

Changes to zooplankton community structure following colonization of a small lake by *Leptodora kindti*

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Abstract

The predaceous cladoceran *Leptodora kindti* (Focke) became established in Third Sister Lake, Michigan, after individuals escaped from experimental enclosures in 1987. By 1988, the *Leptodora* population exhibited seasonal dynamics characteristic of natural populations. The maximum seasonal abundance of *Leptodora* increased to 85 individuals m⁻³ 3 yr following the introduction. After the appearance of *Leptodora*, small-bodied cladocerans (*Ceriodaphnia* and *Bosmina*) virtually disappeared from the lake. There were strong seasonal shifts in the dominance patterns of both cladocerans and copepods, and *Daphnia* species diversity increased. Results from this unplanned introduction suggest that invertebrate predators can have a rapid and lasting effect on prey populations, even in the presence of planktivorous fish. Small-scale (<20 km) geographic barriers might be as important as large-scale barriers to dispersal of planktonic animals.

Both planktivorous fish and invertebrate predators have the potential to structure crustacean zooplankton communities through size selective predation. Planktivorous fish that feed visually select the largest available prey while invertebrate predators remove smaller individuals (Zaret 1980). Whereas the effects of planktivorous fish on zooplankton community structure are well established (Brooks and Dodson 1965; Hall et al. 1976), the effects of invertebrate predators are less clear. Large predatory zooplankton, such as *Chaoborus* and certain calanoid copepods (e.g., *Hesperodiaptomus*, *Heterocope*), are often abundant in the absence of fish and can inflict considerable mortality on populations of small-bodied prey (Von Ende and Dempsey 1981; Luecke and O'Brien 1983; Elser et al. 1987; McNaught et al. 1999). Such intense predation can lead to the exclusion of small-bodied species, thereby changing the size structure of the zooplankton community (Dodson 1974; Luecke and O'Brien 1983; Black and Hairston 1988; Hanazato and Yasuno 1989). When fish are present, large nonmigratory inverte-

brate predators are often replaced by species that are less conspicuous to fish by virtue of their small size (cyclopoid copepods, the cladoceran *Polyphemus*, the rotifer *Asplanchna*), high transparency (*Leptodora*), or ability to migrate downward during the day (small chaoborids, *Leptodora*, *Bythotrephes*, mysids).

Some large migratory invertebrate predators can have long-term effects on the structure of zooplankton communities in the presence of planktivorous fish. *Mysis*, *Neomysis*, and *Bythotrephes* readily select large-bodied prey (Lazenby and Langford 1973; Murtaugh 1981; Yurista and Schulz 1995) and have been implicated in the decline or disappearance of *Daphnia* populations (Richards et al. 1975; Hanazato and Yasuno 1988; Lehman 1988). Most of our information on the community-wide effects of large migratory invertebrates comes from field studies following exotic introductions. Such "natural" experiments are rarely performed with locally occurring species.

Invertebrate predators exert their influence on prey populations primarily by increasing in number (Hall et al. 1976). They can inflict considerable mortality on prey populations even in lakes with fish (Mordukhai-Boltovskaya 1958; Lane 1979). However, this predation pressure is usually short lived (Hall 1964; Elser et al. 1987; Lunte and Luecke 1990), sporadic (Herzig and Auer 1990), or restricted to certain regions within the lake by fish predation on the invertebrate predator (Kerfoot 1977; Baker et al. 1992). Sometimes, long development times and developmental bottlenecks limit the ability of invertebrate predators to respond to growing prey populations (Neill and Peacock 1980; Stenson 1990). Unless they can escape fish predation and attain high densities for a sufficient length of time, it seems unlikely that invertebrate

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predators will be able to alter the structure or composition of aquatic communities to a degree comparable to that of planktivorous fish.

Among those invertebrate predators that coexist with fish, the cladoceran *Leptodora* could have significant community-wide effects. *Leptodora* reproduces parthenogenetically and can quickly respond to growing prey populations. This predatory cladoceran is able to impose high death rates on *Daphnia* populations (Hall 1964; de Bernardi 1974; Lunte and Luecke 1990) and has been implicated in the late summer decline of *Bosmina* populations (Branstrator and Lehman 1991). Results from laboratory feeding trials and short-term enclosure experiments indicate that *Leptodora* has the potential to alter the size structure of the zooplankton community by removing small cladocerans, colonial rotifers, and copepod nauplii (Mordukhai-Boltovskaya 1958; Herzig and Auer 1990; Lunte and Luecke 1990; McNaught 1993a). *Leptodora* rarely eats adult copepods, which have a rapid escape response (Browman et al. 1989).

The conclusions that one can draw from these laboratory and short-term enclosure experiments are limited in their applicability to natural systems. Artificially high predator densities, spatial restrictions, and temporal limitations often confound the interpretation of experimental results. The events surrounding the invasion of a lake by an exotic invertebrate predator provide information that a controlled experiment cannot. Because an entire habitat is manipulated during an invasion, the invertebrate predator is restricted neither spatially nor temporally. Species interactions that have been forced in experimental enclosures might be unimportant when the organisms are naturally segregated in the environment. Weak interactions during a short-term enclosure experiment could become significant when the organisms are allowed to interact for long periods of time in the natural environment.

Disadvantages to whole-lake experiments include limited or no replication and the absence of true controls. Few whole-lake experiments are replicated because of logistical constraints and the inability to find two or more lakes in a given watershed that are geologically, morphologically, or chemically similar. If two similar lakes are available within a watershed, investigators can select one lake as a treatment site and the second as a reference site. Investigators can control for temporal variability by sampling both lakes simultaneously. Controlled before and after designs have been successfully employed by Gonzalez et al. (1990) to demonstrate the effect of acidification on rotifer populations and by Schindler and Fee (1974) to show the effect of phosphorus addition on algal biomass and productivity. A reference site is often not available for unplanned whole-lake manipulations, yet such "natural" experiments have provided useful information. Edmondson (1991) showed that reduced nutrient and chlorophyll *a* (Chl *a*) concentrations in Lake Washington were associated with sewage diversion in the mid-1960s. Mittelbach et al. (1995) examined zooplankton composition and size structure following the elimination and reintroduction of largemouth bass (*Micropterus salmoides*) from a small Michigan Lake. They concluded that largemouth bass act as a keystone species, depressing the domi-

nant planktivore and permitting herbivorous cladocerans to thrive.

