Hydrobiologia **198**: 215–226, 1990.
H. J. Dumont, J. G. Tundisi and K. Roche (eds), Intrazooplankton Predation.

Chaoborus predation and zooplankton community structure in a rotifer-dominated lake

Karl E. Havens
Department of Biological Sciences and Water Resources Research Institute, Kent State University, Kent, OH 44242, USA

Key words: Predation, *Chaoborus*, zooplankton, rotifers

Abstract

During summer, *Chaoborus punctipennis* larval densities in the water column of fishless, eutrophic Triangle Lake become very high, and coincidently, the spined loricate rotifer *Kellicottia bostoniensis* becomes the dominant zooplankter. Research was done to test the hypothesis that selective predation by *Chaoborus* on soft-bodied rotifers controls species dominance in the mid-summer zooplankton of this lake. *In situ* predation experiments showed positive selection by *Chaoborus* for the soft-bodied *Synchaeta oblonga*, negative selection for *K. bostoniensis*, and intermediate selection for *Polyarthra vulgaris*, a species with rapid escape tactics. However, during a 21 day *in situ* mesocosm experiment, zooplankton dominance and succession in *Chaoborus*-free enclosures was identical to that in enclosures with *Chaoborus* at lake density. Despite the selective predation, *Chaoborus* larvae may not exert significant top-down control on rotifers, whose intense reproductive output during mid-summer in temperate eutrophic lakes results in new individuals at rates that exceed predatory losses.

Introduction

In the fifteen years since Dodson's (1974) statement of the Balanced Predation Hypothesis, considerable research has been done to assess the impact of invertebrate predation on the zooplankton. One of the most intensively studied predators is the larva of the 'phantom midge' *Chaoborus*. This animal is an important component of the limnetic food web, because it is a consumer of zooplankton (Yan *et al.*, 1982) and a food source for fish (Pastorok, 1980). Numerous studies have documented its predatory behavior and selective feeding (Swift & Fedorenko, 1975; Kajak & Ryback, 1979; Pastorok, 1980, 1981; Smyly, 1980; Winner & Greber, 1980; Chimney *et al.*, 1981; Riessen *et al.*, 1984), and the impact of its predation on crustacean zooplankton community structure (Yan *et al.*, 1982; Vanni, 1988) and morphology (Stenson, 1987; Dodson, 1988, 1989). It has also been shown that the larvae feed on rotifers (Hillbricht-Ilkowska *et al.*, 1975; Lewis, 1977), and that high *Chaoborus* densities coincide with dense rotifer populations (Neill & Peacock, 1980; Neill, 1985). However, only one study (Moore & Gilbert, 1987) has assessed the vulnerability of various rotifer species to *Chaoborus* predation, and no studies have examined the impacts of *Chaoborus* predation on rotifer species dominance in the limnetic plankton community. The objective of the present study is to examine the interaction between *Chaoborus* and the rotiferan zooplankton in fishless Triangle Lake, Ohio

USA, where rotifers account for over 90% of the limnetic zooplankton biomass. Specifically, I tested the hypothesis that selective predation by *Chaoborus* controls the mid-summer dominance among the rotiferan species assemblage.

Methods

Triangle Lake is a small (Area 0.38 ha, z_{max} 8 m) glacial kettle lake located in Portage Co., Ohio, USA. The naturally acidic lake is highly stained with humics, such that the euphotic zone is limited to the upper meter, and is eutrophic, based on summer total phosphorus and chlorophyll levels (Cotner, 1984). The phytoplankton is dominated by large flagellates, and the zooplankton is rotifer-dominated year round (Havens, 1989). During summer 1989, a series of *in situ* predation experiments were performed to determine the feeding selectivity of *Chaoborus punctipennis* on the natural zooplankton assemblage. In July, an *in situ* mesocosm experiment was performed, to evaluate the effects of *Chaoborus* exclosure on zooplankton community structure.

