Invertebrate predation in Lake Michigan: Regulation of *Bosmina longirostris* by *Leptodora kindtii*

Donn K. Branstrator and John T. Lehman

Department of Biology, Natural Science Building, University of Michigan, Ann Arbor 48109

Abstract

The density of *Bosmina longirostris* (O. F. Mueller) declined 100-fold between 25 June and 20 August 1985 in Lake Michigan; a similar pattern of changing abundances was observed in 1986 but not in 1987 or 1988. *Bosmina* collected from periods before and during the decline in 1985 and 1986 were examined for size at maturity and clutch size. Population size-frequency distributions suggest that some animals began to mature at smaller sizes during the decline in 1985. In some cases, the average clutch size for *Bosmina* of similar body lengths was significantly reduced during the decline in 1985 and 1986. These data suggest that food limitation was a factor in the species decline in both years. Gut content analyses indicate that of seven potential predators, *Leptodora kindtii* (Focke) was probably most responsible for *Bosmina* mortality. There is ample evidence that *Leptodora* does not consume strictly fluid from its prey: juvenile *Leptodora* ate mainly smaller prey that included *Bosmina* and the rotifer *Conochilus*; adults ate a broader size range of prey that included mainly *Bosmina*, *Daphnia*, and copepods. In 1987 and 1988, *Bythotrephes cederstroemii* Schoedler was abundant in Lake Michigan and was contemporaneous with collapse of the *Leptodora* population and concurrent increase of the *Bosmina* population in August and September. Predation by the large copepods *Epischura lacustris* S. A. Forbes and *Limnocalanus macrurus* Sars did not appear to have any significant effect on the population dynamics of *Bosmina*.

Lake Michigan has long been regarded as an ecosystem in which visual planktivory by fish exerts a dominant structuring influence. The exposition by Wells (1970) documenting changes in zooplankton populations in response to predation by alewife, *Alosa pseudoharengus* (Wilson), helped to establish size-selective predation as one of the paradigms of plankton community ecology. Wells observed that the successful invasion of alewife into Lake Michigan was associated with depressed densities of *Daphnia*, *Leptodora*, *Limnocalanus*, *Epischura*, and other large-bodied crustacean taxa and with increased densities of smaller taxa, particularly *Bosmina longirostris*.

Although Wells (1970) argued convincingly that the large plankton were removed by selective planktivory, no rationale was advanced for the numerical increase in *Bosmina*. In retrospect, the taxon's success may have stemmed from relaxed competition for food resources or from reduced planktivory by invertebrates. That planktivory played a role in *Bosmina*'s dynamics seems plausible but because several putative predators declined simultaneously the relative importance of each is indecipherable from his data.

Recent changes of Lake Michigan's zooplankton community, wrought by a new invading species, provide an opportunity to further understand factors controlling *Bosmina* dynamics there. In summers 1985 and 1986, *Bosmina* populations in offshore Lake Michigan experienced similar abundance cycles. Populations quickly reached peak densities in late June of 31,000 m^{-2} (1985) and early July of 70,000 m^{-2} (1986), and then decreased steadily to densities of 600 m^{-2} (1985) and 9,000 m^{-2} (1986) by mid-August. In 1987, however, major changes occurred in the composition of the offshore zooplankton community; they were attributed in part to predation by the invading cladoceran, *Bythotrephes cederstroemii* (Lehman 1988). That summer, and in 1988, *Bosmina* did not decline in August and September as it had in 1985 and 1986 during those months. In this report we use the population changes associated with this event to investigate the controls on *Bosmina* in Lake Michigan.

General approach

Factors responsible for the seasonal declines of *Bosmina* in Lake Michigan in 1985 and 1986 were hypothesized to be resource limitation, predation, or a combination of the two. Because populations in 1985 and 1986 declined at summer epilimnetic water temperatures that permitted continued growth in 1987 and 1988, ambient temperature was not considered to be a cause. *Bosmina* size-frequency distributions and size-specific egg ratios (average clutch size per body-length class) were examined for changes that would suggest food limitation as a factor. Gut analyses were performed on the potential predators to determine if any were eating *Bosmina*. On the basis of physical presence and potential for carnivory, these predators were young-of-the-year (YOY) *Coregonus hoyi* (Gill), and the crustacean zooplankton *Mysis relicta* (Lovén), *Leptodora kindtii, Epischura lacustris, Limnocalanus macrurus, Senecella calanoides* Juday, and cyclopoids [mainly *Diacyclops bicuspidatus thomasi* (S. A. Forbes)]. Planktivory on *Bosmina* by YOY *C. hoyi* was immediately rejected based on results of gut analyses from 1985 (Warren and Lehman 1988), which showed that these vertebrates consumed cyclopoid copepodids and *Daphnia pulicaria* Forbes almost exclusively during the time when *Bosmina* declined. Evidence for the potential carnivory of *M. relicta* (Bowers and Vanderploeg 1982), *L. kindtii* (Mordukhai-Boltovskaia 1958), *E. lacustris* (Chow-Fraser and Wong 1986), *L. macrurus,* and *S. calanoides* (Nero and Sprules 1986) and cyclopoids (Fryer 1957) made these species candidates for study.