Here, we describe the response of the zooplankton community of Third Sister Lake, Michigan, to the inadvertent introduction of *Leptodora kindti* (Focke). This large (up to 18 mm), transparent cladoceran is present between May and November at low densities (<100 individuals m⁻³) in many surrounding lakes in the study region. *Leptodora* occurs exclusively in the presence of planktivorous fish and is most frequently observed in large lakes (>4 ha) that have an abundant supply of *Daphnia* (McNaught 1993b). Except for its size, Third Sister Lake was a typical *Leptodora* habitat with established populations of planktivorous fish (*Lepomis macrochirus*, *M. salmoides*, *Notropis* spp.) and *Daphnia*.

During summer 1987, an enclosure experiment was conducted to measure the effect of *Leptodora* on the zooplankton community of Third Sister Lake. In July, six large enclosures (~12 m³) were deployed and stocked with *Leptodora* from nearby (16 km) Whitmore Lake. On several occasions during the summer, one or more enclosures became partially detached from their flotation collars, enabling the exchange of water between the enclosure and lake. The enclosures were removed on 15 September, and on this day *Leptodora* was first identified in plankton samples from Third Sister Lake. Prior to this, *Leptodora* had not been observed in Third Sister Lake (Ball 1943; Korstad 1980; Dorazio 1986; Kiesling 1990). The unplanned introduction provided a unique opportunity to evaluate the capacity of a widely distributed invertebrate predator to alter the composition and structure of the resident zooplankton community despite its low density in the presence of planktivorous fish.

Study site and methods

Third Sister Lake is a small (3.85 ha) seepage lake located in the Saginaw Forest (University of Michigan property), 1 km west of Ann Arbor, Michigan (Fig. 1). Third Sister Lake is rather deep for its size, with maximum and mean depths of 16.5 and 7.2 m, respectively (Lehman and Naumoski 1986). The lake has no permanent surface inlets or outlets, and the water level is maintained by overland runoff and groundwater input (Eggleton 1931). Occasionally, water drains westward into the Huron River via Honey Creek (Ball 1943). Third Sister and nearby First and Second Sister Lakes are isolated from other lakes in the Huron River watershed (Fig. 1). First and Second Sister Lakes are small (<3 ha), shallow (<7 m) waterbodies, and *Leptodora* has never been observed in the plankton. Except for one large storm sewer settling pond in NW Ann Arbor, Barton Pond, an impoundment of the Huron River, is the closest (4.1 km) large (>4 ha) lake. Barton Pond might contain *Leptodora* from connected upstream water bodies. The closest lake known to contain *Leptodora* is Whitmore Lake located 16.4 km from Third Sister (Fig. 1).

Third Sister Lake is moderately eutrophic, with 5–40 µg L⁻¹ Chl *a* and 0.5–1.5 µmol L⁻¹ total phosphorus during the summer months (Lehman and Naumoski 1986). Stratification occurs in early spring following a brief mixing period, and the hypolimnion quickly becomes anoxic (Bridgeman et

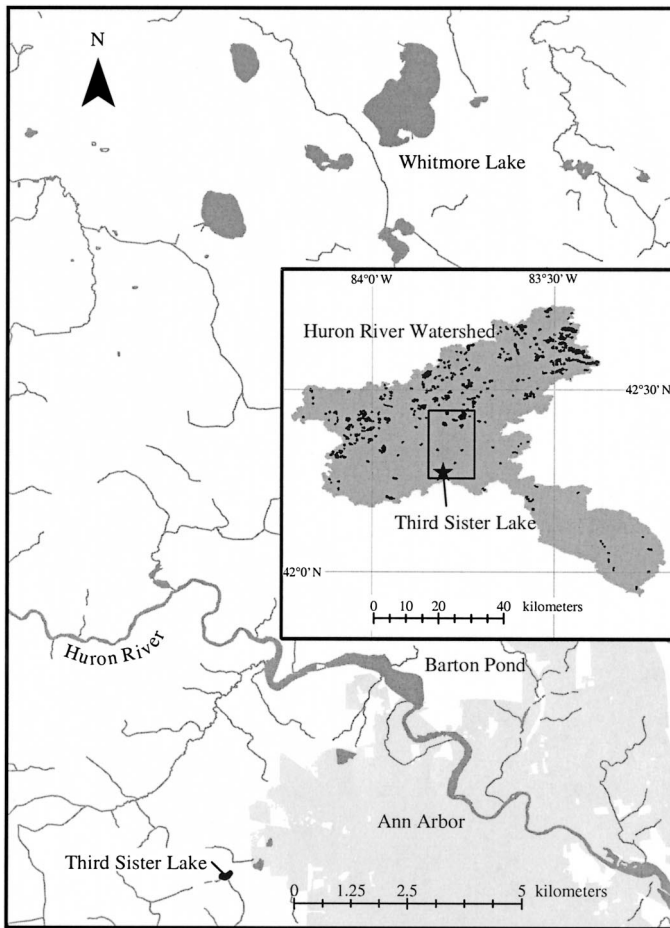


Fig. 1. Location of Third Sister Lake near Ann Arbor, Michigan, within the Huron River watershed (inset). Only water bodies ≥ 4 ha are shown.

al. 2000). By late summer, the thermocline is at 5–6 m. Physical and chemical parameters were consistent from year to year during the course of this study (Table 1), with the exception of conductivity, which increased steadily from 362 $\mu\text{S cm}^{-1}$ in 1982 to 1,040 $\mu\text{S cm}^{-1}$ in 1988, largely as a result of sodium chloride input (Bridgeman et al. 2000). The phytoplankton assemblage of Third Sister Lake is dominated by diatoms, chrysophytes, and cryptomonads during the spring and autumn and by cyanobacteria during the summer (Korstad 1980; Kiesling 1990). During the ice-free period, phytoplankton and zooplankton are concentrated in the upper 5 m of water (Dorazio 1986). *Chaoborus* resides in the anoxic hypolimnion during daylight hours (Bridgeman et al. 2000).

The zooplankton community of Third Sister Lake was monitored during ice-free months (June–October) from 1983 to 1991. In 1983, 1985, and 1986, zooplankton were primarily collected with a 15- or 24-liter Schindler–Patalas trap at 1, 3, and 5 m (Table 2). Average water column densities were estimated by integrating over the upper 5 m. In 1984 and occasionally in 1985 and 1986, zooplankton were collected with small-diameter, fine-mesh plankton nets. In 1988–1991, zooplankton were collected with large-diameter, coarse-mesh plankton nets (Table 2). Plankton nets were usually towed once through the entire water column (13 m) during daylight hours. In 1987, zooplankton were collected with a fine-mesh Wisconsin net towed eight times through the upper 4 m during daylight hours. All plankton samples were preserved in a 4% sugar-formalin solution (Haney and Hall 1973). Zooplankton data from 1983 were obtained from Dorazio (1986).