In situ predation experiments were performed on 16 May, 30 May, 12 June, 7 July and 21 July. *Chaoborus* larvae were collected from the lake via several hauls of a 363 μm plankton net (20 cm mouth opening). The contents of the first haul were preserved with chilled formalin/sucrose, while *Chaoborus* from subsequent hauls were placed into a small plastic chamber and covered with a black plastic cover, for later use in the experiment. Lakewater was collected from the upper 0.5 m of the water column, and placed into a 20 l plastic bucket. After gentle mixing, the water was used to fill ten 1 l plastic bottles. Five Control bottles were immediately capped, while five Predation bottles each received 10 *Chaoborus* larvae. The larvae were added to the bottles using a transparent plastic dropper, and additions were done under a dark tarp, to minimize disturbance of feeding habits. The Predation bottles were capped, and all ten bottles were suspended at a depth of 0.5 m in the lake. Water temperature was determined at the incubation depth, and five replicate 300 ml samples from the 20 l bucket were preserved with formalin/sucrose. After a 4 hr incubation (0900 to 1300), the bottles were retrieved, mixed by gentle shaking, and 300 ml from each poured into seperate Whirl-Pak bags. These samples were immediately preserved with formalin/sucrose. The remaining contents of each bottle were filtered through a 363 μm mesh, and the number of retained *Chaoborus* larvae counted on site. Later, these numbers were added to those determined from scanning the preserved portions of the samples. With only a single exception, ten larvae were recovered from each Predation bottle, and none were found in the Controls. At the end of the 7 July experiment, one of the Control bottles contained a single larva. Counts from that bottle were not used in subsequent calculations.

In the lab, the preserved samples were concentrated to a known volume, using a small plastic cup with a 20 μm mesh port. In May and June, when zooplankton densities were low, the entire concentrated samples were enumerated in a plexiglass chamber at 30 ×. In July, when densities were high, triplicate 1 ml aliquots were enumerated in a Sedgewick-Rafter cell at 30 ×. The mean density of each prey species in the environment was determined from counts of the three samples from the 20 l bucket. These mean values were never significantly different from mean densities calculated from the final Control bottle counts (t-tests, $p > 0.5$ in all cases).

Chaoborus predation rates on the various prey types (prey $Chaoborus^{-1}$ hr^{-1}) were calculated by subtracting the mean final density of each prey type in the Predation treatment from its density in the Control, and dividing the resultant values by 40, to correct for feeding time (4 hrs) and the total number of larvae (10) in each Predation bottle. Indices of selectivity (W) were calculated from normalized predation rates, as described in Vanderploeg & Scavia (1979). W values range from 0 to 1, with neutral selectivity corresponding to 1/n, where n equals the total number of prey types in the experiment.

Chaoborus densities (No. m^{-3}) in the lake were determined by counting the entire unconcentrated net haul samples at 10 ×. Counts were not corrected for sampling efficiency, since the net was unmetered. Hence, it is likely that the densities presented herein are underestimates, especially since the chloromonad *Gonyostomum semen* was very abundant in the lake from May to August. This alga has trichocysts which discharge mucilagenous threads when disturbed (Cronberg, 1988), and hence, it caused marked clogging of the plankton net. However, the underestimated larval densities do not affect the conclusions of this study.

An *in situ* mesocosm experiment was performed from 5 to 26 July. On day zero, six transparent polyethylene bags (0.5 m diameter, 1.5 m deep, open at the top and sealed at the bottom) were suspended from a wooden raft in the lake. The bags were filled manually, by pouring in lakewater collected in a 20 l bucket from the upper 0.5 m of the water column. The final volume of each enclosure was 250 l. Numerous net tows in the upper 1 m of the water column at the start of the experiment showed that *Chaoborus* larvae were located below that depth in the lake. Therefore, unfiltered surface water was used.

Immediately thereafter, *Chaoborus* larvae were collected from the lake with several 8 m hauls of the 363 μm net. The contents of the first haul were preserved with formalin/sucrose and unumerated on site, to determine their density in the water column. Larvae from the later hauls were placed into a plastic holding chamber until addition to the bags. Three bags were untreated, and as such, represented the *Chaoborus*-free Exclosure treatment. The remaining three Control bags each received 40 *Chaoborus* larvae, which produced the measured lake density of 160 larvae m^{-3}. During the experiment, additional larvae were added to the Control bags (20 each on day 10, and 100 each on day 13), as lake densities increased. Following sampling on day 21, the contents of each bag were mixed with a wooden stirrer. Five successive water samples were collected from each bag with a 4 l trap, and the contents poured through the 363 μm net, to collect *Chaoborus* larvae. Final larval densities (No. m^{-3}) in the bags were calculated, assuming bag volumes of 244 l, since 6 l were removed from each bag during sampling on earlier days.