Methods

Zooplankton collections — Zooplankton were collected during summer 1985–1988 in Lake Michigan at a reference station (43°N, 86°40'W), 36 km offshore from Grand Haven, Michigan (Lehman et al. 1990). In 1985 and 1986, large crustacean zooplankton were collected by Tucker trawl with a mouth opening of 1 m² and a net aperture of 300 µm and by 1-m-diameter Puget Sound vertical closing nets with 130- or 300-µm mesh. Trawl and nets were towed

at 0.5–1 m s⁻¹. Large- and small-bodied zooplankton were collected by submersible pump discharged through either 63- or 130-µm mesh (Dorazio et al. 1987; Lehman et al. 1990). Pump collections were integrated over 10-m intervals. Temperatures were measured by mechanical bathythermograph (1985 and 1986) and by electronic bathythermograph (1987 and 1988). In 1987 and 1988, zooplankton were collected exclusively by closing nets fitted with 130-µm mesh. Zooplankton were immediately narcotized with carbonated water and preserved in a sugar-Formalin solution (Haney and Hall 1973). Samples collected by the trawl and closing nets were split by volume with a Folsom plankton splitter. Representative fractioned samples were counted to determine population densities of species by date and depth. Pump samples were subsampled by pipette and counted.

Bosmina — The potential effects of resource limitation on *Bosmina* were determined by examining the animals for changes in size at maturity and clutch size. Goulden et al. (1982) reported that *Bosmina* grown under low-food conditions matures at a smaller size than better fed individuals. The smallest sizes at which Lake Michigan *Bosmina* reached second and third (primaparous) instars were determined from population size-frequency distributions. Instars were identified from modes of the distributions and numbers of barren vs. fecund females in individual frequency cells. We hypothesized that declining resources would have caused *Bosmina* to mature at a smaller size.

Somatic growth in *Bosmina* continues after primaparity; thus later adult instars have larger brood chambers and can carry more eggs. Kerfoot (1974) found that *Bosmina* grown under low-food conditions carries fewer eggs per clutch than well-fed individuals; this relationship held over a range of carapace lengths. We hypothesized that declining resources would have forced *Bosmina* to decrease clutch size.

To test both hypotheses, we measured *Bosmina* for body length and clutch size. Plankton samples were filtered on 50-µm mesh and rinsed with filtered tapwater (50 µm) to remove excess Formalin. After re-

suspension, random subsamples of 5 ml were extracted with a widebore Finn injection pipette and discharged into a zooplankton counting chamber. Animals were viewed on a Wild M5A stereo dissecting microscope at 25× magnification. As encountered, individuals were removed to and mounted on glass microscope slides in 50% glycerin. Coverslips were sealed with Permount histological mounting medium (Fisher SO-P-15). Individuals were measured for total body length (Kerfoot 1980) with the aid of an ocular micrometer under 190× magnification on an Olympus BHA compound stereo microscope. Clutch size was recorded.

Bosmina egg volume was also estimated to determine whether egg size could explain differences in clutch size across dates. For individuals carrying eggs in an early stage of embryonic growth, dimensions of one egg per clutch were measured. The yolk of these eggs was transparent and nongranular, the oil droplet was visible, and the membrane had not been cast off. Egg volume (V) was approximated as

$$V = \tfrac{4}{3}\pi AB^2. \qquad (1)$$

where A and B are the longest and shortest radii.

Death rates for *Bosmina* were calculated in order to determine predation rates necessary to account for the decline (Paloheimo 1974). The instantaneous birth rate (b) was taken as

$$b = \ln(1 + E)/D \qquad (2)$$

where E is the egg ratio (average number of eggs per female) and D the egg development time. Because the animals were distributed throughout the water column, they experienced different temperatures, thus different egg development times. To compute an average population egg development time for each date, we determined the population density of *Bosmina* in each stratum from pump samples. Between two and six series of samples were taken over 24 h to determine the diurnal vertical distribution of *Bosmina*.

The corresponding fraction of eggs in each stratum was estimated by multiplying a total population egg ratio (E) times *Bosmina*

density in that stratum for each period. χ^2 homogeneity tests showed that E was not significantly different by stratum on any date ($P > 0.05$). Values for the dependency of egg development rate on temperature were taken from Vijverberg (1980). The population egg development time was then computed as an average, weighted to account for the time that different percentages of eggs experienced different temperatures over 24 h. The instantaneous population growth rate (r) was taken as

$$r = (\ln N_t - \ln N_0)/t \qquad (3)$$

where N_t and N_0 are the population densities at time t and 0, and t is the time between sample dates. The instantaneous death rate (d) was taken as

$$d = b - r. \qquad (4)$$

Daily death rate (DR) was then taken as

$$\text{DR} = d(N_0 + N_t)/2. \qquad (5)$$

Copepods and Leptodora—Animals were examined for prey remains in their digestive tracts. Results were used chiefly to identify predators of *Bosmina*. Subsamples of 5 ml were prepared as for *Bosmina* and then discharged into a glass Petri dish. Species were identified under bright-field microscopy on the Wild microscope at 25× magnification. Zooplankton were removed as encountered and placed individually on glass slides. *Leptodora* was measured from the center of the eye to the base of the bifurcation in the tail spine. Each animal was completely covered with Hoyer's mounting medium (200 g of chloral hydrate crystals, 20 ml of glycerin, 30 g of photopurified gum arabic, and 50 ml of water), then covered with a coverslip and sealed with Permount. Hoyer's medium dissolves organic tissue and allows observation of the contents in the digestive tract without dissection.

The contents of each gut were identified by differential interference contrast microscopy on the Olympus microscope at 190× and 750× magnifications. This technique made it possible to distinguish slight structural details in the remains of ingested food. As we became skilled at assigning prey remains to specific taxa, animals were re-examined to ensure that remains in earlier

specimens had not been overlooked. Each animal was examined at ~2 weeks and 3, 6, and 12 months after preparation. Rotifers in gut contents were identified by trophi and loricas.