In the laboratory, planktonic animals were enumerated by counting replicate 5-ml subsamples in a Bogorov tray with a stereomicroscope at $\times 30$. Taxa were identified to species by the method of Edmondson (1959). Microcrustaceans were measured and classified as either small (< 1.0 mm) or large (> 1.0 mm). Entire samples were examined for *Leptodora* and *Chaoborus* because these large taxa were much less abundant than other zooplankton taxa. Because the Schindler–Patalas trap was not able to detect plankton densities

Table 1. Physical and chemical conditions of Third Sister Lake before and after the introduction of *Leptodora*. The depicted values (range) are from epilimnetic samples taken in mid-September each year except for 1983 and 1991, when no samples were collected.

	Before <i>Leptodora</i> (1982–1987)	After <i>Leptodora</i> (1988–1990)
Thermocline depth (m)	5.0–6.0	4.5–6.5
Epilimnetic temperature ($^{\circ}\text{C}$)	18.0–20.4	19.4–22.4
Light extinction coefficient	0.70–0.80	0.59–0.84
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	3.8–6.9	3.3–3.8
Epilimnetic oxygen (mg L^{-1})	7.8–10.0	7.8–8.8
pH	7.7–8.3	8.0–8.2
Alkalinity (meq L^{-1})	2.0–2.2	2.0–2.1
Conductivity ($\mu\text{S cm}^{-1}$)	362–948	635–1,040
Chloride (meq L^{-1})*	2.85 (1,982)	7.0 (1,988)
Soluble reactive phosphorus ($\mu\text{mol L}^{-1}$)	0.0–0.2	0.0–0.6
Ammonium ($\mu\text{mol L}^{-1}$)	0.0–9.8	0.0–1.2
Silica ($\mu\text{mol L}^{-1}$)	9.0–20.8	4.2–16.0

* Chloride was measured only once in each time period as indicated by the date in parentheses.

Table 2. Sampling gear used to collect zooplankton from Third Sister Lake during 1983–1991. Detection limit is one animal per volume sampled.

Date	Sampling gear	Mesh size (mm)	Depth sampled (m)	Volume sampled (L)	Detection limit (m ⁻³)
Jun 83	15-liter trap	25	1, 3, 5	45	22.2
Jul 83*	15-liter trap	25	1, 3, 5	45	22.2
Aug 83*	15-liter trap	25	1, 3, 5	45	22.2
Sep 83	15-liter trap	25	1, 3, 5	45	22.2
Jul 84	13-cm-diam. net	153	0–13	173	5.8
Sep 84	25-cm-diam. net	73	0–10	491	2.0
Jun 85*	25-cm-diam. net	73	0–7	344	2.9
Jul 85*	24-liter trap	64	1, 5	48	20.8
Aug 85*	25-liter trap	64	1	24	41.7
Sep 85	25-cm-diam. net	73	0–13	638	1.6
Jun 86*	24-liter trap	64	3	24	41.7
Jul 86*	25-liter trap	64	3	24	41.7
Aug 86	24-liter trap	64	3	24	41.7
Jun 87*	24-liter trap	64	3	24	41.7
Jul 87*	13-cm-diam. net	153	0–4	425	2.4
Aug 87*	13-cm-diam. net	153	0–4	425	2.4
Sep 87*	13-cm-diam. net	153	0–4	425	2.4
Jun 88	50-cm-diam. net	202	0–13	2,553	0.4
Jul 88*	50-cm-diam. net	202	0–13	2,553	0.4
Aug 88*	50-cm-diam. net	202	0–13	2,553	0.4
Sep 88*	13-cm-diam. net	153	0–13	173	5.8
Jul 89	50-cm-diam. net	500	0–10	1,963	0.5
Aug 89	50-cm-diam. net	243	0–13	2,553	0.4
Oct 89	50-cm-diam. net	243	0–13	2,553	0.4
Sep 90*	50-cm-diam. net	243	0–13	2,553	0.4
Oct 90*	50-cm-diam. net	243	0–13	2,553	0.4
Jun 91	50-cm-diam. net	243	0–13	2,553	0.4
Aug 91	50-cm-diam. net	130	0–12	2,356	0.4
Sep 91*	50-cm-diam. net	243	0–13	2,553	0.4
Oct 91	50-cm-diam. net	243	0–13	2,553	0.4

* Two samples collected per month versus usual one sample per month.

of <20 individuals L⁻¹ in 1983, 1985, and 1986 (Table 2), we estimated *Leptodora* and *Chaoborus* densities from net samples only. Rotifers and copepod nauplii were excluded from our analysis because they were not adequately sampled with 153- μ m or larger mesh.

Mesh sizes used prior to 1988 were able to trap copepodites and cladocerans of all sizes; however, some *Ceriodaphnia* and *Bosmina* might have passed through the 202- and 243- μ m mesh used in 1988–1991. We measured body length and depth of *Ceriodaphnia* and *Bosmina* collected in June 1984 when both populations were abundant and growing. The 202- and 243- μ m mesh would trap all sizes of both

cladoceran species if all individuals encountered the net in a lateral orientation. The 202- μ m mesh would underestimate *Ceriodaphnia* and *Bosmina* densities by 3% if all individuals encountered the net in an anterior–posterior orientation (Table 3). The 243- μ m mesh would underestimate *Ceriodaphnia* and *Bosmina* densities by 17% and 11%, respectively, if all individuals encountered the net in an anterior–posterior orientation. The 500- μ m mesh could not adequately sample small zooplankters but was useful for estimating densities of large species.

Because few zooplankton species occur below the thermocline in Third Sister Lake (Dorazio 1986), density esti-

Table 3. Body size measurements of *Ceriodaphnia* and *Bosmina* collected from Third Sister Lake on 21 June 1984 and percentage of each population that would pass through various mesh sizes.

Taxon	Measurement (μ m)	Mean \pm 1 SD	Range	Percent passing through mesh		
				202 μ m	243 μ m	500 μ m
<i>Ceriodaphnia</i> (n = 69)	Length	544 \pm 108	336–799	0	0	37.7
	Depth	337 \pm 92	193–606	2.9	17.4	98.6
<i>Bosmina</i> (n = 61)	Length	403 \pm 47	281–495	0	0	100
	Depth	294 \pm 43	188–372	3.3	11.5	100

mates from epilimnetic trap samples always exceeded estimates from net tows of 0 to 13 m. Therefore, zooplankton counts from integrated trap samples and 4-m net tows were adjusted to approximate a 13-m net tow (multiplication factor = 5/13). Zooplankton counts from net samples compared well (<2-fold difference) with standardized counts from integrated trap samples taken on the same date. Regardless of sampling technique, all count data were converted to numbers per cubic meter.