Sampling was done on days 0, 1, 2, 4, 6, 9, 12, 14, 16, 19 and 21. Zooplankton were collected with a 6 cm diameter PVC integrated sampler, which sampled the entire 1.5 m water column in the bags, and the upper 1.5 m in the lake. After collection, the contents of the sampler were released into a 5 L bucket, and after gentle mixing, a 200 ml subsample was placed into a Whirl-Pak bag and fixed with formalin/sucrose. The remaining contents of the bucket were then returned to the sampled bag, to minimize volume reduction. On each sampling date, a single 8 m vertical haul of the 363 μm net was done in the lake, to collect *Chaoborus* larvae. The animals were placed into Whirl-Pak bags and preserved as above. The vertical hauls were not replicated, due to net clogging by *Gonyostomum.*

All zooplankton samples were concentrated to a known volume, as described for the predation experiments, and triplicate 1 ml aliquots were enumerated at 30 × in a Sedgewick-Rafter cell. Densities (No. ml^{-1}) were determined by multiplying counts by a factor which accounted for sample size and percent of sample volume counted (10 to 30%). I assumed a sampling efficiency of 100% for the integrated sampler. *Chaoborus* densities were determined by counting entire unconcentrated net haul samples at 10 ×, and were expressed as No. m^{-3}, uncorrected for sampling efficiency.

Data organization, calculation of means and standard errors, t-tests and linear regressions were done using SAS (SAS Institute, 1985). All zooplankton data presented from the mesocosm experiment are means of three replicate bags per treatment, and unreplicated lake samples. An exception is that for the Exclosure treatment, data after day 16 are means of only two replicates, since one bag developed a hole below the water line.

Results

There was a highly significant ($p = 0.01$) positive relationship between *Kellicottia bostoniensis* frequencies and *Chaoborus punctipennis* densities in the limnetic plankton of Triangle Lake during summer 1989 (Fig. 1). This is similar to the relationship seen in previous summers.

Table 1 shows the abundances of the zooplankton prey during the predation experiments. On 16 May, 30 May and 12 June, zooplankton abundances in the lake were low, and the soft-bodied rotifer *Synchaeta oblonga* was the dominant prey. On 7 and 21 July, zooplankton abundances were much higher, and the dominant prey were *Kellicottia bostoniensis* and *Polyarthra vulgaris*. For the two May experiments, second instar *Chaoborus* larvae were the predators. In June and July, the predators were both second and third instars.

The results of the experiments are shown in Table 2. During May and June, when the zooplankton was dominated by *S. oblonga*, the selectivity indices for the various prey indicated near-neutral selection (random feeding). An exception was that on 12 June, *K. bostoniensis* accounted for 2% of the available prey, but none were consumed. Hence, for this species, a *W* value of 0 indicates maximally negative selection. In the two July experiments, when the prey consisted of the three rotifer species, selective predation was observed. The selectivity values indicate positive selection by *Chaoborus* for *S. oblonga*, highly negative selection for *K. bostoniensis*, and intermediate selection for *P. vulgaris*.