We identified *Bosmina* by postabdominal claw morphology. Postabdominal claw length was recorded for those claws lying in favorable orientations. A regression equation relating the body length of *Bosmina* to claw length was used to estimate the body lengths of ingested *Bosmina* (Eq. 6).

$$TL = 15.38 \, CL - 0.12$$
$$(n = 207, \, r^2 = 0.888) \tag{6}$$

where TL is total body length (mm) and CL is claw length (mm). We also identified *Bosmina* by the diagnostic second antennae. Although *Eubosmina coregoni* (Baird) possesses morphologically similar antennae, this species was not detected in 1985 and was rare in 1986 (18 individuals m^{-2} on 8 July 1986).

We identified *Daphnia* by postabdominal claw morphology and thoracic comb appendages. Claw length was recorded for claws lying in favorable orientations. A regression equation from Warren and Lehman (1988) was used to estimate the total length (center of eyespot to base of tail spine) of ingested *Daphnia.*

Copepods were identified by caudal rami, mandibles, and setous appendages including first antennae and thoracic legs.

Some prey appendages were assignable only to the following two general categories: Cladocera (*Daphnia* and *Bosmina*) and Cladocera-copepod. Cladocera were distinguished by mandibles. Cladocera-copepod possessed setous appendages but could not be discriminated further.

It was possible to count and verify the number of animals ingested only when specific parts such as trophi, postabdominal claws, or mandibles were present. These structures usually do not break apart during ingestion and gut passage, and because each animal possesses a small number of these parts, it was easy to verify number of prey.

Mysis—For each specimen, the crop was excised and placed on a glass slide. Contents were teased apart, covered with Hoyer's medium and a coverslip, and then sealed with Permount. Prey identification was the same as for copepods and *Leptodora*. We also identified *Bosmina* by rostra and antennules. The one *Leptodora* found was identified by a mandible.

Results

Sampling precision—The mean C.V. for crustacean zooplankton in No. of animals m^{-2} equals 19% for pump collections (Dorazio et al. 1987) and 18.5% for vertical net collections (Lehman et al. 1990). Because two or more replicates were always taken, the standard error (SE) for the mean areal estimates in Fig. 1 is usually <15% of the reported value.

Bosmina—On most dates, population size-frequency distributions have multiple modes that represent first, second, and adult instars (Fig. 2). In 1985, some animals matured at smaller sizes in July than in June, and some matured at smaller sizes in August than in July. Some second-instar individuals also appeared at reduced size later in summer 1985. No consistent seasonal pattern was evident in 1986.

The effect of date on average clutch size was significant in half of the body-length classes in 1985 (Table 1). For these classes, average clutch size was larger in June than in July and August. Among July and August dates only, the effect of date on clutch size was not significant in any body-length class (Kruskal-Wallis $P > 0.05$, df = 2). In 1986, we collected no *Bosmina* in June samples, and the effect of date on clutch size was not significant in any body-length class (Kruskal-Wallis $P > 0.05$, df = 2). Egg volume did not change significantly during either year (Table 2, one-way ANOVA 1985, $P = 0.518$; 1986, $P = 0.065$).

