

Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan

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Abstract

Several developments in the offshore plankton community accompanied the invasion of *Bythotrephes cederstroemi* Schoedler (Crustacea: Cladocera: Cercopagidae) into Lake Michigan. A native predatory cladoceran, *Leptodora kindtii*, became significantly reduced in abundance and biomass in the presence of *Bythotrephes*. The offshore *Daphnia* assemblage, which had consisted of three species before the arrival of *Bythotrephes*, was reduced to dominance by only *D. galeata mendotae*. Abundances of *Daphnia* species exhibited reciprocal relationships to *Bythotrephes* abundance in both space and time. The surviving *Daphnia* populations offshore exhibited altered daytime vertical distributions which reduced spatial overlap with the invading predator. Model calculations indicate that energetic requirements by *Bythotrephes* equaled or exceeded replacement production by *Daphnia* during midsummer of the first years of species invasion. Decreases in midsummer *Daphnia* biomass did not produce significant increases in midsummer algal biomass, measured as particulate chlorophyll *a*. Instead, physical mixing depth and epilimnetic temperature, a correlate of the intensity of density stratification, exhibited the strongest statistical relationship to Chl *a* over the years studied.

Bythotrephes cederstroemi Schoedler (syn. *B. cederstroemii*; Crustacea: Cladocera) is a zooplanktivore first collected in North America from Lake Huron in December 1984 (N. Andresen, cited by Bur et al. 1986). Specimens were collected subsequently from Lakes Erie and Ontario in 1985 (Bur et al. 1986; Lange and Cap 1986), from Lake Michigan in 1986 (Lehman 1987), and from Lake Superior in 1987 (Cullis and Johnson 1988). The species has its native distribution in the Palearctic, and its arrival in North America has fostered speculation about its mode of transport and date of introduction (Bur et al. 1986; Lange

and Cap 1986; Evans 1988; Keilty 1988). In Lake Michigan, the rise of *Bythotrephes* was associated with changes in the resident zooplankton community that have been attributed to intense invertebrate planktivory (Lehman 1988, 1991).

Species invasion of the Great Lakes constitutes a biomanipulation on a vast scale. As such, it offers the opportunity to explore changing relationships among resident species and to discover patterns of interaction which may have remained cryptic otherwise. Of particular interest is the relationship between herbivory and algal biomass in Lake Michigan. Several investigators have noted that phytoplankton growth and grazing loss are in approximate balance in summer and that algal biomass might be controlled by herbivory (Scavia et al. 1986, 1988; Dorazio et al. 1987; Scavia and Fahnenstiel 1987). Changes of the grazer community ecosystem-wide presented an opportunity to investigate this premise.

Methods

Time-series data presented here were collected at a 100-m reference station at 43°N, 86°40.0'W, 36 km offshore from Grand Haven, Michigan. Sampling frequency varied from 1 to 3 weeks from May to September. Additional stations from 43–45°N were visited less frequently in order to provide information about spatial distributions.

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Acknowledgments

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Water temperatures were measured by mechanical (1985–1986) or electronic (1987–1988) bathythermograph or by CTD (1989–1990). Bathythermograph (BT) temperatures were calibrated against a Whitney TC-5C thermistor, which was itself calibrated against a NBS certified mercury thermometer. Temperatures in 1983 were measured with the thermistor directly. Mechanical BT traces were read at 5-m intervals to a precision of 0.1°C. Electronic BT data were recorded at 0.1-m intervals to a precision of 0.01°C; data at meter intervals were used in subsequent calculations. CTD (Seabird) temperature records were of high precision (0.001°C); raw data files were interpolated to produce values at meter intervals with software provided by the manufacturer. Specific volume anomalies and in situ densities were calculated from the international equation of state for seawater (Fofonoff and Millard 1983), using $S = 0.13\text{‰}$ as the salinity of Lake Michigan water. Discrete densities were fit by cubic spline and stability ($d\rho/\rho dz$) was calculated from first derivatives at 1-m intervals.

For comparison among dates and years, diel mixing depth was defined as the shallowest depth for which $d\rho/\rho dz > 0.0001 \text{ m}^{-1}$, which corresponded well by visual inspection with the isopycnal surface layer sustained against diel convective mixing.

Particulate chlorophyll was measured from Niskin casts. Samples were filtered shipboard (GF/F) and Chl *a* was determined fluorometrically after grinding the filters in 90% vol/vol acetone. Pheopigment contribution to fluorescence was estimated by acidification, and Chl *a* from *Anacyctis* (Sigma), verified spectrophotometrically for concentration, was used as a standard. Usual sampling depths were 2, 10, 15, 20, 30, and 60 m from surface and 10 m above bottom. Mean concentrations over depth strata were calculated by trapezoidal integration.

Zooplankton were collected by submersible pump (1983–1986: Dorazio et al. 1987) and with 1-m-diameter Puget Sound closing nets (1985–1990: Lehman 1987) of 130- μm aperture deployed while the ship lay at anchor. The entire water column, from near bottom to surface, was sampled at each station except in 1983 when only depths to 40 m were sampled. Abundance estimates are typically based on

triplicate nighttime samples which are combined mechanically before enumeration. On most dates these counts were supplemented with additional vertical stage series collected both day and night. In 1985 and 1986, samples were collected throughout diel series (4–6 vertical series per date). Animals were preserved in sucrose-Formalin (Haney and Hall 1973). Collections were split, if necessary, with a Folsom plankton splitter, and then subsampled by widebore injection pipette for enumerations. At least 100 specimens of each taxon were counted from each sample, unless low densities precluded doing so.

Bythotrephes was removed from each collection for further study. Age-specific morphological stages were determined by the number of paired barbs present at the base of the spine of each specimen (Ischreyt 1930, 1934). Adult females were classified by their reproductive conditions: barren, fecund parthenogenic, or fecund gametogenic. Clutch sizes were recorded for fecund specimens.

