Algal biomass unaltered by food-web changes in Lake Michigan

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***Bythotrephes cederstroemii* Schoedler (Crustacea: Cladocera), a predator previously confined to the Palearctic, has successfully invaded the North American Great Lakes[1-3]. *Bythotrephes* is a voracious predator on herbivorous Cladocera, including the dominant grazers in Lake Michigan during the summer. Lake Michigan has been the source of active debate regarding the relative importance of nutrient income versus food-web relations to its trophic state and water quality[4-6]. The recent species invasion has directly altered the lake's food web at a middle trophic level. During summer 1987 *Bythotrephes* populations increased rapidly in the offshore regions of Lake Michigan and abundances of herbivorous zooplankton simultaneously declined. Despite the resulting relaxation of herbivory, particulate chlorophyll concentrations, an index of algal biomass, did not increase. These results suggest that primary producers are most constrained by abiotic forces in this deep oligotrophic lake.**

The arrival of *Bythotrephes* in North America[1-3] has caused a novel perturbation of existing plankton communities. The rising abundances of *Bythotrephes* at an offshore reference station at 43° N 86°40′ W (36-km offshore; depth, 100 m) in Lake Michigan were associated with pronounced changes in the abundances of other zooplankton taxa. Zooplankton abundances on 30 June 1987, when *Bythotrephes* was rare, in most cases equalled or exceeded abundances recorded during 1985 and 1986 before the arrival of the predator (Table 1). Epilimnion temperatures were warmer in 1987 than in the previous two years, and the warm water promoted the early success of most crustacean taxa other than *Limnocalanus* and *Senecella*, which are hypolimnion-dwelling cold stenothermic copepods[7]. By 22 July 1987 *Bythotrephes* had increased to more than 200 individuals m^{-2}, and the abundances of five other plankton species were significantly different from levels recorded in 1985 and 1986 (Table 1).

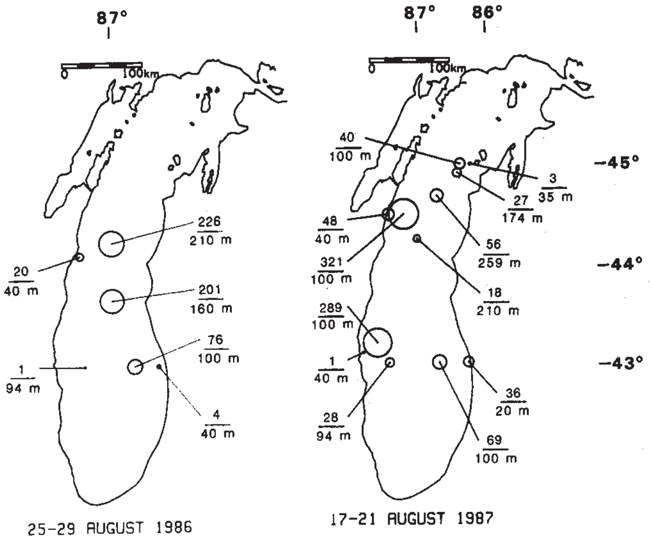

Fig. 1 Abundances (individuals m^{-2}) of *Bythotrephes* in Lake Michigan during survey cruises in August 1986 and 1987. Areas of the plotted circles are proportional to abundances. Numerators, individuals m^{-2} in water column from surface to within 5 m of bottom; denominators, depth of water column.

The depth-integrated plankton abundances reported in Table 1 have only a 20% estimation error[8]. By first-order error propagation[9], abundance ratios between years are subject to standard errors of estimation equal to 28% of the ratio. Ratios are thus not regarded to be significantly different from 1.0 at the 0.05 probability level (1.0 ± 2 s.e.m.) unless they are less than 0.44 or greater than 2.27 (the reciprocal of 0.44). All three *Daphnia* species (*D. pulicaria*, *D. galeata mendotae* and *D. retrocurva*), as well as *Leptodora kindtii*, declined in July 1987 and subsequently remained low during sampling cruises in August and September. The only crustacean to increase substantially, other than *Bythotrephes* itself, was *Epischura lacustris*. *Epischura* is univoltine and its population growth was due to accelerated recruitment of copepodids from naupliar stages earlier than usual because of warm temperatures. *Epischura* is carnivorous only in its late copepodid stages, and although capable of consuming *Daphnia* occasionally, it preys principally on zooplankton much smaller than *Daphnia*[10].