Several statistical techniques were used to identify changes in the zooplankton community following the introduction of *Leptodora*. First, we compared pre- and postintroduction densities and size ratios (small:large) with randomized intervention analysis (RIA; Carpenter et al. 1989). RIA is essentially a resampling technique that allows one to quantify the uncertainty associated with observed differences before and after a disturbance (intervention). Observed abundance values (including zeros) were randomly shuffled to create 999 time series permutations. We calculated the absolute difference between average pre- and postintroduction values for each permutation. We considered the boundary between pre- and postintroduction periods to be 15 September 1987, because on this date, *Leptodora* was first seen in the lake. We then ranked all absolute differences ($|\text{avg.PRE} - \text{avg.POST}|$) along with our actual difference (AD). The AD ranking produces a *P*-value (e.g., 5 out of 1,000 = 0.005). Our uncertainty estimate (*P*-value) is fairly conservative because we did not use a time series model to correct for seasonal variability (Carpenter et al. 1989).

We also performed a Fisher's exact test to determine whether the presence of *Leptodora* was associated with a dramatic reduction in any zooplankton taxon. We considered "dramatic" to be $\leq 1\%$ of the average annual preintroduction peak abundance.

Finally, we performed a temporally constrained cluster analysis by the method of incremental sum of squares (Grimm 1987) to identify those sampling dates during the 9 yr that had similar zooplankton community composition. We used TILIA (version 1.09) to create dendrograms that were based on square root transformations and Euclidean distances. The height of each node connecting clusters in the dendrogram was defined by total dispersion at each stage.

Results

Before the introduction of *Leptodora*, the crustacean zooplankton assemblage of Third Sister Lake was composed of small-bodied cladocerans (*Ceriodaphnia*, *Bosmina*, *Diaphanosoma*, *Daphnia rosea*, *Daphnia parvula*), as well as diaptomid and cyclopoid copepods (Fig. 2). *Mesocyclops edax* and *Chaoborus punctipennis* were the two important invertebrate predators identified during these years. From 1983 to 1987, there was a consistent seasonal pattern of cladoceran species succession from a *D. parvula*-*Bosmina longirostris* assemblage in spring and early summer to a *Ceriodaphnia reticulata*-*D. rosea* assemblage in mid- to late summer (Fig. 3A,B). Copepods represented <30% of the zooplankton community, and their proportional representation did not change much during the ice-free season (Fig.

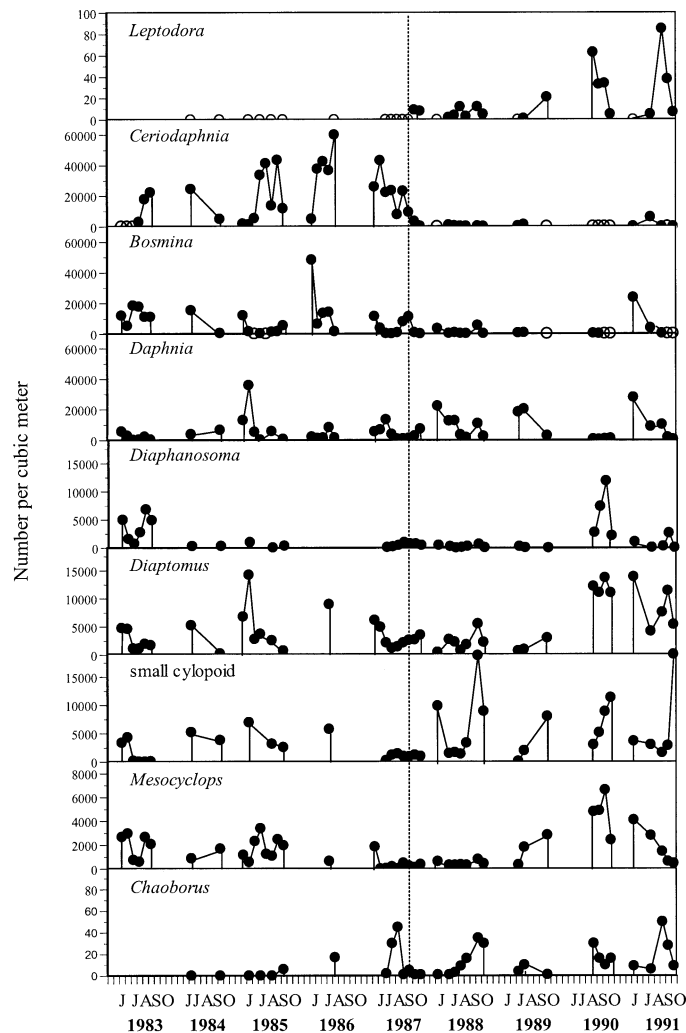


Fig. 2. Density of microcrustaceans and *Chaoborus punctipennis* in Third Sister Lake from June to October 1983–1991. Data are based on vertical net hauls, except 1983, 1986, and June–July 1985, when integrated samples were collected with a Schindler–Patalas trap. Vertical dashed line indicates first appearance of *Leptodora* in Third Sister Lake. Open circles indicate no organisms detected.

3A). As a result of dominance by small-bodied species, the size structure of the crustacean assemblage was skewed toward smaller individuals (Fig. 3C).

Once introduced, *Leptodora* quickly became established in the lake and, as early as 1988, exhibited a phenology characteristic of natural populations (Fig. 2). Juveniles appeared in late July or early August, and the population increased in size until it reached its maximum abundance in early September. As autumn approached, the population declined until early November, when *Leptodora* could no longer be found in the lake. Since its introduction, *Leptodora* attained higher peak abundance in every subsequent year monitored, culminating with 85 individuals m^{-3} in September 1991.