For biomass estimates of copepods and herbivorous Cladocera, lengths were measured for at least 30 specimens of each taxon from each sample and dry mass was estimated with the same equations used by Dorazio et al. (1987). For *Bythotrephes*, the total wet mass of individuals removed from the quantitative samples was measured directly and an empirically determined dry: wet mass ratio of 0.12 used. Dry masses of individual life stages were determined from specimens picked individually from live collections, frozen on Teflon disks over Dry Ice, and then freeze-dried. Females with parthenogenic embryos in the advanced black-eye stage were isolated in filtered lake water until neonates were released. Masses of neonates, adult females, and exoskeletal molts were measured on freeze-dried material. For *Leptodora*, the average figure of 80 μg individual⁻¹ was used based on length-weight regression for freeze-dried animals ($\mu\text{g DW} = 0.479 \text{ mm}^{2.408}$, $r^2 = 0.93$, $n = 67$) and measured size frequencies of *Leptodora* in Lake Michigan (Branstrator and Lehman 1991).

Respiration rates were measured by Winkler titration and converted to carbon equivalents with $\text{RQ} = 1 \text{ mol CO}_2 (\text{mol O}_2)^{-1}$. Individuals were isolated from net collections and after acclimatization at 16°C for at least 6 h, they were incubated individually in 10-ml volu-

metric flasks. After 4–8.5 h, the entire flask contents were fixed and titrated by microburette with 0.019 N sodium thiosulfate. Because the incubated specimens were destroyed by chemical fixation, treatments were by instar, and mean instar weights were determined from weights of freeze-dried proxy specimens. Control incubations of filtered lake water accompanied all treatments.

Birth rates for *Daphnia* species were estimated from fecundity data and temperatures. For each species, relative frequencies of eggs by vertical depth stratum (f_z) were estimated from sample counts, and egg development rates for each stratum ($1/D_z$, d^{-1}) were estimated from stratum mean temperatures by the equation of Pastorok (1978) and Edmondson and Litt (1982). Because stations were sampled both day and night in order to record diel vertical distributions, individual estimates of $\Sigma f_z/D_z$ were averaged to obtain the mean daily rate of egg development for the entire water column. Mean development rates were multiplied by the mean ratio of eggs m^{-2} to *Daphnia* m^{-2} in order to obtain the mean finite birth rate, B . Instantaneous birth rates, b (d^{-1}), were estimated with the formula of Paloheimo (1974). Temperature-dependent postembryonic development rates of juvenile *Daphnia* were calculated by the formula of Geller (1985: table 1).

Spatial overlaps of invertebrate predators with potential prey were estimated according to Schoener (1970). Population mean depths and mean temperatures were calculated by summing the products of relative frequencies of abundance (by stratum) with either stratum mean depth or stratum mean temperature. SYSTAT version 5.0 (Wilkinson 1990) was used for statistical analyses.

Results

Temporal changes in Lake Michigan Cladocera—The typical seasonal pattern of biomass for herbivorous Cladocera parallels the onset of thermal stratification and epilimnetic warming. Cladoceran biomass plotted in Fig. 1 is positively correlated with epilimnion temperature ($R = 0.448$, $P = 0.002$, $n = 45$) over all years, but important differences exist among years. The offshore *Daphnia* community has been dominated by *D. pulicaria*, *D. galeata mendotae*, and *D. retrocurva* in 1983, 1985,

and 1986 before the arrival of *Bythotrephes* (Fig. 1). After a striking episode of depressed biomass during 1987, *D. galeata mendotae* has dominated the herbivore community, particularly in late summer. The changes in the *Daphnia* species complex are coincident with changes in the species composition of predatory Cladocera (Fig. 2). *Leptodora kindti* declined after the arrival of *Bythotrephes* in late summer 1986 and has not subsequently developed midsummer biomasses approaching those seen before the arrival of the new predator.

Zooplankton have been sampled at numerous stations in Lake Michigan and Green Bay (Fig. 3) from 1986 to 1989, as well as at the main reference station from 1985 to 1990. Marked reciprocal relationships exist between simultaneous abundances of *Bythotrephes* and those of *D. pulicaria*, *D. retrocurva*, and *Leptodora* (Fig. 4). A less striking inverse relationship exists between abundances of *Bythotrephes* and *D. galeata mendotae*, but no simple pattern is evident between abundances of *Bosmina* and *Bythotrephes*. Data are categorized by epilimnetic water temperatures at the sampling stations in Fig. 4 to illustrate that the reciprocal relationships do not result from differing seasonalities or temperature tolerances of the plotted species. The data are consistent with the reported gradient in *Bythotrephes* abundance from shallow inshore regions to the offshore (Lehman 1987). Low abundances of *Bythotrephes* nearshore are associated with refuge populations of *Leptodora* and *D. retrocurva*. Higher abundances of *Bythotrephes* offshore are associated with few *Leptodora* or *D. retrocurva*, and with dominance by *D. galeata mendotae* (Fig. 5).

Despite changes in the biomass and species composition of *Daphnia*, no significant changes occurred in midsummer total algal biomass, estimated from Chl *a*. Mean concentrations of Chl *a* in July and August from 0 to 20 m as well as from 0 to 30 m were not significantly different among years (one-way parametric AOV, $P > 0.2$ in both cases). Instead, there emerged strong statistical relationships between physical characteristics of the water column and algal biomass. Mean concentrations of Chl *a* from 0 to 20 m (Fig. 6) showed the strong effect of mixing depth, when isothermal and stratified periods were contrasted (Kruskal