In 1985, the frequency of fecund to barren females was significantly different among dates (Table 3, χ^2 homogeneity, $P = 0.027$). The proportion of fecund females appears to have been larger in June than during the rest of the season; the frequency of fecund to barren females was not significantly different among July and August dates alone (χ^2 homogeneity, $P = 0.494$). In 1986, the frequency of fecund to barren females was not significantly different among dates (χ^2 homogeneity, $P = 0.489$).
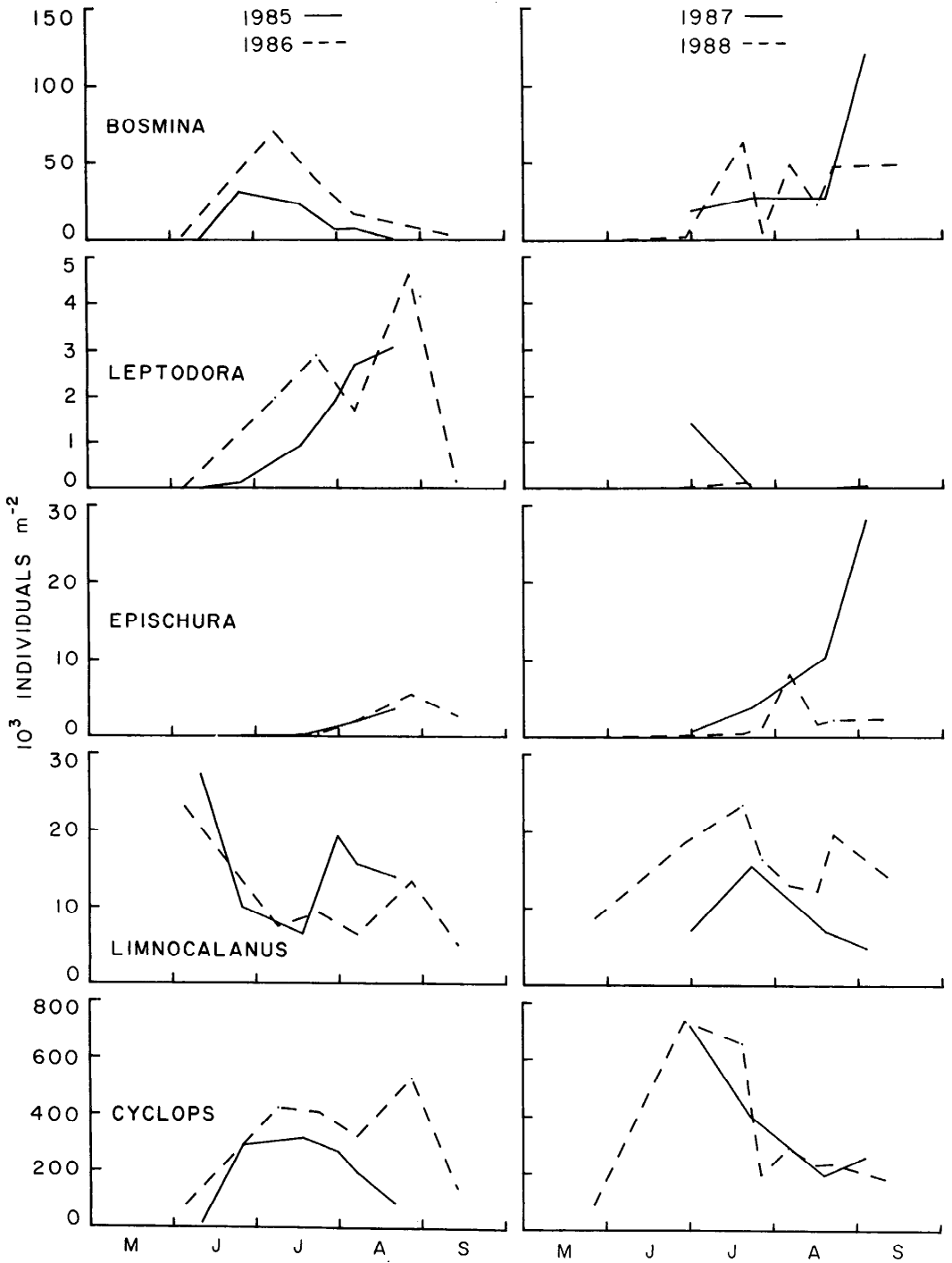
Fig. 1. Densities of *Bosmina longirostris* and potential predators at the offshore reference station from May to September 1985–1988. Copepod densities are stages C1–C6.
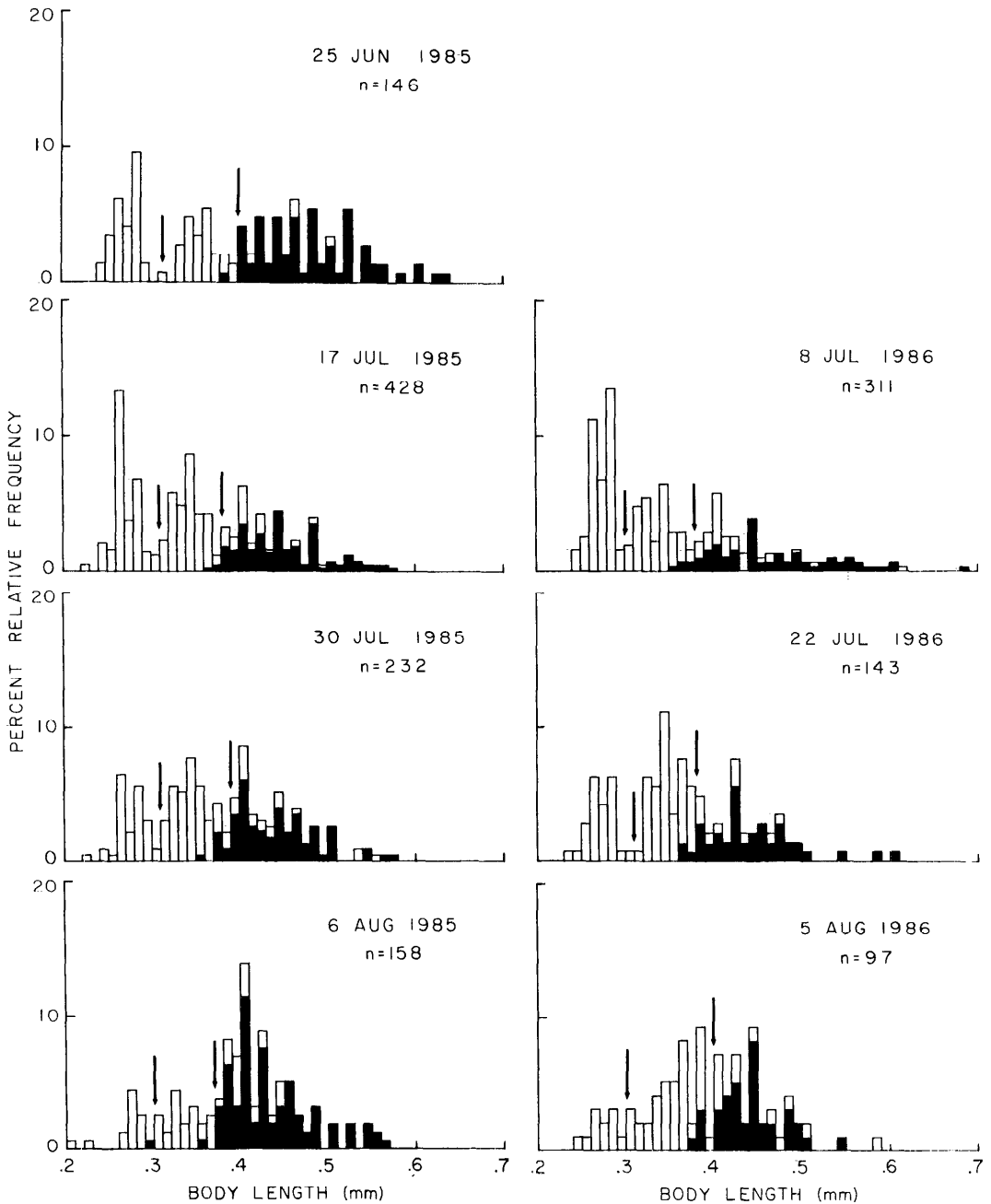
Fig. 2. Population size-frequency distributions for *Bosmina longirostris* at the offshore reference station for four 1985 and three 1986 dates. Black bars indicate fecund individuals. Arrows indicate estimates of the smallest second- and third-instar individuals on each date.