The crustacean zooplankton community of Third Sister Lake underwent significant changes immediately following the appearance of *Leptodora*. *Ceriodaphnia*, which had dom-

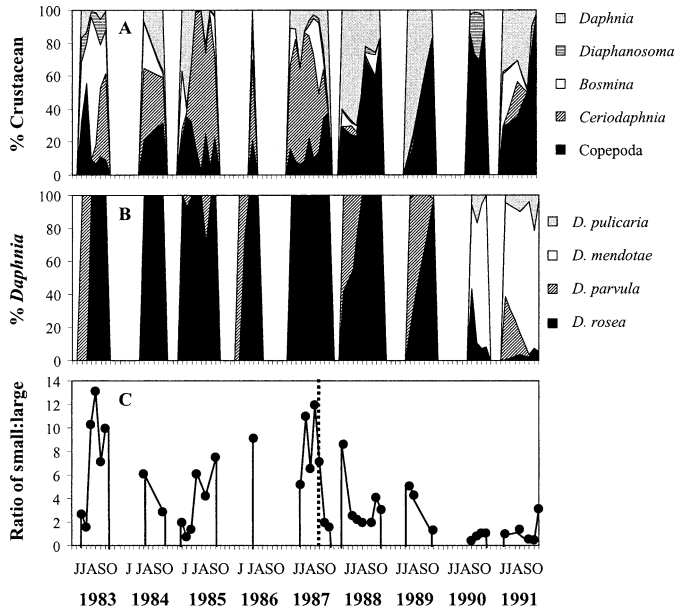


Fig. 3. Percent composition of zooplankton and crustacean size ratio in Third Sister Lake from 1983 to 1991. (A) Percentage of cladocerans and copepods. (B) Percentage of *Daphnia* species. (C) Ratio of small (<1 mm) to large (>1 mm) crustaceans, excluding copepod nauplii. Vertical dashed line indicates first appearance of *Leptodora*.

inated the zooplankton during the summer months, was virtually eliminated, and *Bosmina* populations were drastically reduced (Fig. 2; Table 4). Indeed, the probability of observing *Ceriodaphnia* and *Bosmina* was significantly lower in the presence of *Leptodora* than in its absence (Fisher's exact probability, 0.008 and 0.006, respectively). *Bosmina* did become abundant in spring 1991 at a time when *Leptodora* was absent from the water column, but it did not exhibit a late summer abundance peak characteristic of earlier years

(1983, 1985–1988). There was also a significant increase in small cyclopoid species and a marginally significant increase in *Diaptomus* after the introduction (Fig. 2; Table 4).

The disappearance of *Ceriodaphnia* and *Bosmina* resulted in a threefold reduction in the small:large crustacean ratio and a change in the proportional representation of cladocerans and copepods (Table 4; Fig. 3A,C). The declining size ratio can best be explained by the removal of the small-bodied cladocerans and not by a concomitant increase in large-bodied species (i.e., *Daphnia* and *Mesocyclops*). Even when small and large *Daphnia* were considered separately, there was no significant change in abundance associated with the introduction of *Leptodora* (Table 4). However, the proportional representation of copepods did change. Prior to the introduction, copepods were 20% of the zooplankton community throughout the ice-free season. After the introduction, copepods were >50% of the zooplankton community (Table 4), and their seasonal representation grew from <30% in the early summer to >80% in September and October (Fig. 3A). With the decline of *Ceriodaphnia* and *Bosmina*, the remaining cladoceran assemblage was dominated by *Daphnia* throughout the ice-free season.

Another intriguing event associated with the introduction of *Leptodora* was a change in the species composition of the *Daphnia* assemblage. Prior to the introduction of *Leptodora*, the *Daphnia* assemblage was dominated by *D. parvula* in the spring and *D. rosea* in the summer and autumn (Fig. 3B; also see Dorazio 1986). After the introduction, *D. parvula* persisted longer into the summer months (1988, 1989), and *Daphnia mendotae* became the most abundant species. *Daphnia pulicaria*, once present in only trace numbers, became a significant member of the daphnid assemblage during the summers of 1990 and 1991 (Fig. 3B). An assemblage dominated by two species in 1983 became an assemblage of four well-represented species by 1991.

Cluster analysis demonstrates that the zooplankton communities sampled before the introduction of *Leptodora* were

Table 4. Results of randomized intervention analysis for zooplankton taxa in Third Sister Lake before and after the introduction of *Leptodora* in 1987. The actual difference (AD) between pre- and postintervention averages (± 1 SD, sample size in parentheses) is compared to 999 permutations of the data to produce a *P* value.

Group	Abundance (individuals L ⁻¹)		AD	<i>P</i>
	Preintroduction	Postintroduction		
<i>Ceriodaphnia</i>	20.0 \pm 16.9 (28)	0.65 \pm 1.45 (21)	19.4	0.001
<i>Bosmina</i>	8.31 \pm 9.91 (28)	1.92 \pm 5.19 (21)	6.39	0.005
<i>Diaphanosoma</i>	3.42 \pm 7.65 (17)	1.49 \pm 2.92 (21)	1.92	0.371
<i>Daphnia</i>	4.99 \pm 7.26 (26)	8.09 \pm 8.23 (21)	-3.10	0.183
Small <i>Daphnia</i>	3.13 \pm 3.46 (26)	5.45 \pm 6.16 (21)	-2.32	0.112
Large <i>Daphnia</i>	1.87 \pm 4.16 (26)	2.62 \pm 4.19 (21)	-0.750	0.535
<i>Diaptomus</i>	3.68 \pm 2.24 (22)	5.58 \pm 4.67 (21)	-1.90	0.061
Cyclopoids	2.36 \pm 2.24 (17)	5.54 \pm 5.53 (21)	-3.18	0.025
<i>Mesocyclops</i>	1.38 \pm 1.08 (24)	1.75 \pm 1.91 (21)	-0.38	0.432
<i>Chaoborus</i>	0.009 \pm 0.015 (12)	0.014 \pm 0.014 (21)	-0.005	0.197
Crustaceans	35.6 \pm 20.9 (20)	25.0 \pm 15.0 (21)	10.6	0.063
Small : large	6.26 \pm 3.76 (20)	2.28 \pm 1.95 (21)	3.98	0.001
Cladocera : copepod	6.04 \pm 4.18 (20)	2.07 \pm 3.55 (21)	3.97	0.001
% cladocerans	79.7 \pm 12.5 (20)	47.3 \pm 27.2 (21)	32.4	0.001
% copepods	20.3 \pm 12.5 (20)	52.8 \pm 27.2 (21)	-32.5	0.001