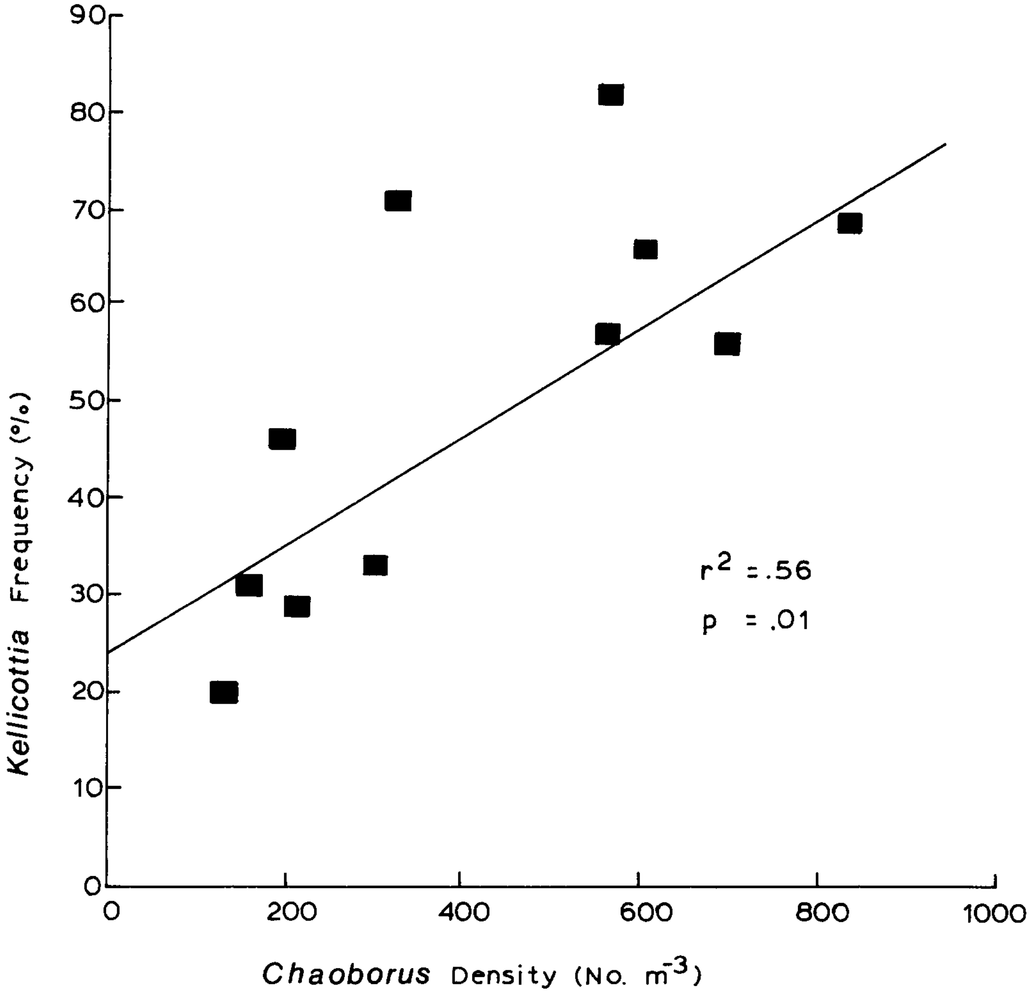


Fig. 1. The relationship between *Kellicottia bostoniensis* frequencies and *Chaoborus punctipennis* larval densities in the limnetic plankton of Triangle Lake during summer 1989.

Table 1. Prey densities (means ± one standard error) and incubation temperatures during the five in situ predation experiments.

	Experiment				
	16 May	30 May	12 June	7 July	21 July
Prey Densities (No. l^{-1})					
Synchaeta oblonga	220 ± 17	717 ± 17	230 ± 21	208 ± 38	320 ± 35
Kellicottia bostoniensis	0	0	4 ± 2	996 ± 62	3751 ± 423
Polyarthra vulgaris	0	0	0	871 ± 168	1400 ± 177
cyclopoid nauplii	27 ± 2	14 ± 2	8 ± 3	0	0
cyclopoid copepodids	0	7 ± 3	0	0	0
Temperature (°C)	12	16	19	19	20