Daily death rates (DR) for *Bosmina* were calculated for two 1985 time periods: DR for 25 June–17 July = 2,780 *Bosmina* m^{-2} d^{-1}; DR for 17–30 July = 2,215 *Bosmina* m^{-2} d^{-1}.

Predator densities —During 1985 and 1986 when *Bosmina* was declining, *Leptodora* and *Epischura* were increasing in densities (Fig. 1). Densities of other predators during that time did not demonstrate con-

Table 1. Average clutch size ± SE (*n*) per body-length class for fecund *Bosmina longirostris* during 1985 and 1986 at the offshore reference station.

Body length (mm)	25–26 Jun 85*	17 Jul 85	30 Jul 85	6 Aug 85
0.40–<0.42†	1.48±0.11 (23)	1.05±0.05 (22)	1.15±0.08 (20)	1.05±0.05 (21)
0.42–<0.44†	1.79±0.09 (28)	1.50±0.17 (18)	1.44±0.18 (9)	1.13±0.09 (15)
0.44–<0.46	1.97±0.12 (31)	1.81±0.10 (26)	2.00±0.15 (14)	1.92±0.14 (13)
0.46–<0.48	2.79±0.19 (14)	1.90±0.10 (10)	2.27±0.20 (11)	2.33±0.42 (6)
0.48–<0.50	3.24±0.24 (21)	2.38±0.20 (16)	2.57±0.30 (7)	2.40±0.25 (5)
0.50–<0.52†	3.88±0.26 (16)	2.80±0.20 (5)	3.17±0.31 (6)	2.67±0.33 (3)

	8 Jul 86	22 Jul 86	5 Aug 86
0.40–<0.42	1.22±0.15 (9)	1.00±0.00 (5)	1.00±0.00 (7)
0.42–<0.44	1.60±0.24 (5)	1.30±0.15 (10)	1.00±0.00 (7)
0.44–<0.46	1.71±0.13 (14)	2.00±0.00 (7)	2.10±0.10 (10)
0.46–<0.48	2.50±0.22 (6)	2.33±0.33 (6)	2.00±0.00 (2)
0.48–<0.50	3.00±0.37 (6)	2.75±0.48 (4)	2.40±0.40 (5)

* Some individuals were selected nonrandomly from samples.
† Mean clutch sizes are significantly different across all dates (Kruskal-Wallis $P < 0.05$, df = 3).

tinued increase. *Bythotrephes* was then first detected in Lake Michigan on 25 August 1986 (Lehman 1987). In 1987 and 1988, *Bosmina* did not decline through August and September as it had in the previous 2 yr. *Leptodora* was present briefly in 1987 and 1988 in June and mid-July but then became virtually undetectable. Copepod densities were comparable to 1985 and 1986 values on most dates. Areal *Mysis* densities remained constant for the period 1985–1989 (mean = 110 individuals m^{-2}) (Lehman et al. 1990). *Senecella* was always <1,000 individuals m^{-2} during the months relevant here for 1985–1988.

Predator gut analyses—Animals cleared progressively in Hoyer's medium over periods of several weeks. After 3 months, most food items were visible. We occasionally found and identified additional prey after 3

months, but such data were the results of our increasing familiarity with the prey remains and not related to the clearing agent. In copepods, food was usually found packaged in small boluses throughout the entire length of the gut. In *Leptodora*, almost all prey remains were found in the stomach portion of the gut. In *Mysis*, examination was confined to the crop. Occasional analyses of the intestine revealed diatom frustules only.

Senecella showed no evidence of predation on *Bosmina* and only minimal selection for animal food compared to the other predators (Table 4). *Limnocalanus* consumed a range of prey including one *Bosmina*. Cyclopoids were eating *Bosmina*, but, as with *Limnocalanus*, direct evidence is limited to one specimen. *Epischura* con-

Table 2. Average volume ($\mu m^3 \times 10^5$) ± SE (*n*) for *Bosmina longirostris* eggs at the offshore reference station.

	Egg volume
1985	
25–26 Jun	6.13±0.14 (46)
17 Jul	5.88±0.12 (31)
30 Jul	6.19±0.30 (12)
6 Aug	5.82±0.35 (12)
1986	
8 Jul	6.62±0.21 (23)
22 Jul	5.79±0.24 (11)
5 Aug	6.26±0.32 (9)

Table 3. Number of fecund and barren female *Bosmina longirostris* (≥0.40-mm body length) at the offshore reference station. All animals were selected randomly from samples.

	Fecund	Barren
1985		
25 June	71	4
17 Jul	112	26
30 Jul	71	19
6 Aug	72	12
1986		
8 Jul	26	8
22 Jul	36	7
5 Aug	33	12

Table 4. Number of copepods examined and total prey found in specimens from the offshore reference station, 1985. Number of animals selected from certain dates reported as taxon: number (date). *Senecella*: 24 (18 July); *Limnocalanus*: 45 (25–26 June), 66 (17–18 July), 29 (30 July), 21 (6 August); cyclopoids: 32 (25 June), 41 (17–18 July), 11 (30 July), 13 (6 August); *Epischura*: 20 (17 July), 26 (30 July), 14 (6 August).

Predator	No. examined	Prey type					
		Daphnia	*Bosmina*	Copepod	Clad/cope	Rotifer*	*Peridinium*
Senecella	24	0	0	0	0	3	0
Limnocalanus	161	0	1	3	5	3	1
Cyclopoids†	97	1	1	0	3	2	0
Epischura	60	1	0	3	0	21	78

* Includes *Keratella cochlearis* (Gosse), *Kellicottia longispina* (Kellicott), *Conochilus*, and unidentifiable taxa.
† Includes *Diacyclops bicuspidatus thomasi* and *Acanthocyclops vernalis* (Fischer).

sumed a variety of food items and, based on frequency of presence in the guts, *Peridinium* and rotifers, mainly *Keratella cochlearis*, were most common. Algal taxa other than *Peridinium* are excluded from Table 4. *Limnocalanus* and *Senecella* guts were usually filled with diatoms, mainly *Melosira* and *Tabellaria*. Cyclopoid and *Epischura* guts occasionally contained algae.