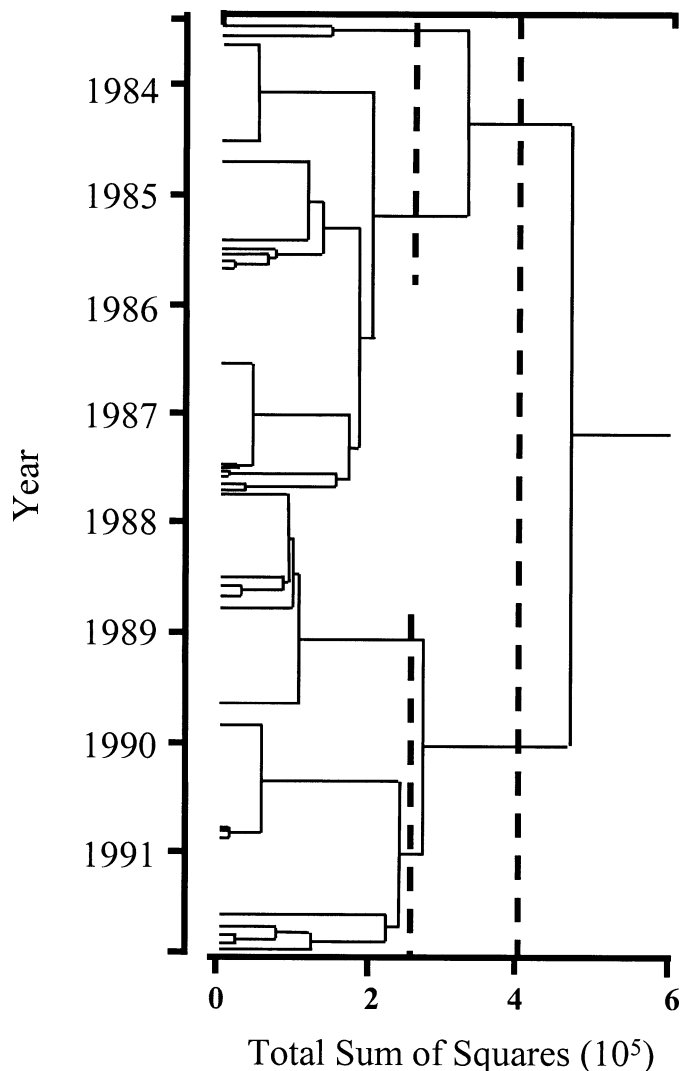


Fig. 4. Cluster analysis of Third Sister Lake zooplankton community from 1983 to 1991. Dendrogram based on Euclidean distances using all crustacean species except *Leptodora*. A square root transformation was used to de-emphasize the effects of numerically dominant species. Similar zooplankton communities are joined at low levels (small sum of squares), whereas dissimilar communities are not joined until high levels (large sum of squares). Distinct temporal patterns are defined by dashed lines cutting the dendrogram of total dispersion.

distinctly different from those sampled following the introduction of *Leptodora* (Fig. 4). A vertical cut across the dendrogram at sum of squares = 4×10^5 indicates that pre- and postintroduction communities are most distinct from one another. The point of separation occurs in late September 1987, exactly when *Leptodora* was first observed in Third Sister Lake. These two clusters are best distinguished by the presence or absence of small-bodied cladocerans. A second cut at sum of squares = 2.6×10^5 shows that the early 1983 community was different from the other preintroduction communities and that the 1988–1989 communities were different from the 1990–1991 communities (Fig. 4). The early 1983 community was characterized by relatively abundant

populations of *Bosmina* and copepods compared with the other preintroduction communities. The 1990–1991 communities had measurable densities of *Ceriodaphnia*, *Bosmina*, and *Diaphanosoma*, whereas the 1988–1989 communities did not.

The appearance of *Leptodora* in Third Sister Lake was not associated with a change in the density of the insect larva *C. punctipennis* (Table 4) and did not alter the probability of observing *C. punctipennis* in our net samples (Fisher's probability, 0.061). A graphical examination indicates that densities of the predaceous midge larva were already high in 1986 and early 1987 (Fig. 2). As a result, the actual difference (AD) was not significant when compared to shuffled data. We caution that the apparent increase in *Chaoborus* might be, in part, an artifact of different sampling methods. Our pre-1987 data might underestimate *Chaoborus* abundance because samples were collected with small-diameter nets (rather than the 50-cm nets used in 1988–1991). Small-diameter nets can miss low-density organisms that are patchily distributed.

Although we did not have a reference site in this study, data collected from a nearby lake during the past 30 yr suggest that small-bodied cladocerans did not experience a regional decline concurrent with the disappearance of *Ceriodaphnia* and *Bosmina* from Third Sister Lake. Frain's Lake, an 8-m-deep kettle lake located in the Huron River watershed 16.6 km from Third Sister, is dominated by small cyclopoid copepods and small-bodied cladocerans (*D. rosea*, *D. parvula*, *Ceriodaphnia lacustris*, *B. longirostris*). In Frain's Lake, the proportional representation of *Ceriodaphnia* has changed little since 1964, and the proportional representation of *Bosmina* has changed little since 1971 (Table 5). *Daphnia* was more prominent in 1962–1963 than in 1964–1992, and copepods (mostly cyclopoid) were more prominent in 1964–1992 than in 1962–1963. Daytime densities of *Chaoborus* (15 individuals m^{-3}) in 1992 were similar to those in Third Sister Lake after 1987.

Discussion

Past researchers have discounted the capacity of invertebrate predators to influence zooplankton communities in lakes with fish (e.g., Hall et al. 1976). Large invertebrate predators—notably *Leptodora*, *Bythotrephes*, certain calanoid copepods, mysids, and small *Chaoborus* species—are typically present at low densities relative to herbivorous zooplankton. Because they are vulnerable to planktivorous fish, these predators might never achieve sufficient numbers to influence plankton communities for extended periods of time. Our results, however, suggest that at least one invertebrate predator, *Leptodora*, can have a lasting effect on community composition and structure despite its low density and vulnerability to planktivorous fish.

Dramatic changes to the composition and size structure of the crustacean zooplankton community following the introduction of *Leptodora* provide circumstantial evidence that the predaceous cladoceran has become an important selective force in Third Sister Lake. Small-bodied cladocerans (*Ceriodaphnia* and *Bosmina*) decreased following the ap-

Table 5. Percent composition of crustacean zooplankton community in Frain's Lake, Michigan, 1962–1992. Sampling methods: Juday trap in 1962–1964; 1-liter Kemmerer bottle in 1971; 25-cm-diameter, 73- μ m mesh net in 1992.