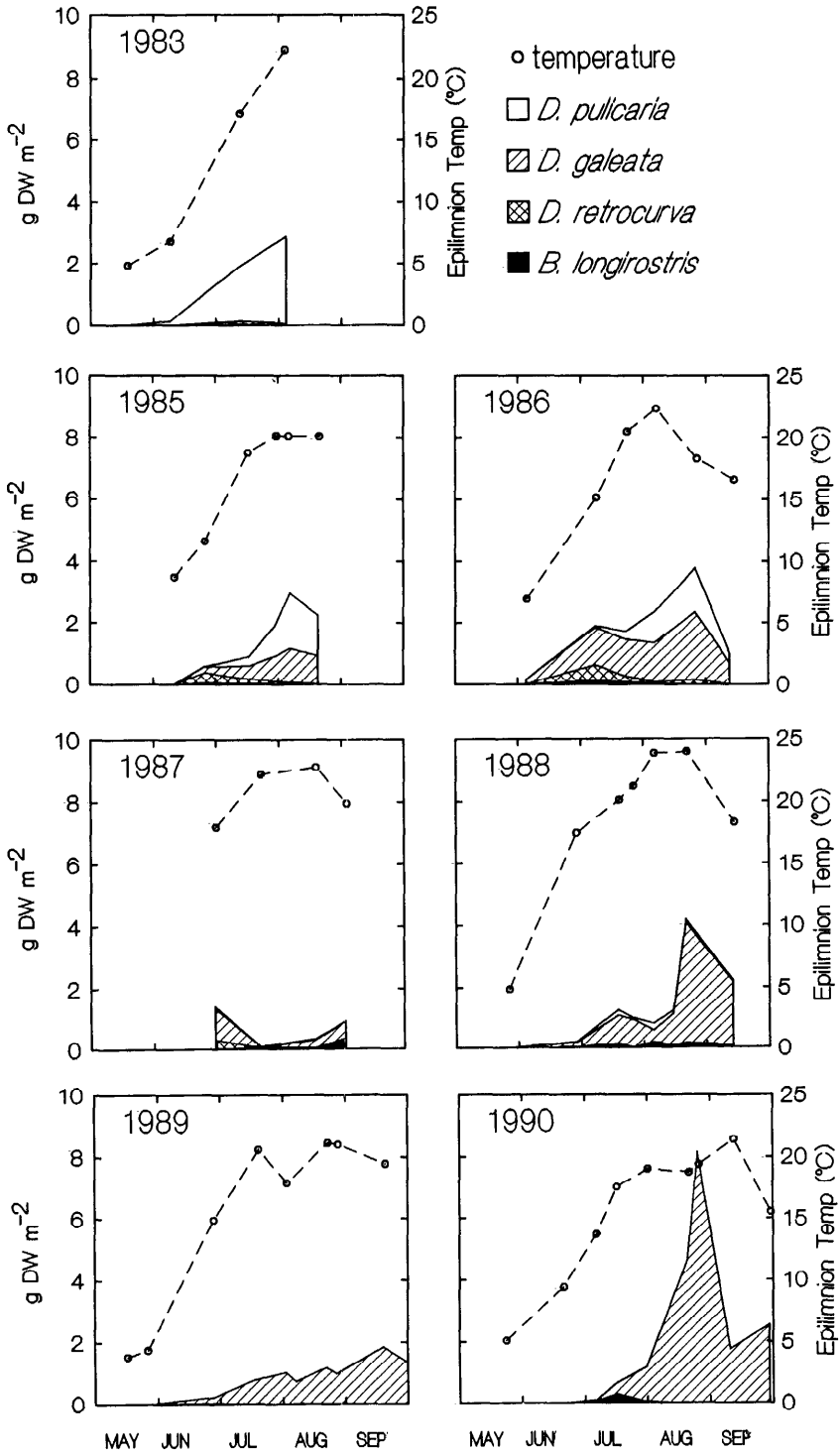


Fig. 1. Epilimnion temperature and biomass of herbivorous Cladocera at the offshore reference (100 m) station in Lake Michigan.

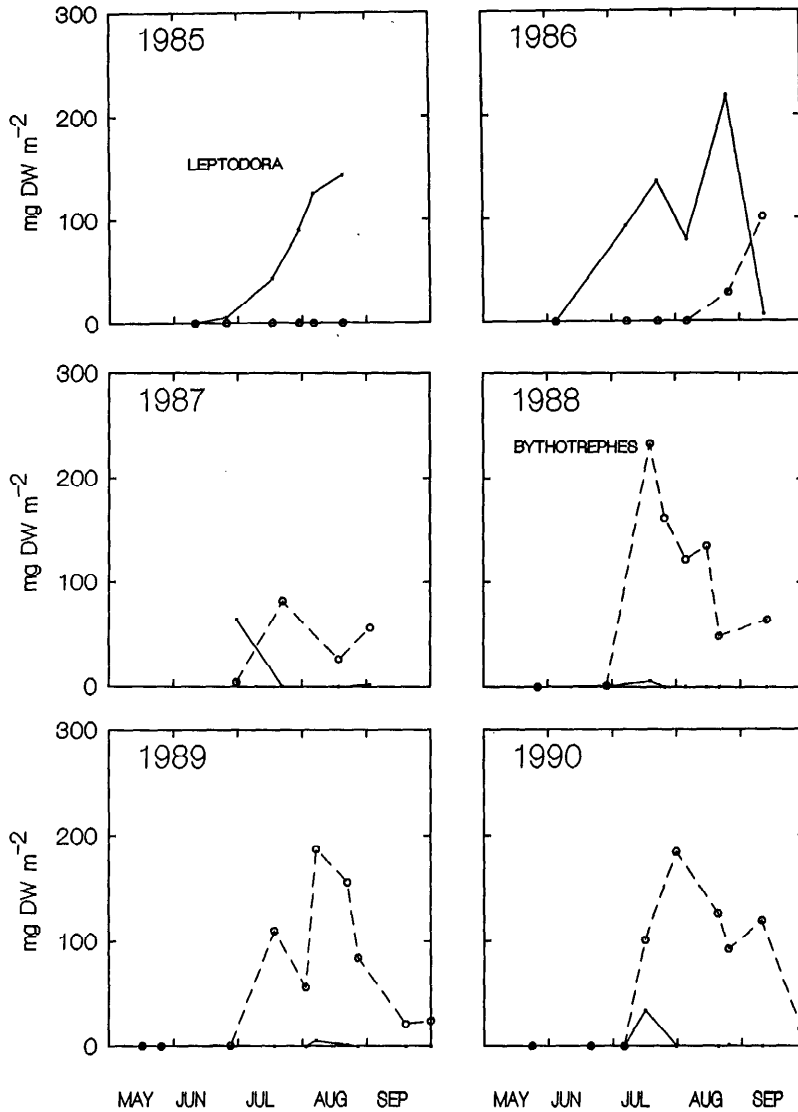


Fig. 2. Biomass of *Leptodora* and *Bythotrephes* at the main offshore reference station, 1985–1990.