The spatial distribution of *Bythotrephes* during late August 1986 was consistent with a presumed invasion route from Lake Huron in the north (Fig. 1). By 1987, *Bythotrephes* was no longer in an early colonizing phase, but populations nonetheless developed asynchronously in different regions of the lake. In August 1987, *Bythotrephes* was in greatest abundance at deep (100 m) stations in western Lake Michigan. Populations on the east side of the lake had declined from similar high abundances one month earlier (Table 2).

Generation times for parthenogenically reproducing *Bythotrephes* are less than two weeks[11]. Females are iteroparous, and clutch sizes averaged 4.4 embryos per female in 1987. With

Table 1 Abundances of dominant crustacean zooplankton at an offshore reference station in Lake Michigan (43° N 86°40′ W) during comparable cruise periods in 1985-87

Taxon	Individuals m^{-2} 1985	1986	1987	Ratios 1987/1985	1987/1986
	(25-26 June)	(7-8 July)	(30 June)		
Diaptomus spp. C1-C6	472,600	663,700	832,200	1.76	1.25
Cyclops spp. C1-C6	290,100	423,700	719,000	2.48	1.70
Daphnia galeata mendotae	17,800	84,280	97,460	5.48	1.16
Daphnia pulicaria	345	3,473	2,300	6.67	0.66
Daphnia retrocurva	32,400	56,480	46,170	1.42	0.82
Bosmina longirostris	30,800	70,360	18,540	0.60	0.26
Limnocalanus macrurus C1-C6	14,600	7,480	7,210	0.49	0.96
Senecella calanoides C1-C6	456	380	318	0.70	0.84
Epischura lacustris C1-C6	110	64	738	6.71	11.53*
Leptodora kindtii	169	1,975	1,388	8.21	0.70
Bythotrephes cederstroemii	0	0	11		
Temperature at 5 m (°C)	11.5	14.9	18.0		
	16-18 July	22-23 July	22 July		
Diaptomus spp. C1-C6	383,800	705,100	646,400	1.68	0.92
Cyclops spp. C1-C6	316,300	408,400	404,000	1.28	0.99
Daphnia galeata mendotae	28,040	67,360	2,260	0.08	0.03*
Daphnia pulicaria	18,800	17,440	345	0.02	0.02*
Daphnia retrocurva	15,740	18,380	16	0.00	0.00*
Bosmina longirostris	23,090	39,300	26,610	1.15	0.68
Limnocalanus macrurus C1-C6	9,550	9,260	15,520	1.62	1.68
Senecella calanoides C1-C6	456	292	512	1.12	1.75
Epischura lacustris C1-C6	522	340	3,842	7.32	11.30*
Leptodora kindtii	2,677	2,892	0	0.00	0.00*
Bythotrephes cederstroemii	0	0	239		
Temperature at 5 m (°C)	18.6	20.6	22.4		

Only copepodid stages (C1-C6) are tabulated for copepods. Abundances significantly different in 1987 from both previous years are denoted by an asterisk.

Table 2 Reproductive condition of adult female *Bythotrephes* collected from offshore Lake Michigan in 1987

	June	July	August	September
Fecund parthenogenic females	60	368	15	71
Barren females	10	200	8	31
Gametogenic females with resting eggs	0	72	12	31
Bythotrephes m^{-2}	11	239	69	164
Abundance ratios *Daphnia* : *Bythotrephes*	13,270	11	318	380

Frequency distributions change significantly through time (overall $\chi^2 = 52.8$, 6 d.f.; $P = 1.3 \times 10^{-9}$). There were proportionally more barren and gametogenic females in July than in June, and proportionally more gametogenic females in August than in July. Reproductive conditions of females in August and September were statistically indistinguishable.

its short generation time, *Bythotrephes* can quickly dominate the dynamics of prey populations, but its influence may subside equally rapidly. The collapse of the *Daphnia* population in Lago Maggiore, for instance, has been attributed to predation from *Leptodora* and *Bythotrephes*[12–14]. Short-lived predators like *Bythotrephes*, however, may become victims of their own success. By mid-July 1987, the ratio of *Daphnia* to *Bythotrephes* had dropped to less than 30 to 1 at the offshore reference station (Table 2). The subsequent decline in *Bythotrephes* in August was associated with production of resting eggs, rather than parthenogenic eggs, an indication of food limitation. The proportions of barren *Bythotrephes* females and those bearing resting eggs increased significantly from June to July, when the *Daphnia* populations declined (Table 2). *Daphnia* species, in contrast, remained parthenogenic and fecund during their decline. Cladocera switch from parthenogenic reproduction to gametogenic production of resting eggs when food levels fall precipitously[15].