	Composition (%)				
	29 Sep 62 (2 m)	07 Sep 63 (2 m)	05 Sep 64 (2 m)	13 Oct 71 (2 m)	07 Sep 92 (0–8 m)
<i>Daphnia</i>	32.6	51.3	2.3	2.8	13.9
<i>Ceriodaphnia</i>	7.1	8.7	14.4	12.7	11.4
<i>Bosmina</i>	2.5	0.5	3.0	9.9	6.0
<i>Diaphanosoma</i>	0.0	0.0	0.1	0.1	0.7
Copepoda	57.8	39.5	80.2	74.5	68.0
Copepodites	18.5	20.9	46.0		30.2
Nauplii	39.3	18.6	34.1		37.8
Total (individuals L ⁻¹)	82	96	79	—*	61

* Absolute density estimate could not be calculated from available records.

pearance of *Leptodora*, and copepods became a dominant component of the zooplankton. Within the *Daphnia* assemblage, there was a shift from small-bodied species (*D. parvula*, *D. rosea*) to large-bodied species (*D. mendotae*, *D. pulicaria*). Although mesh sizes used to collect plankton in 1988–1991 might have underestimated *Ceriodaphnia* and *Bosmina* densities, the underestimate is low (<17% for *Ceriodaphnia* and <11% for *Bosmina*) and cannot account for the observed 99% reduction in both species following the introduction of *Leptodora*. Small-bodied cladocerans are particularly vulnerable to *Leptodora* because they move rather slowly and fit easily inside *Leptodora*'s trap basket (Mordukhai-Boltovskaya 1958; Herzig and Auer 1990). Large *Daphnia* and copepods can be consumed by *Leptodora* (Lunte and Luecke 1990; Branstrator and Lehman 1991), but they are not easily captured. Copepods have an effective escape response, and large *Daphnia* do not fit inside the trap basket (Browman et al. 1989).

Laboratory and field studies have shown that *Leptodora* has the potential to impose significant death rates on cladoceran populations. Maximum predation rates recorded in the laboratory include 12 individuals predator⁻¹ d⁻¹ for quick-moving *Diaphanosoma* (Herzig and Auer 1990), 14 individuals predator⁻¹ d⁻¹ for juvenile *Daphnia pulex* (Browman et al. 1989), and 30 individuals predator⁻¹ d⁻¹ for small-bodied *Polyphemus* (Mordukhai-Boltovskaya 1958). Field studies have focused on the capacity of *Leptodora* to control populations of large-bodied cladocerans. In a study of *Daphnia* population dynamics, Hall (1964) determined that when its density reached 45–130 individuals m⁻³, *Leptodora* could consume 25–35% of *Daphnia* production. The peak seasonal abundance of *Daphnia* (15–30 individuals L⁻¹) was similar to that found in Third Sister Lake. De Bernardi (1974) also observed a close correspondence between the high death rate of *Daphnia hyalina* and the late summer maxima in *Leptodora* abundance (300–500 individuals m⁻³).

The influence of *Leptodora* on small-bodied prey might be overlooked or underestimated. Field studies are typically conducted in habitats where *Leptodora* had long been established and in which the herbivore assemblage had already changed to accommodate the invertebrate predator. *Leptodora* often coexists with *Daphnia* (McNaught 1993b). This

can occur not because the large herbivore is a preferred food resource, but because small-bodied herbivores have been removed from the community. The events surrounding the invasion of Third Sister Lake suggest that *Leptodora* selects small-bodied prey such as *Ceriodaphnia* and *Bosmina* during the initial stages of colonization. After small-bodied cladocerans are gone, *Leptodora* might switch to juvenile and small adult *Daphnia*.

In Third Sister Lake, the effect of *Leptodora* on the small-bodied zooplankton community was both immediate and long lasting. Late summer populations of *Ceriodaphnia* and *Bosmina* that overlap temporally with *Leptodora* were noticeably absent only 1 yr after the introduction. Hellsten and Stenson (1995) also observed a rapid disappearance of *Bosmina longispina* in a Swedish lake when *Leptodora* populations were dense. The rapid shift in size structure and near extirpation of several small-bodied cladoceran species following the introduction of *Leptodora* is comparable to that observed when *Chaoborus* colonizes a lake. Black and Hairston (1988) observed an increase in average zooplankton size and species diversity 3 months after the introduction of *Chaoborus americanus* to a previously fish-dominated system. The small cladoceran *Eubosmina* was virtually eliminated, and the fish-tolerant copepod *Diaptomus sanguineus* was replaced by the *Chaoborus*-tolerant copepod *Diaptomus spatulocrenatus*.

C. americanus and *Leptodora* have a similar effect on zooplankton communities, but *Leptodora* is able to exploit prey resources in the presence of planktivorous fish. The predaceous cladoceran is able to escape visual predators because it is highly transparent and migrates to deeper waters during the day (McNaught 1966; Kerfoot 1985). Smaller *Chaoborus* species (*C. punctipennis*, *Chaoborus flavicans*) also survive in the presence of planktivorous fish and might exert similar pressure on small-bodied zooplankton populations. Ironically, *Leptodora* is unable to influence the zooplankton communities of fishless lakes because it does not occur in these habitats. *C. americanus* preys on juvenile *Leptodora* and might prevent establishment of the cladoceran in fishless lakes (McNaught 1993a).

Species introductions, even at low densities, might so disturb the dynamics of well-established populations that pre-

viously closed niches become filled with rare species released from biotic pressures. Neill and Peacock (1980) observed that low-level *Chaoborus* predation allowed cyclopoid copepods and small cladoceran species to become more abundant in experimental enclosures. In this study, two *Daphnia* species (*D. mendotae* and *D. pulicaria*), previously present in only trace amounts, assumed prominence within the cladoceran assemblage of Third Sister Lake after the appearance of *Leptodora*. These herbivores might be able to coexist with *Leptodora* because they can escape predation by molting to larger sizes (Lynch 1980). Changes in species diversity, however, could be short lived. Although there was an increase in species diversity in Little Bullhead Pond immediately following colonization by *C. americanus*, a process of species sorting eventually led to the extinction of several organisms ill suited to the new predation pressure (Black and Hairston 1988). As of 1991, Third Sister Lake might have been a disturbed system still on its way to a new stable state.

When interpreting the results of an unreplicated whole-lake study, it is important to know whether the system changed following a perturbation and whether the perturbation caused the change. Results from RIA and cluster analysis indicate that there was a clear change in species abundance, size structure, and community composition following the appearance of *Leptodora* in Third Sister Lake. It is more difficult to demonstrate that *Leptodora* caused the observed changes in the zooplankton community. Measured or unmeasured ecosystem parameters could have changed simultaneously with the introduction of *Leptodora*. Alternative explanations for the sudden disappearance of small-bodied cladocerans from Third Sister include climatic change, reduction in the planktivorous fish population, and increase in the population of native invertebrate predators. Without data from a nearby reference site, it is difficult to exclude these alternative explanations. However, we can show that they are less parsimonious than the introduction of a known cladoceran planktivore.