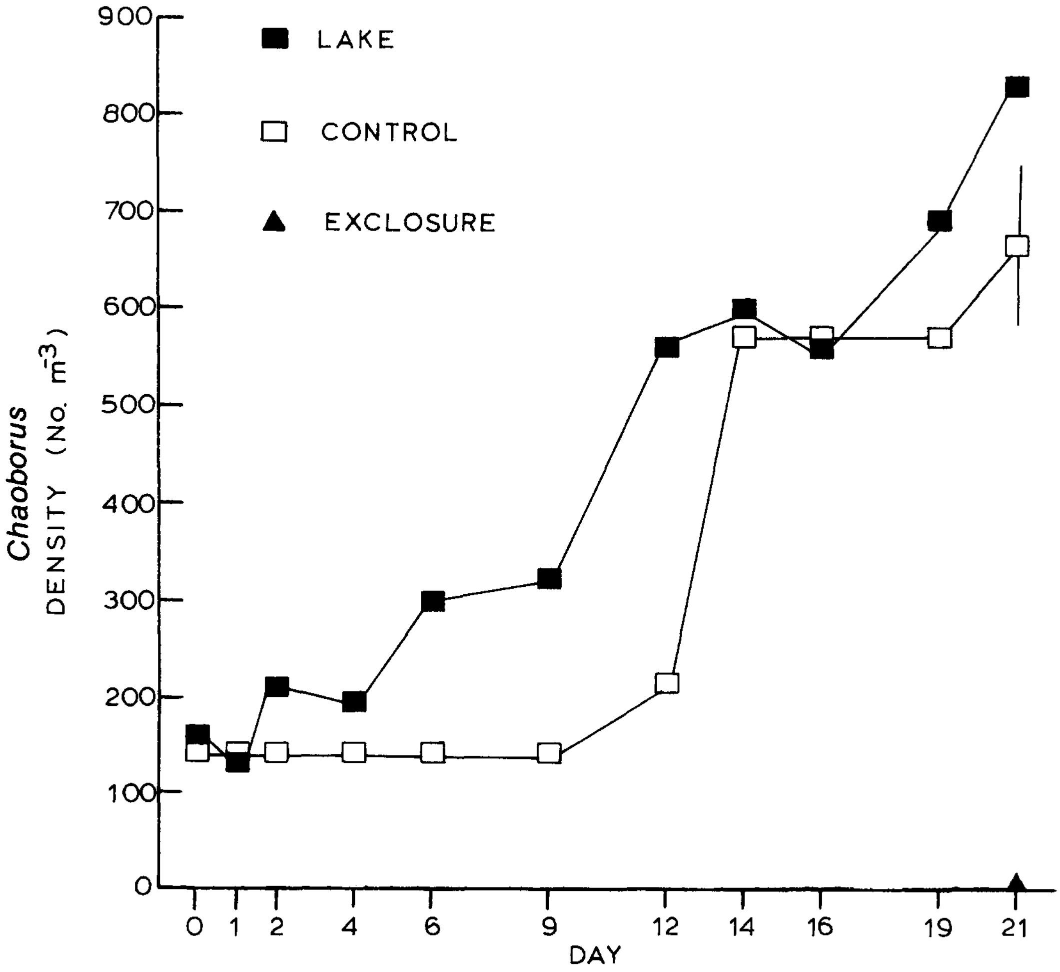


Fig. 2. *Chaoborus* larval densities in the treatments and lake during the *in situ* mesocosm experiment. The lake data represent unreplicated 8 m net haul samples; day 0 to 19 treatment data are estimates based on larval additions to the bags: day 21 treatment data are means of densities calculated from trap samples in the bags of each treatment. The vertical bar is ± one standard error.

Table 2. Selectivity values (*W*) for *Chaoborus* preying on the various zooplankton during the five in situ predation experiments. The values corresponding to neutral selectivities are also given for each experiment. Values above this level during an experiment represent positive selection; values below this level represent negative selection.

Prey Type	Experiment				
	16 May	30 May	12 June	7 July	21 July
Synchaeta oblonga	0.48	0.30	0.44	0.78	0.67
Kellicottia bostoniensis	–	–	0	0.05	0.02
Polyarthra vulgaris	–	–	–	0.17	0.30
cyclopoid nauplii	0.52	0.35	0.56	–	–
cyclopoid copepodids	–	0.35	–	–	–
Neutral Selectivity	0.50	0.33	0.50	0.33	0.33