Leptodora ate Cladocera, copepods, and rotifers (Table 5). Two pairs of incudate trophi, probably assignable to *Asplanchna*, and one pair of malleate trophi are not included in Table 5. *Conochilus* trophi were not assignable to species, but *Conochilus unicornis* Rousselet was the only member of that genus found in sample collections from Lake Michigan during the years relevant here. For all dates, most of the *Leptodora* guts examined contained observable prey remains (Table 5).

Daphnia and copepod remains were found more frequently in larger *Leptodora* while *Conochilus* was found exclusively in *Leptodora* <8 mm long (Fig. 3). The rotifers excluded from Table 5 were found in *Lep-*

todora <6 mm long. We found *Bosmina* more consistently than other prey among a wider range of *Leptodora* sizes. Larger *Leptodora* consumed larger Cladocera (Fig. 4). We found few *Daphnia* >1.0 mm in *Leptodora*.

Given 1985 densities for *Leptodora* and *Bosmina* DRs, we estimated that predation rates of 6 *Bosmina* $(Leptodora)^{-1} d^{-1}$ for the period 25 June–17 July and 2 *Bosmina* $(Leptodora)^{-1} d^{-1}$ for 17–30 July would account for 100% of *Bosmina* mortality between dates.

Mysis consumed a variety of prey taxa including *Bosmina* (Table 6). Given 1985 *Mysis* densities (Lehman et al. 1990) and *Bosmina* DRs, we calculated that each *Mysis* on average would have to consume 19 *Bosmina* d^{-1} for the period 25 June–17 July and 18 *Bosmina* d^{-1} for the period 17–30 July to account for 100% of *Bosmina* mortality between dates.

Discussion

Bosmina *in Lake Michigan* — The decline in density of *Bosmina* in offshore Lake Michigan in 1985 and 1986 appears to be

Table 5. Number of *Leptodora kindtii* examined (number with observable prey remains) and total identifiable prey found in specimens from the offshore reference station.

	No. examined	Prey type					
		*Daphnia**	*Bosmina*	Cladocera	Copepod	Clad/cope	*Conochilus*
1985							
16–18 Jul	193(137)	33	42	2	19	33	69
30 Jul	80(60)	25	5	0	8	8	18
6–7 Aug	54(48)	21	1	0	5	7	1
20 Aug	35(23)	9	0	0	1	6	0
1986							
8 Jul	106(69)	30	7	0	10	5	103

* Includes *D. galeata mendotae* Birge, *D. pulicaria*, and *D. retrocurva* Forbes.
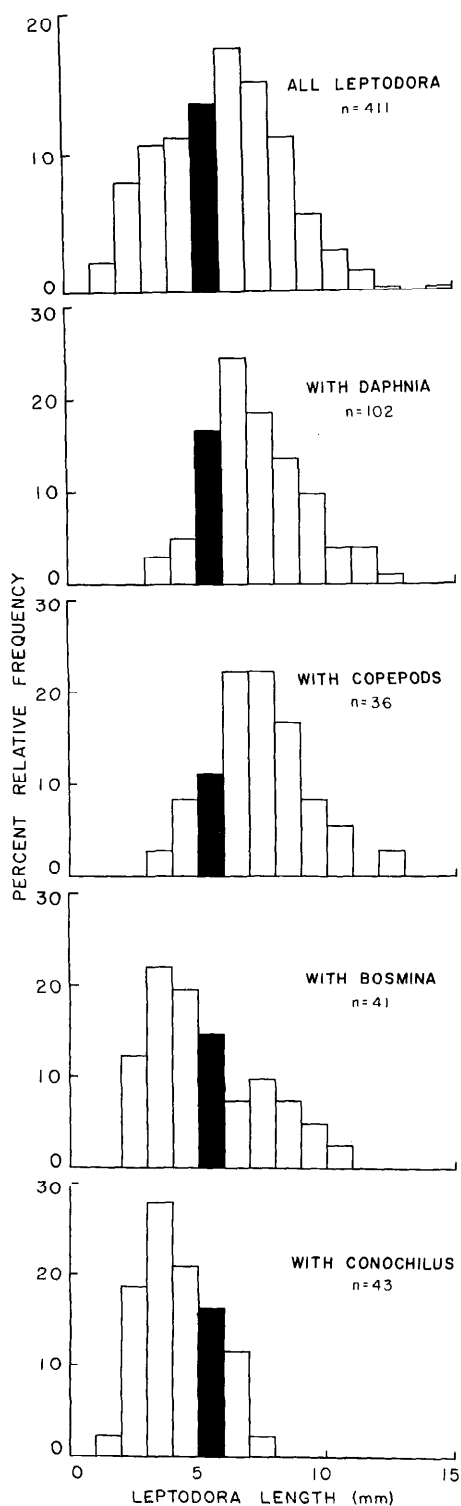
the result of food limitation and predatory mortality, the latter imposed mainly by *Leptodora*.

In 1985, *Bosmina* matured at a larger body length in June than during July and August (Fig. 2). In addition, *Bosmina* in June carried, on average, significantly more eggs per clutch than animals in July or August for 3 of 6 body-length classes (Table 1). During July and August, average clutch size did not differ significantly. The ratio of fecund to barren females ≥ 0.40 mm long was also significantly larger in June than in July or August, but this ratio was not different among July and August dates (Table 3). These data suggest that *Bosmina* experienced food limitation between June and the first July date. During July and August, *Bosmina* showed no further signs of food limitation, except for the presence of some smaller mature individuals in the population.