If regional temperature and precipitation patterns changed in 1988–1991, one would expect surface water temperature and ion concentration to change as well. An examination of late summer data from 1982–1990 revealed little change in epilimnetic temperature or chemistry (Table 1). The conductivity increase that occurred between 1982 and 1988 has been attributed to the cumulative inputs of road salt and not evaporative loss (Bridgeman et al. 2000). It is unlikely that an increased NaCl concentration was responsible for the disappearance of *Ceriodaphnia* and *Bosmina*. Cladocerans (i.e., *D. pulex*, *Ceriodaphnia quadrangula*, and *Alona* spp.) frequently occur in hyposaline lakes whose conductivity approaches 4,000 $\mu\text{S cm}^{-1}$ (Hammer and Forró 1992). Moreover, the abundance of other cladocerans (*Daphnia*, *Diaphanosoma*) remained constant during the same time period.

Another alternative explanation for the disappearance of small-bodied cladocerans in Third Sister Lake is a reduction in the planktivorous fish population. According to the size efficiency hypothesis (Brooks and Dodson 1965), reduced vertebrate planktivory should favor large, competitively dominant zooplankters such as *Daphnia*. In fact, visual sur-

veys of fish populations in Third Sister Lake indicate that dominant planktivore and piscivore populations might have increased between 1985 and 1988. Average abundance of *Lepomis* and *Micropterus* (± 1 SD) along 100-m transects in the littoral zone was 353 ± 159 and 50 ± 35 individuals ha^{-1} on 9 July 1985 ($n = 2$; Dettweiler unpubl. data) and $1,222 \pm 775$ and 372 ± 125 individuals ha^{-1} on 7 May 1988 ($n = 3$; this study). The number of bluegill nests in 100-m shoreline transects was fairly consistent from year to year (>25 in 1987, 25–80 in 1988). Our analysis also shows that *Daphnia* numbers did not increase after 1987 (Table 3). Moreover, *Ceriodaphnia*, not *Daphnia*, is the superior competitor during the summer months in Third Sister Lake (Kiesling 1990). If the numbers of planktivorous fish had decreased after 1987, *Ceriodaphnia* should not have been eliminated.

Recent paleolimnological evidence supports our assertion that enhanced invertebrate predation, rather than relaxed vertebrate predation, was responsible for the observed changes to the Third Sister Lake zooplankton community. Crustacean remains in sediment cores indicate the first appearance of *Leptodora* and subsequent reduction in *Bosmina* abundance (Kerfoot unpubl. data). With an increase in *Leptodora* abundance, *Bosmina* became larger-bodied and the population shifted from short-featured (micro, antennule length) to long-featured morphs. *Bosmina* morphs with long features have lower death rates and higher escape efficiencies than short-featured morphs (Hellsten et al. 1999).

It is possible that *C. punctipennis* facilitated the near elimination of small-bodied cladocerans from Third Sister Lake; however, we do not think that *C. punctipennis* was the primary causative agent. *C. punctipennis* has long been a part of the Third Sister Lake zooplankton community. Eggleton (1931) recorded summertime densities comparable to those observed after 1987 (40–124 individuals m^{-3}). Low *Chaoborus* densities prior to 1987 could reflect suboptimal sampling techniques to target this organism. Even if our analysis could show an increase in *C. punctipennis* numbers in 1986 and early 1987, the observed changes to the prey community corresponded more closely to the introduction of *Leptodora*. *Ceriodaphnia* and *Bosmina* populations were still strong in 1986 and early 1987. Finally, postintroduction *C. punctipennis* densities were often less than *Leptodora* densities, and some of the *C. punctipennis* were first or second instars, which feed only on rotifers (Moore 1988). *Leptodora* of all sizes are able to feed on small cladocerans (Herzig and Auer 1990). At best, *C. punctipennis* might have assisted *Leptodora* in the demise of *Ceriodaphnia* and *Bosmina*.

The successful colonization of Third Sister Lake by *Leptodora* demonstrates that it can become established in small lakes if given the opportunity to disperse to those habitats. Dispersal from lake to lake might be an important determinant of zooplankton community composition, but it has not been tested rigorously. Separated from one another by a terrestrial barrier, inland lakes are analogous to islands and are subject to the same principles of island biogeography. Like islands, lakes exhibit a positive relationship between species richness and area (Browne 1981; Dodson 1992). MacArthur and Wilson (1967) showed that a balance between immigration rates and extinction rates could explain this species-

area relationship. Information on extinction rates might exist in the paleolimnological record or in the species list of a lake that has been monitored for many years, but little information exists on the capacity of aquatic organisms to disperse to and become established in a new habitat.

In nature, dispersal opportunities for *Leptodora* might be rare, and movement from lake to lake might require long periods of time. Vulnerable to handling and desiccation, adult *Leptodora* disperse to new habitats only through connecting waterways. Dispersal to isolated lakes would require the transport of lake sediments that contain *Leptodora* resting eggs (Herzig 1985). Specific dispersal vectors have not been identified for *Leptodora*, but it is possible that their dormant eggs are carried from lake to lake in wet mud clinging to avian or mammalian hosts. This mode of dispersal would favor the colonization of large lakes, where the probability of intercepting an animal vector is greater than that for small lakes. Indeed, McNaught (1993b) showed that lake size was the best predictor of *Leptodora* presence or absence. Without human intervention, the likelihood that *Leptodora* could colonize a small lake (such as Third Sister Lake) that receives no direct input from another body of water is low.

Dispersal is greatest over short distances. Havel and Shurin (2004) compared colonization rates from experimental studies and exotic introductions. They concluded that zooplankton dispersal becomes limiting >20 km from a source. The absence of *Leptodora* from Third Sister Lake for 50+ yr, despite the existence of a known source population 16 km away (Whitmore Lake) and a suspected source population 4 km away (Barton Pond), suggests that *Leptodora* disperses slowly. Why then is *Leptodora* so widely distributed in the northern hemisphere? Although its colonization rate is low, *Leptodora* might have a low or negligible extinction rate once it invades an established community. The ability to coexist with fish and reproduce parthenogenetically are traits that would help *Leptodora* persist in newly colonized lakes.

This study provides strong correlative evidence that, despite the presence of planktivorous fish, a large invertebrate predator, *Leptodora*, is able to modify the composition and size structure of the zooplankton community in a way that is consistent with the results of previous laboratory and field experiments. This study also suggests that *Leptodora* can influence the structure and composition of zooplankton communities even at relatively low densities (<100 individuals m⁻³). Finally, it might be incorrect to assume that all lakes are colonized by all species in a given geographic region. The capacity to disperse over relatively short spatial scales (<20 km) could be an important factor limiting the regional distribution of *Leptodora* and other planktonic animals and deserves further attention. In the future, controlled before and after studies and manipulative experiments should be conducted to further examine the dispersal capacity of invertebrate predators and their effects on zooplankton communities.

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