occur in the littoral zone of Lake Texoma. As the YOY of these species switch from zooplanktivory to piscivory, they are gape-limited (Timmons *et al.*, 1980). By growing rapidly, a juvenile fish can reduce its risk of being eaten by remaining too large for juvenile predators to consume. The presence of *D. lumholtzi* may allow YOY silversides to grow more rapidly during summer and thereby remain too large for YOY predators.

Although silversides have been shown to use *D. lumholtzi* as a food source during summer, no conclusions can be drawn about the effects of *D. lumholtzi* on silverside growth and survival. To evaluate the effect of *D. lumholtzi* invasion on planktivorous fishes, future studies should compare life-history characteristics (e.g. gamete production, longevity, growth rate, recruitment) of planktivorous fishes in the presence and absence of *D. lumholtzi*.

Due to its temporal pattern of abundance, *D. lumholtzi* is probably an additional food source for zooplanktivorous fish in Lake Texoma and is not replacing the food sources available prior to its invasion. It is predicted that the invasion of *D. lumholtzi* will not have a negative effect on silversides in Lake Texoma, and may benefit some zooplanktivorous fishes.

PWL was supported by a Centennial Research Fellowship from the University of Oklahoma. We thank K. Work, M. Craig and J. Stewart for help with field work and C. McCallister for helping prepare the figures. The manuscript benefited from reviews by W. Matthews, W. Shelton and L. Wallace, and anonymous reviewers. The University of Oklahoma Biological Station provided laboratory space and field vehicles. This project was completed as part of a Doctoral Dissertation (PWL) for the University of Oklahoma Department of Zoology.

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