Wallis one-way AOV, $P < 0.001$). Moreover, during thermally stratified conditions, over the measured range of mixed layer temperatures (T_{mix} : 13–25°C), mean Chl *a* concentrations were a strong nonlinear function of mixed layer temperature and hence of density stability:

$$\text{Chl} = c + a \exp(-b \cdot T) \quad (1)$$

where $c = 0.774$ (SE = 0.082), $a = 4.02$ (SE = 0.74), $b = 0.652$ (SE = 0.155), and T is T_{mix} –

13. The model accounts for 73% of the variance ($r^2 = 0.727$). Such a strong empirical relationship with water temperature could conceivably be the consequence of grazing effects because of the observed seasonal pattern of herbivore populations (Fig. 1). Statistical analyses, however, failed to support this notion. Stepwise regression of Chl *a* on cladoceran biomass (B) and on the product of biomass and epilimnion temperature ($B \cdot T_{\text{mix}}$) selected the model

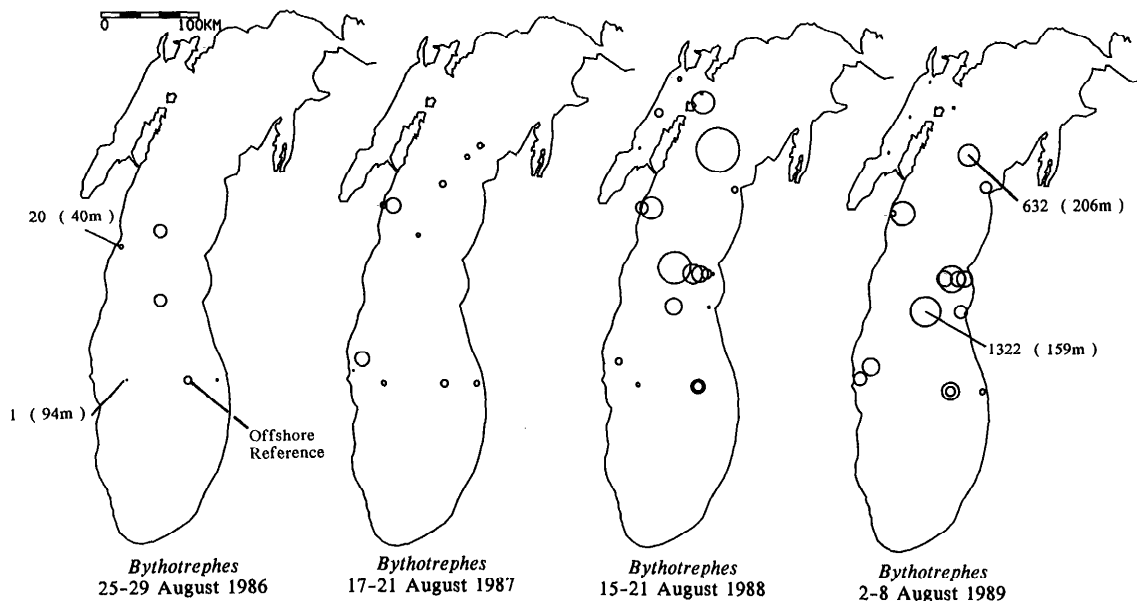


Fig. 3. Spatial distributions and abundances of *Bythotrephes* in Lake Michigan and Green Bay during August periods. Areas of circles are proportional to abundance (individuals m^{-2}).

$$\text{Chl} = 1.253 - 0.007 B \cdot T_{\text{mix}} \\ (r^2 = 0.152, n = 35, P = 0.02) \quad (2)$$

as being superior to one based on *B* alone, but the fitted relationship had poor statistical power and included large residual outliers. Fifty percent of the large residual variance ($r^2 = 0.500$) could be explained by the nonlinear term reported in Eq. 1. In contrast, neither *B* nor *B* *T* were significantly correlated with the residual errors resulting from application of Eq. 1 alone ($P > 0.2$).

Diel vertical distributions—*Bythotrephes* does not display strong diel vertical migration during midsummer (July–August) in offshore Lake Michigan, although diel migrations become a feature of the populations in fall (Fig. 7). Vertical distributions constructed from closing net collections during July and August from 1987 to 1990 show no significant differences between proportions of the population found in any stratum during day (0800–1900 hours) vs. night (2100–0300 hours) (t -test, $P > 0.15$). It is therefore possible to investigate whether the populations which declined in 1987 had occupied vertical distributions that would have caused them to overlap substantially with the new predator and whether the most successful species, *D. galeata mendotae*, demonstrated

any altered vertical distributions that reduced overlap.

Overlap between *Bythotrephes* and other taxa were calculated from vertical closing net collections in summer 1987, 1989, and 1990. For 1985 and 1986 the potential overlaps of *Bythotrephes* with the same taxa were estimated from the mean vertical distribution of *Bythotrephes* after invasion. The data were subjected to two-way AOV with invasion (before vs. after) and sampling time (day vs. night) as treatments. For some taxa, particularly *D. retrocurva* and *Leptodora*, postinvasion comparisons were hampered by the fact that populations were too rare to permit reliable abundance estimates on most dates. Summary overlap statistics are reported in Table 1. AOV detected strong effects ($P < 0.005$) correlated with the arrival of *Bythotrephes* on vertical distributions of *D. pulicaria*, *D. galeata mendotae*, and *Bosmina*. Diel effects were significant ($P < 0.05$) for all *Daphnia* species, and significant interactions between the invasion and diel distributions were found for *D. galeata mendotae* and *D. retrocurva*. Identical analyses for copepodids (C1–C6) of the taxa *Diaptomus* spp., *Cyclops* spp., and *Epischura lacustris* detected no significant effects or interactions ($\alpha = 0.05$).

The invasion of *Bythotrephes* into Lake Michigan was thus contemporaneous with altered vertical distributions of *Daphnia* species and *Bosmina*. In the case of *Bosmina*, the mean depth of the population changed both day and night ($P < 0.001$, two-way AOV) coincident with the arrival of *Bythotrephes* (Fig. 8) and with the loss of *Leptodora* (Fig. 2). In 1985 and 1986, *Bosmina* mean depths had been 39.1 m (SE = 2.0, $n = 25$), but the animals occupied more shallow strata (mean = 23.2, SE = 2.1, $n = 22$) in subsequent years. *Leptodora* is believed to have been the principal predator on *Bosmina* in offshore Lake Michigan (Branstrator and Lehman 1991).

The effects inferred for *Daphnia* species are the result of changes in the daytime vertical distribution of the taxa (Table 2). The proportions of the midsummer *D. galeata mendotae* population found in the 0–10-m stratum during the day declined from 22.9% before the population collapse of mid-July 1987 to 6.2% afterward (t -test, $P < 0.05$), and proportions from 0 to 20 m declined from 71.2 to 38.1% ($P < 0.05$). Distributions at night did not exhibit detectable changes ($P > 0.2$).