In 1986, there was no pattern in size at maturity to indicate that *Bosmina* was food limited (Fig. 2). In addition, average clutch size did not decrease significantly for any body-length class, but a trend of decreasing clutch size was evident among most body-length classes (Table 1). This trend suggests that food limitation may have been a factor in the 1986 decline of *Bosmina*. The ratio of fecund to barren females was not significantly different among dates, however (Table 3). For neither 1985 nor 1986 did average egg volume change significantly (Table 2). Clutch size alone was probably an adequate representation of reproductive investment on each date.

There is other indirect evidence that resource conditions declined for *Bosmina* both years. Chl *a* concentration, a measure of algal biomass, decreased from the surface to 20 m at the reference station from June through July in 1985 and 1986 (Lehman

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Fig. 3. Size-frequency distribution for all *Leptodora kindtii* examined from the offshore reference station, 1985 and 1986, and distributions for those animals whose guts contained various prey items. The 5–6-mm cell is blackened throughout.
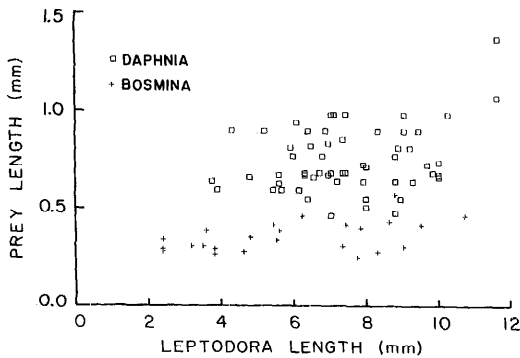
Fig. 4. Cladoceran prey eaten by *Leptodora kindtii* from the offshore reference station, 1985 and 1986. *Daphnia* includes *D. galeata mendotae*, *D. pulicaria*, and *D. retrocurva*.

1988). This decline is consistent with our evidence for food limitation.

Gut content analyses revealed that two copepod taxa, *Limnocalanus* and cyclopoids, were eating *Bosmina* in 1985 (Table 4). Reports suggest, however, that these copepods are not effective predators on *Bosmina*. Nero and Sprules (1986) found very low clearance rates for *Limnocalanus* on *Bosmina* and attributed them in part to *Bosmina*'s defensive mucro. Kerfoot (1977) showed under laboratory conditions that the attack success rate of cyclopoids on *Bosmina* is low. Direct evidence for predation by *Epischura* on *Bosmina* was not detected in our samples, even though it is a predator on *Bosmina*.

Leptodora guts contained substantial evidence for predation on *Bosmina* (Table 5). Calculated predation rates of 2–6 *Bosmina* $(Leptodora)^{-1} d^{-1}$ were necessary to account for 100% of *Bosmina* mortality from 25 June–30 July 1985. Mordukhai-Boltovskaia (1958) reported that a *Leptodora* 3 mm long can eat 11–12 *Polyphemus pedic-*

ulus Linnaeus d^{-1} and that individuals 5–6 mm long can eat 30 d^{-1}. Browman et al. (1989) reported that a *Leptodora* can eat 14 *Daphnia pulex* Leydig d^{-1}. *Leptodora* could probably account for 100% of 1985 *Bosmina* mortality.

Mysis was also consuming *Bosmina* (Table 6). Calculated predation rates of 18–19 *Bosmina* $(Mysis)^{-1} d^{-1}$ were necessary to account for 100% of observed mortality. Bowers and Vanderploeg (1982) reported in situ predation rates for Lake Michigan *Mysis*, held in enclosures, of about 30 *Bosmina* $(Mysis)^{-1} d^{-1}$, which could account for all of the requisite *Bosmina* mortality observed here. The enclosure experiments, however, do not mimic temporal patterns of interaction between *Mysis* and *Bosmina* in situ. *Bosmina* is susceptible to predation by *Mysis* for only a fraction of each day. *Bosmina* remains almost exclusively in the metalimnion and epilimnion, while *Mysis* ascends to the metalimnion only at night (Lehman et al. 1990). Beeton and Bowers (1982) reported data from sample collections and echo location that suggest Lake Michigan *Mysis* spends only 7–8 h d^{-1} in the metalimnion and epilimnion during the summer months relevant here. *Mysis* predation rates would have to be about 2× rates reported by Bowers and Vanderploeg (1982) to account for 100% of observed *Bosmina* mortality. *Mysis*, moreover, was as abundant in 1987 and 1988 as in 1985 and 1986 (Lehman et al. 1990).

In 1986, *Bosmina* demographic trends were similar to 1985 patterns (Fig. 1). All predators examined for gut contents from 1985 were present in comparable densities in 1986. In addition, gut analyses revealed that *Leptodora* collected on 8 July 1986 was eating *Bosmina* (Table 5). These data sug-

Table 6. Number of *Mysis relicta* examined and total prey found in specimens from the offshore reference station.

1985	Prey type							
	Mysis	*Daphnia**	*Bosmina*	Cladocera	*Leptodora*	Copepod	Rotifer†	*Peridinium*
26 Jun	10	9	10	0	0	12	8	0
18 Jul	9	10	18	10	1	24	81	17
31 Jul	9	14	5	4	0	49	15	7

* Includes *D. galeata mendotae*, *D. pulicaria*, and *D. retrocurva*.
† Includes *Kellicottia longispina*, *Keratella cochlearis*, and unidentifiable taxa.

gest that predation by *Leptodora* was also a major source of mortality for *Bosmina* in 1986.