Leptodora, another predatory cladoceran, was virtually absent by July 1987 during the peak population development of *Bythotrephes*. *Bythotrephes* co-exists with *Leptodora* in European lakes[16], and so the loss of *Leptodora* in Lake Michigan was an unusual development. The two predators forage in different ways, but they both take small Cladocera as prey. *Bythotrephes* is the stronger swimmer and it possesses a stout (~1 cm) abdominal spine with up to three recurved barbs[17]. *Leptodora* is an almost transparent, soft-bodied animal with no sclerotized structures besides its mandibles. In June, *Bythotrephes* were found with remains of *Leptodora* trailing from their spines. Thus some incidental direct mortality may have caused the decline of *Leptodora*.

Nutrient income to Lake Michigan and per capita loading of phosphate by human activities have been restricted for more than a decade, in an effort to maintain the oligotrophic condition of the lake[18]. Owing to the century-long hydraulic residence time of the basin the responses have been relatively gradual, but evidence is accumulating that the measures are having success[4]. Lake Michigan has also been stocked with piscivorous salmon for two decades. Resulting changes in abundances of forage fish, primarily the planktivorous alewife (*Alosa pseudoharengus*) have been expected to cause changes that rival the effects of nutrient reduction. In Lake Michigan this dichotomy of management themes has initiated debate about the strength of nutrient controls and fishery management on trophic state and water quality[4–6]. Now, however, the lake ecosystem has endured a rapid manipulation at a middle trophic level by direct species invasion. Coincidentally, the invasion has provided evidence to refute the hypothesis that trophic interactions control the total biomass of algae in Lake Michigan. *Daphnia* are biomass dominants and the major epilimnetic herbivores during summer in Lake Michigan[8], and alterations in their abundance have been linked to changes in algal concentrations in other lakes[19]. Figure 2 shows the mean concentrations of chlorophyll *a* from surface to 20 m at the reference

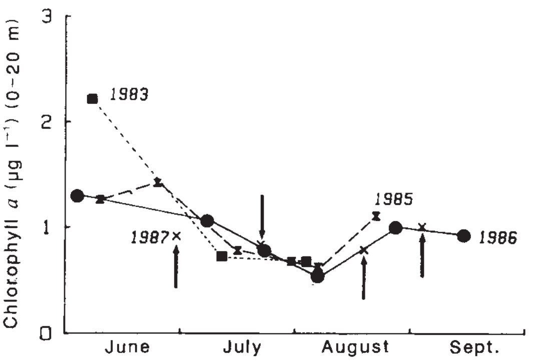

Fig. 2 Mean concentrations of chlorophyll *a* from surface to 20 m at the offshore reference station at Lake Michigan. Values in 1987 are indicated by arrows.

station in 1985, 1986 and 1987, as well as chlorophyll *a* measured at nearby stations in 1983 (ref. 14). During July and August 1987, when *Daphnia* populations were at 10-50-fold lower abundance than in previous years, the biomass of algae measured as chlorophyll *a* was unchanged from previous values. Evidentally, the maximum biomass of algae in Lake Michigan is constrained by forces other than herbivory.

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Rapid changes in genetic structure of epidemic populations of *Ophiostoma ulmi*

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The Northern Hemisphere is currently experiencing simultaneous epidemics of Dutch elm disease, caused by two new and highly pathogenic forms of *Ophiostoma (Ceratocystis) ulmi*, termed the Eurasian (EAN) and North American (NAN) races of the aggressive subgroup. The NAN aggressive has spread across North America[1,2] and into western Europe, probably through Britain[3,4]; the EAN has migrated westwards across Europe, and into south-western and central Asia[4,5]. They are now replacing the 'old' non-aggressive subgroup believed to be responsible for the first milder epidemic of the disease during the 1920s to 1940s (refs 5–9), and most mature elms are likely to be killed in affected areas[5]. This situation has provided an opportunity to examine