Birth rates for *Daphnia*—Estimated birth rates for *Daphnia* species at the main reference station are listed in Table 3. Birth rates did not decline during the episode of population collapse in 1987 and were not lower than birth rates observed for the *Daphnia* assemblage present during the same time in 1985, well before *Bythotrephes* appeared in Lake Michigan. Given the fact that reproductive rates were similar to those observed before the arrival of *Bythotrephes*, it seems necessary to conclude that *Daphnia* declined in 1987 because of significant incremental mortality.

Energetic requirements of *Bythotrephes* populations—Total consumption demands by *Bythotrephes* populations in situ (C : $\mu\text{g prey} \cdot \text{C m}^{-2} \text{ d}^{-1}$) can be defined as

$$C = c_B(\Delta w/D \cdot N + R \cdot B)/(IE \cdot AE) \quad (3)$$

where Δw is mass gain from neonate to fecund adult, D is duration of postembryonic development to primiparity, N is population abundance (individuals m^{-2}), R is the mass-specific rate of respiration (d^{-1}), B is population biomass ($\mu\text{g C m}^{-2}$), c_B is the ratio of C to dry mass, and IE and AE are ingestion efficiency and assimilation efficiency.

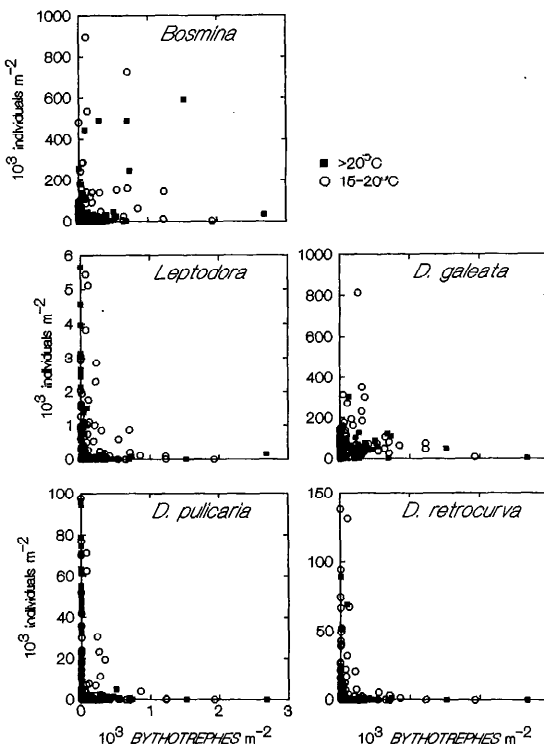


Fig. 4. Simultaneous abundances of *Bythotrephes* and other cladoceran species at sites throughout Lake Michigan and Green Bay from 1985 to 1990 ($n = 123$). Station depths vary from 20 to 200 m. Data are categorized by local epilimnion temperatures.

Neonatal weights of *Bythotrephes* collected in July 1991 were $105.3 \mu\text{g}$ (SE = 5.6, $n = 20$ clutches). Females bearing parthenogenic embryos in the black eye stage weighed $844.6 \mu\text{g}$ (SE = 30.7, $n = 26$). Thus, $\Delta w = 739.3 \mu\text{g DW}$. The mean temperature occupied by *Bythotrephes* populations during July and August 1987–1990, was 15.0°C (SE = 0.6, $n = 20$) during daytime, and 15.9°C (SE = 0.6, $n = 19$) at night. Yurista (1992) estimated that the duration of development (D) from neonate to primiparous adult is ~ 11 d at 15°C . IE , measured directly using radiolabeled prey is $\sim 50\%$ (unpubl. data). AE was assumed to be 80%, and c_B was measured to be 0.52 (Perkin-Elmer 2400 CHN). R , measured at 16°C , was 0.128 d^{-1} (SE = 0.016, $n = 9$) for first instar, 0.108 d^{-1} (SE = 0.008, $n = 10$) for second instar, and 0.096 d^{-1} (SE = 0.007, $n = 11$) for third (adult) instars. The mean value of $R = 0.11 \text{ d}^{-1}$ was used for calculations.

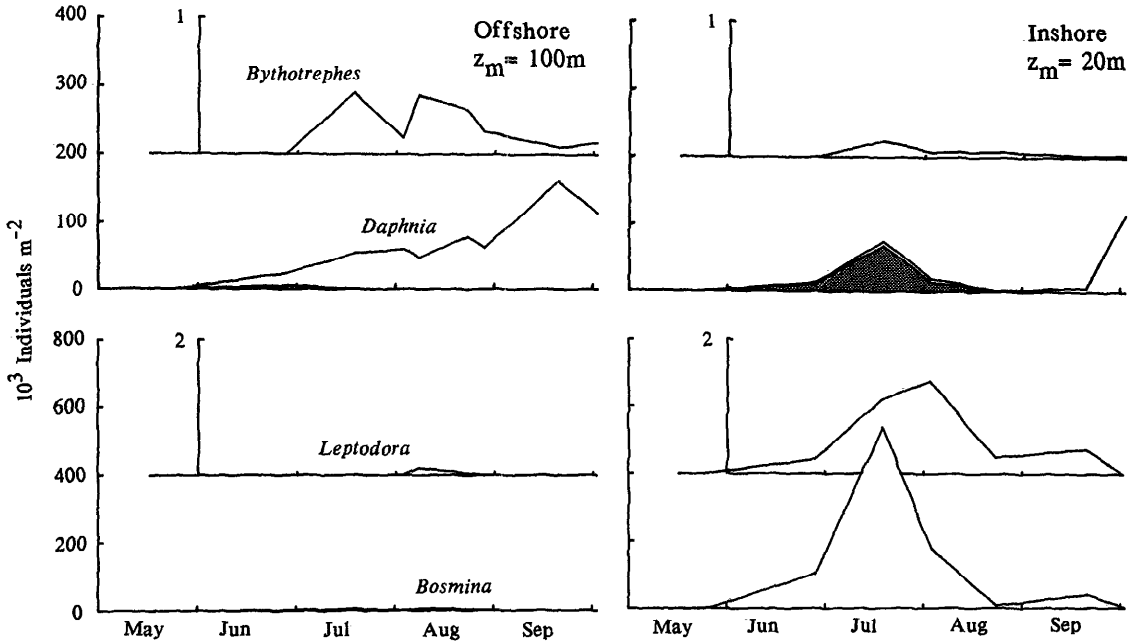


Fig. 5. Seasonal abundances of cladoceran species at inshore and offshore locations 30 km apart in Lake Michigan in summer 1989. Offshore station—43°N, 86°40.0'W; inshore station—43°N, 86°16.3'W. *Daphnia*: open—*D. galeata mendotae*; shaded—*D. retrocurva*.