Zooplankton population dynamics in 1987 and 1988 support the notion that *Leptodora* was responsible for much of the *Bosmina* mortality in 1985 and 1986. In 1987 and 1988, *Leptodora* was present in late June but was undetectable in July and August. Its decline was concurrent with the establishment of *Bythotrephes* in Lake Michigan (Lehman 1988). *Leptodora* failed to coexist with *Bythotrephes* when the latter reached high abundance. Berg and Garton (1988) also reported a negative correlation between seasonal *Bythotrephes* and *Leptodora* densities in western Lake Erie. The mechanism for displacement of *Leptodora* is still under study; the main reason may be direct mortality by *Bythotrephes* or competition for food, particularly for small *Daphnia*. Zooplankton predators other than *Leptodora* remained in 1987 and 1988; they reached densities at least as high as in 1985 and 1986 (Fig. 1). *Bosmina* densities, in the absence of *Leptodora* in 1987 and 1988, were higher in August and September than in 1985 and 1986. Although other predators were probably eating *Bosmina* in 1987 and 1988, their combined effect was apparently not great enough to prevent continued population growth in those years. By comparison, we suggest that additional mortality imposed by *Leptodora* in 1985 and 1986 was a key factor in the decline in *Bosmina* densities in both years.

Previous studies indicate that mortality imposed by *Leptodora* can reduce the densities of cladoceran populations. Field studies have illustrated the impact of *Leptodora* on populations of *Daphnia galeata mendotae* in Baseline Lake, Michigan (Hall 1964), *Daphnia schoedleri* Sars in Canyon Ferry Reservoir, Montana (Wright 1965), and *Daphnia hyalina* Leydig in Lago Maggiore, Italy (De Bernardi 1974). Prophet (1982) reported that decreased densities of *Bosmina* in Reading Lake, Kansas, were associated with increased densities of *Leptodora*. Our data complement these reports.

We conclude that predation on populations themselves constrained by seasonal food limitation was responsible for the de-clines in *Bosmina* densities in offshore Lake Michigan in 1985 and 1986. In 1985, it appears that food limitation was more severe from June to July. Predation, mainly by *Leptodora*, appears to be most responsible for *Bosmina* mortality during July and August. *Mysis* was probably also an important predator during that time. There is some evidence that *Bosmina* was also food limited in 1986 during the dates reported here. Changes in the zooplankton community in 1987 and 1988 suggest that *Leptodora* predation was perhaps the key factor in 1985 and 1986.

Wells (1970) attributed depressed densities of large crustacean zooplankton in Lake Michigan in 1966 to selective planktivory by alewife. Among the taxa that had declined was a suite of invertebrate predators including *Leptodora*, *Epischura*, and *Limnocalanus*. Associated with that event was an increase in *Bosmina* densities during the same year. Given the results of this report, we suggest, by analogy, that reduced predation by *Leptodora* was a pivotal factor in the success of *Bosmina* during that period as well.

Predatory behavior by Leptodora—Suggestions exist that *Leptodora* ingests primarily fluid from prey (Mordukhai-Boltovskaia 1958; Cummins et al. 1969). However, like Edmondson and Litt (1987), we found entire copepods in the guts of *Leptodora*. Furthermore, most *Leptodora* guts examined here contained hard parts from prey (Table 5). Gut analyses reported by Edmondson and Litt (1987) and results here confirm that *Leptodora* in the field feeds on Cladocera, copepods, and rotifers (Table 5).

By number, *Conochilus* represented an important item in *Leptodora*'s diet (Table 5). Correlative data suggest that *Leptodora* may be a primary predator of *Conochilus* in Lake Michigan. In 1987 and 1988, *Conochilus* increased in abundance over 1985 and 1986 densities (Sandgren and Lehman 1990). This shift is also correlated with the invasion of *Bythotrephes* and the decline of *Leptodora*. Thus, the loss of a key predator, *Leptodora*, may have permitted increased densities of *Conochilus*. Edmondson and Litt (1987) suggested that *Leptodora* may control population dynamics of *Conochilus* spp.

in Lake Washington, Seattle. Their conclusion is also based on gut analyses and correlations of annual predator-prey densities.

The size-frequency distributions of *Leptodora* containing *Daphnia*, copepods, *Bosmina*, and *Conochilus* suggest that juveniles and adults ate different prey (Fig. 3). Juveniles (<5 mm long: Andrews 1948) ate mainly smaller prey—*Bosmina* and *Conochilus*—while adults ate a broader size range of prey that included mainly *Bosmina*, copepods, and *Daphnia*. The size relationships of predators and prey also suggest that larger prey are consumed by larger *Leptodora* (Fig. 4). Because juvenile and adult *Leptodora* were collected from the same depth strata, it is doubtful that the life stages encountered fundamentally different prey assemblages. We suggest that this empirical shift in diet may be a function of the larger body size and length of adult feeding appendages. It is not apparent that larger individuals can swim faster (Browman et al. 1989).

Our data support previous observations that invertebrate predators are size selective in their prey choice (Dodson 1974) and that large species of Cladocera attain sizes that reduce or eliminate their risk of predation by invertebrate predators, but small Cladocera never outgrow a vulnerable size (Lynch 1980). *Leptodora* rarely ate *Daphnia* >1.0 mm in total length (Fig. 4). Furthermore, *Leptodora* <5 mm long rarely ate *Daphnia* (Fig. 3). In contrast, *Leptodora* ate large *Bosmina*, >0.5 mm in body length (Fig. 4). *Bosmina* was also vulnerable to juvenile *Leptodora*—some <3 mm long. In general, it appears that larger *Leptodora* can consume larger prey; *Daphnia* is less vulnerable to *Leptodora* after growing to >1.0 mm; and smaller prey taxa, such as *Bosmina*, are vulnerable to *Leptodora* at all sizes.

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