Time-series solutions of Eq. 3 are graphed in Fig. 9 for 1987–1990. Also shown is net replacement production for herbivorous Cladocera (*Bosmina* + *Daphnia*), calculated by the “recruitment-time method” used by Geller

(1985) for *Daphnia* in Lake Constance. Egg and juvenile development times (d) were calculated from mean temperatures for day and night population distributions, and the reciprocal for their sum was used as turnover rate.

Table 1. Measured (1987–1990) and potential (inferred: 1985–1986) percent spatial overlaps with *Bythotrephes* in offshore Lake Michigan. Upper rows: mean, SE, and N by year and sampling time; lower rows: *F*-ratios and significance (asterisks: *—0.05; **—0.01) of effects and interactions. Dpul—*Daphnia pulicaria*; Dgm—*Daphnia galeata mendotae*; Dret—*Daphnia retrocurva*; Lepto—*Leptodora kindtii*.

	<i>Bosmina</i>	Dpul	Dgm	Dret	Lepto
1985–1986	26.6	67.5	48.0	45.8	64.7
(day)	5.5	4.9	5.9	3.9	6.2
	12	12	11	12	10
1985–1986	23.6	79.1	66.9	73.0	65.1
(night)	5.7	3.1	7.4	4.2	6.1
	10	10	10	10	9
1987–1990	47.9	36.7	26.9	24.9	57.2
(day)	7.3	6.1	8.0	11.4	7.9
	11	11	6	4	4
1987–1990	47.7	70.0	39.3	87.6	69.8
(night)	6.2	5.6	9.0	5.2	8.3
	14	14	8	4	7
Effect					
Year	13.0**	10.07**	14.23**	0.27	0.04
Time	0.06	4.16*	18.08**	56.66**	0.76
Year × time	0.05	0.18	4.23*	8.82**	0.66

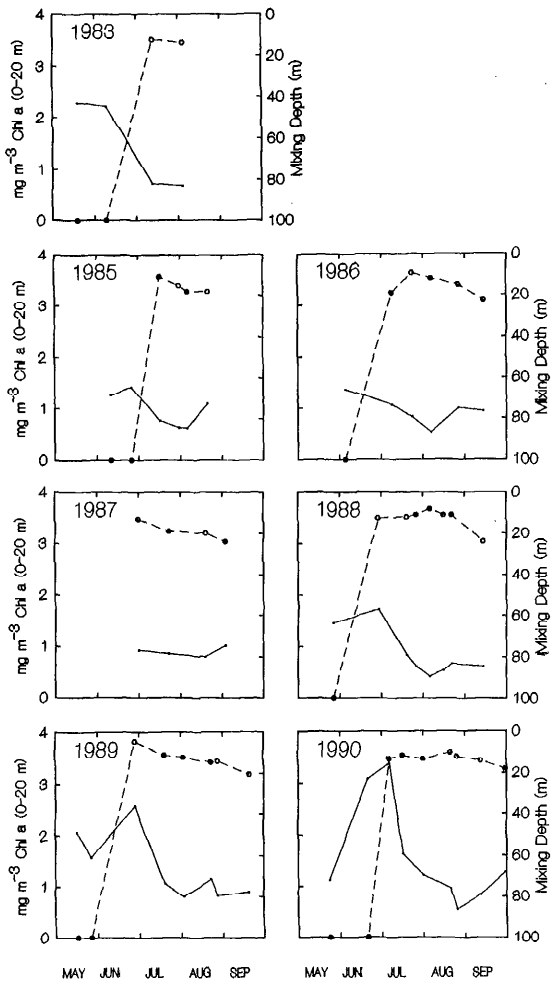


Fig. 6. Mean concentrations of Chl *a* (solid line) and depth of vertical mixing (broken line), offshore reference station.

Rates at day and night mean temperatures were averaged. Consumption demand by *Bythotrephes* equals or exceeds daily cladoceran replacement production (biomass \times turnover rate) in early summer of each year, but when predator populations subsequently decline (Fig. 2), demand decreases and the herbivores increase. Rigler and Downing (1984) suggested that replacement production calculated from population turnover rate may underestimate biomass replacement by $\sim 50\%$. If so, consumption demand and *Daphnia* production would be in approximate balance in midsummer.

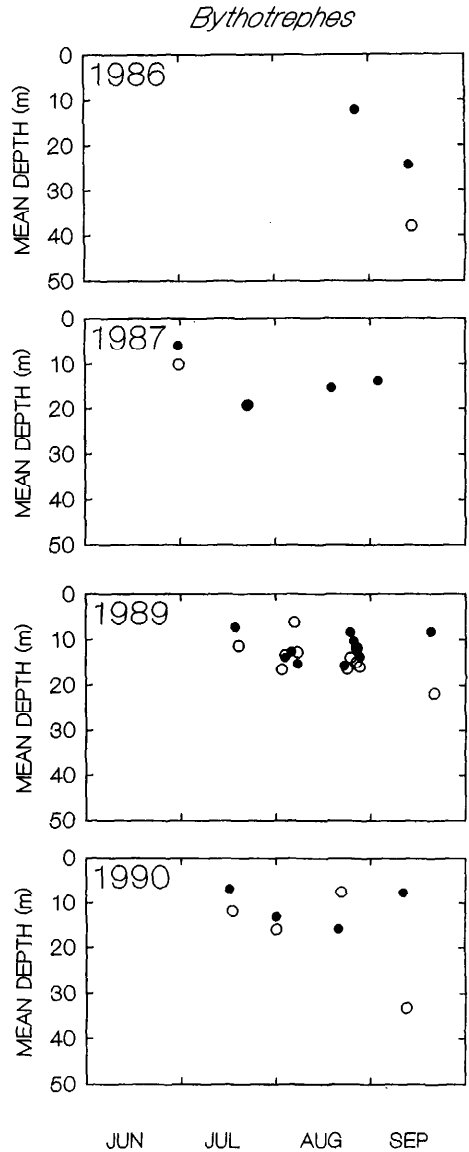


Fig. 7. Mean depths of *Bythotrephes* populations sampled by vertical closing net. Sample intervals were 0–10, 10–20, 20–30, 30–40, and 40–90 m. Day—O; night—●.

Discussion

Bioenergetic calculations suggest that consumptive demands of *Bythotrephes* populations in Lake Michigan equal or exceed replacement production of *Daphnia* populations in midsummer. Moreover, it appears that at times alternative prey might be necessary to satisfy the physiological requirements of the predator population.

Table 2. Proportions of *Daphnia galeata mendotae* population offshore occupying either the upper 10 m or the upper 20 m before and after the mid-July 1987 collapse of *Daphnia* populations and establishment of *Bythotrephes*. Values are mean (SD) and *n*.

	Day		Night	
	Mean (SD)	<i>n</i>	Mean (SD)	<i>n</i>
Before Jul 87				
0–10 m	0.229(0.215)	15	0.598(0.225)	11
0–20 m	0.712(0.194)	15	0.932(0.126)	11
After Jul 87				
0–10 m	0.062(0.061)	9	0.582(0.339)	9
0–20 m	0.381(0.380)	9	0.800(0.316)	11

The predatory potential of *Bythotrephes* may be larger than many workers have previously suspected. The animal has been reported to feed in the laboratory on various small Crustacea, including nauplii, copepodids, and small Cladocera such as *Bosmina* and *Ceriodaphnia* (Monakov 1972). Some confusion has probably developed from literature accounts that do not differentiate between the two Palearctic species *B. cederstroemi* and *B. longimanus*. *B. cederstroemi* is the larger of the two (Ischreyt 1930, 1934), and is the only species present in Lake Michigan where specimens occasionally attain individual dry weights > 1 mg. This species is known by direct observations to be a voracious predator on even large adult *Daphnia*.

The striking differences between spatial overlaps in day and at night between *Daphnia* and *Bythotrephes* (Table 1) suggest that vision may play a role in prey capture by *Bythotrephes*, as it does in *Polyphemus* (Young and Taylor 1988), a morphologically similar predatory cladoceran.

The fact that neither cladoceran biomass nor its interaction with temperature can account for more than a trivial amount of variation in algal biomass measured as Chl *a* confirms an earlier conclusion drawn when phytoplankton failed to increase in response to the decline of *Daphnia* in 1987 (Lehman 1988). Instead, the major environmental feature contributing to the seasonal declines of algae in Lake Michigan is the onset of thermal stratification (Fig. 6). Physical factors influence the vertical transport of nutrients and most likely contribute to the development of nutrient limitations measured through bioassays both before and after

Table 3. Birth rates for *Daphnia* at the main offshore reference station in 1985 (before *Bythotrephes*) and in 1987. Finite birth rate—*B*; instantaneous birth rate—*b*.

		<i>B</i> (d ⁻¹)	<i>b</i> (d ⁻¹)
1985			
10–11 Jun	<i>Daphnia</i> spp.	0.061	0.045
25–26 Jun	<i>Daphnia</i> spp.	0.121	0.089
16–18 Jul	<i>Daphnia</i> spp.	0.038	0.035
30–31 Jul	<i>Daphnia</i> spp.	0.061	0.051
1987			
1 Jul	<i>D. galeata</i>	0.135	0.109
	<i>D. pulicaria</i>	0.083	0.071
	<i>D. retrocurva</i>	0.187	0.141
22 Jul	<i>D. galeata</i>	0.143	0.093
	<i>D. pulicaria</i>	0.109	0.084
	<i>D. retrocurva</i>	NA*	NA*
18 Aug	<i>D. galeata</i> †	0.230	0.162
	<i>D. pulicaria</i> †	0.095	0.067

* Insufficient sample size for estimation.

† Based on vertical distribution at 0100 hours only.

biomanipulation by species invasion (Lehman and Sandgren 1990). The very strong influence of physical factors on the phytoplankton of Lake Michigan thus makes the lake a poor candidate for management strategies based on food-web controls.

Planktivorous fish are known to play an important role in the Lake Michigan ecosystem. Both alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) have been implicated as important and influential planktivores in offshore waters either historically (Wells 1970), or in recent years (Scavia et al. 1986; Dorazio et al. 1987; Warren and Lehman 1988). Large-bodied *Daphnia* such as *D. pulicaria* and *D. galeata mendotae* are particular targets of these planktivores. As a consequence, one competing hypothesis to explain the declines by *Daphnia* in Lake Michigan after the arrival of *Bythotrephes*, offered by Sprules et al. (1990), is that planktivory by fish accelerated coincidentally at the same times that *Bythotrephes* increased. Species compositional changes in recent years, however, are not consistent with good historical evidence about the roles of planktivory by fish, notably alewife, in Lake Michigan. Wells (1970) had found that the large-bodied *D. galeata mendotae* was lost during episodes of strong alewife planktivory and that only the smaller *D. retrocurva* persisted with the fish. Recent events in Lake Michigan have been exactly opposite to this

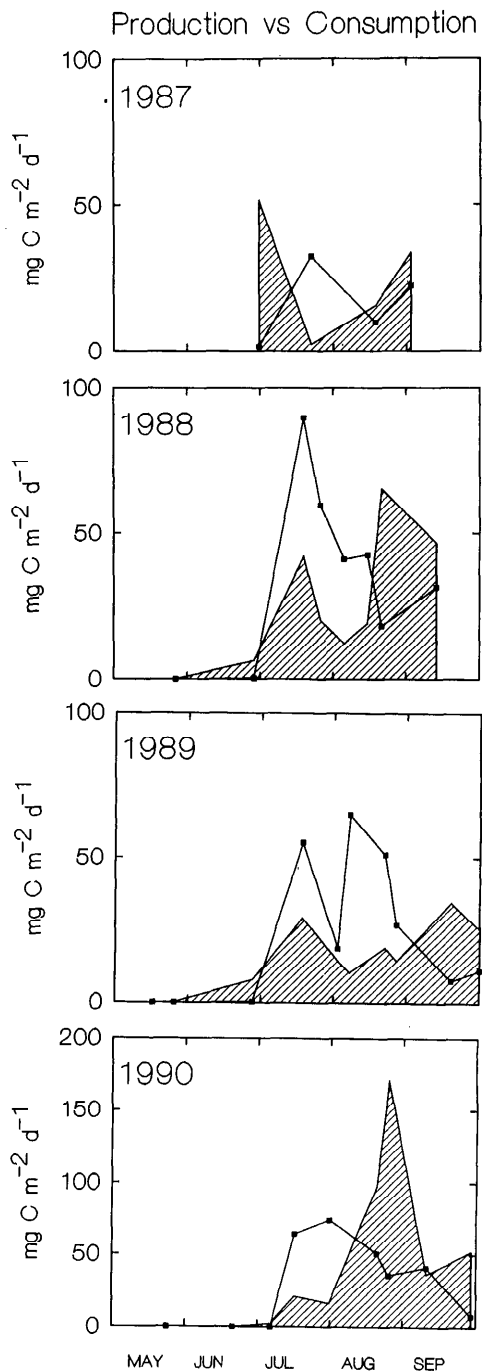
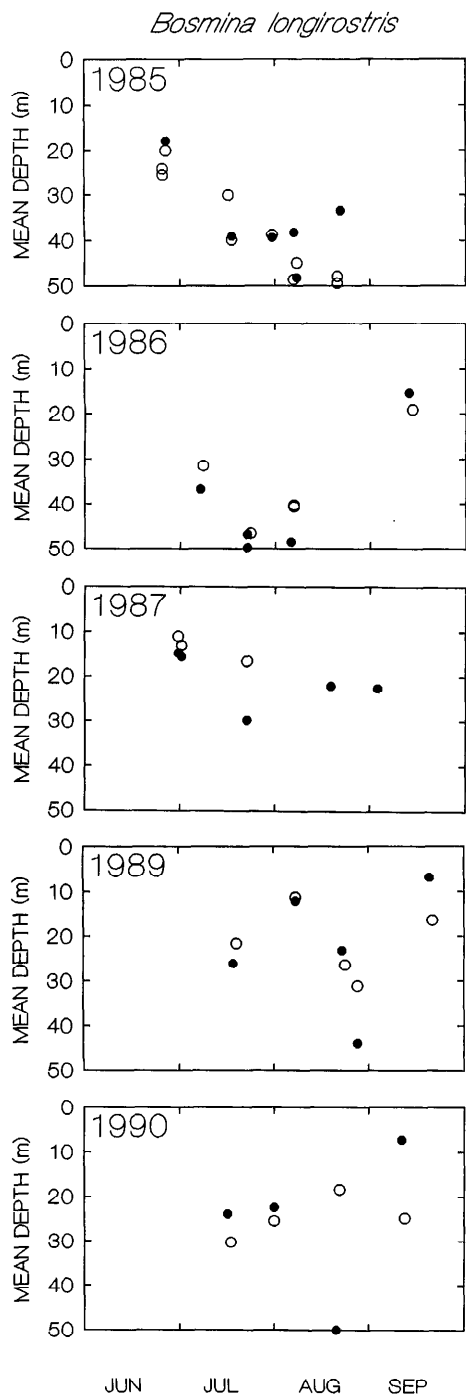


Fig. 8. Mean depths of *Bosmina longirostris* sampled by submersible pump (1985–1986) and by closing net (1986–1990). Sampling intervals and symbols as in Fig. 7.

Fig. 9. Consumption demand by *Bythotrephes* (■) estimated from bioenergetics model (Eq. 3) and estimated net daily replacement production by herbivorous Cladocera (hatched).

pattern. *D. retrocurva* has become extremely rare offshore and only occurs in abundance at places and times when *Bythotrephes* is rare (Fig. 5). In contrast, *D. galeata mendotae* has become the dominant daphnid species, and the size frequency distributions of surviving *Daphnia* populations offshore are consistent with planktivory by invertebrates, rather than vertebrates (Lehman 1991).

In addition to the loss of *D. retrocurva*, abundances of both *D. pulicaria* and *Leptodora* declined after the invasion of *Bythotrephes* and have not recovered in the offshore regions of the lake. The loss of *Leptodora* is believed to have triggered further changes, including increased abundances of both *Conochilus* and *Bosmina*, which had been important prey items for *Leptodora* (Sandgren and Lehman 1990; Branstrator and Lehman 1991). Whether *Leptodora* was lost by direct predation or by competition for food is presently under study. The loss of *D. pulicaria*, however, at first glance appears enigmatic. It is large as an adult, achieving body lengths in excess of 3 mm in offshore Lake Michigan, even during its population decline in 1987 (Lehman 1991). The success of *D. pulicaria* in 1983 was ascribed to the relative absence of alewife planktivory (Scavia et al. 1986). Its decreasing success in 1985 and 1986 (Fig. 1) was ascribed to the increasing planktivory exerted by young-of-year *C. hoyi* (Dorazio et al. 1987; Warren and Lehman 1988). The population decline in 1987 was triggered by incremental mortality and not by depressed birth rate (Table 2). It seems plausible that *Bythotrephes* would feed most aggressively on the smaller size classes of its prey, based on general experience with invertebrate predators (Zaret 1980), and thus the new predator may have accelerated a trend of decreasing abundance that was already occurring for *D. pulicaria*.

Bythotrephes is known to be a favored prey of numerous fish species (Giussani 1974; Guma'a 1978; Stenson 1978). Owing to its large size (~1 cm including the spine) and conspicuous eye, large fish have high positive electivities for *Bythotrephes* in natural plankton assemblages. Evans and Jude (1986) have noted that intense planktivory by fish is a perennial feature of the nearshore environment in Lake Michigan. Planktivory on *Bythotrephes* by fish is consequently the plausible cause of dimin-

ished abundances nearshore. Abundant populations of *Bythotrephes* offshore is itself an indirect indication that fish predation is relaxed there.

Empirical evidence supports the conclusion that when *Bythotrephes* invaded Lake Michigan it produced a substantial decline in *Daphnia* populations by elevating the mortality rates experienced by those populations. The invasion triggered other changes in the zooplankton, but failed to produce detectable effects on algal biomass. The effects of this invertebrate predator are strongly influenced by its local abundance, which may in turn be controlled by the sizes and abundances of planktivorous fish. The true scope of the environmental effects of *Bythotrephes* will best be judged, however, from repetition of the patterns and events observed in Lake Michigan in other lakes of the Nearctic.

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