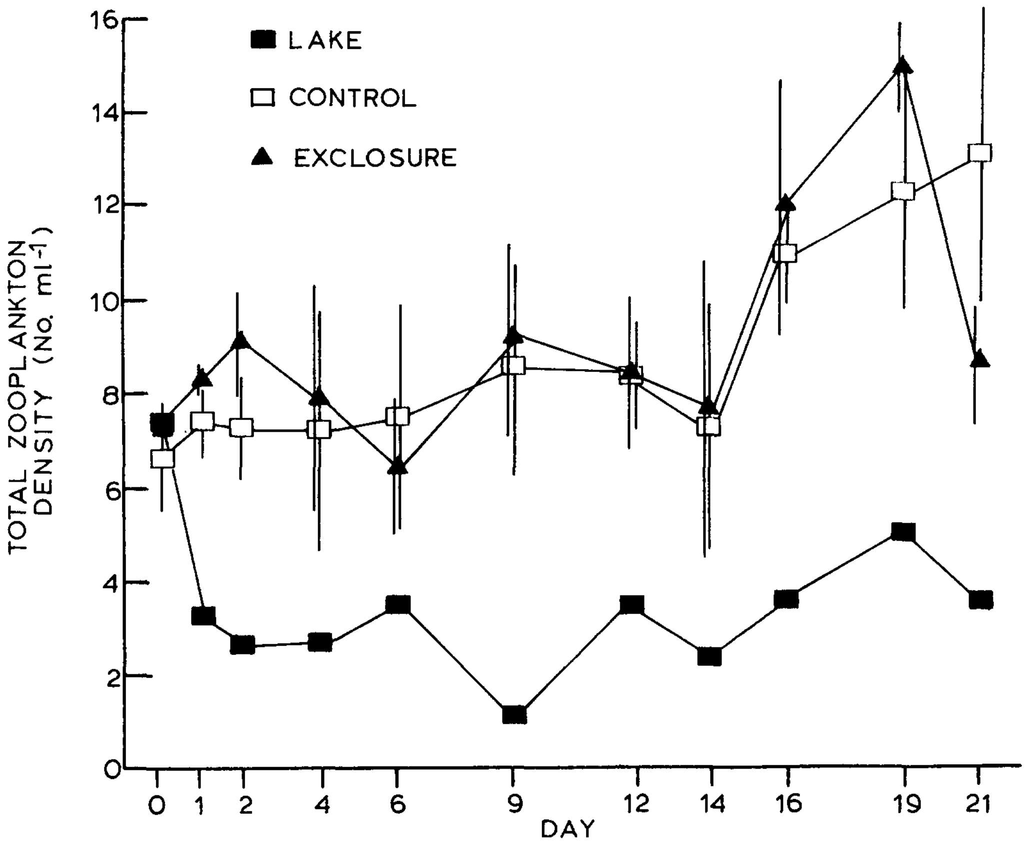


Fig. 3. Total zooplankton densities in the treatments and lake during the *in situ* mesocosm experiment (vertical bars are ± one standard error).

Chaoborus densities increased in the lake during the *in situ* mesocosm experiment, from an initial 160 m^{-3} to over 800 m^{-3} on day 21 (Fig. 2). They also increased in the Control enclosures, as a result of larval additions, from the initial 160 m^{-3}, to a final 690 m^{-3}. *Chaoborus* densities were zero in the Exclosure treatment throughout the experiment, as confirmed by the results of sampling on day 21, when no larvae were collected in 20 l samples from the bags.

Total zooplankton densities were roughly 7 ml^{-1} on day zero in the lake and treatments, and remained at that level through day 14 in both the Control and Exclosure (Fig. 3). Densities then increased in both treatments, to roughly 12 ml^{-1} in the later days of the experiment. There was no significant treatment effect on total zooplankton density ($P > 0.05$ for t-tests on any given day). In the lake, zooplankton densities declined after day zero, and were roughly 3 ml^{-1} throughout the experiment.

The relative abundances of the various zooplankton species in the lake and treatments are shown in Fig. 4. Only species accounting for > 1% of total zooplankton density are shown. Because the four dominant zooplankton species (*Synchaeta oblonga*, *Polyarthra vulgaris*, *Kellicottia bostoniensis* and *Ascomorpha ecaudis*) are of similar size, the relative density data also reflect relative biomass. On day 0, the lake and treatments showed dominance by *P. vulgaris*, which accounted for roughly 70% of the zooplankton. In the lake, *P. vulgaris* declined over time, and *K. bostoniensis* became increasingly dominant. As noted previously, this was coincident with increasing *Chaoborus* densities. *S. oblonga* accounted for < 10% of the lake zooplankton until day 4, increased to roughly 15% on days 6 xoto 12, and then declined to less than 10% on days 14 to 21. *A. ecaudis*, an important littoral rotifer in Triangle Lake, increased in importance in the lake during the later days of the experiment. In both treat-

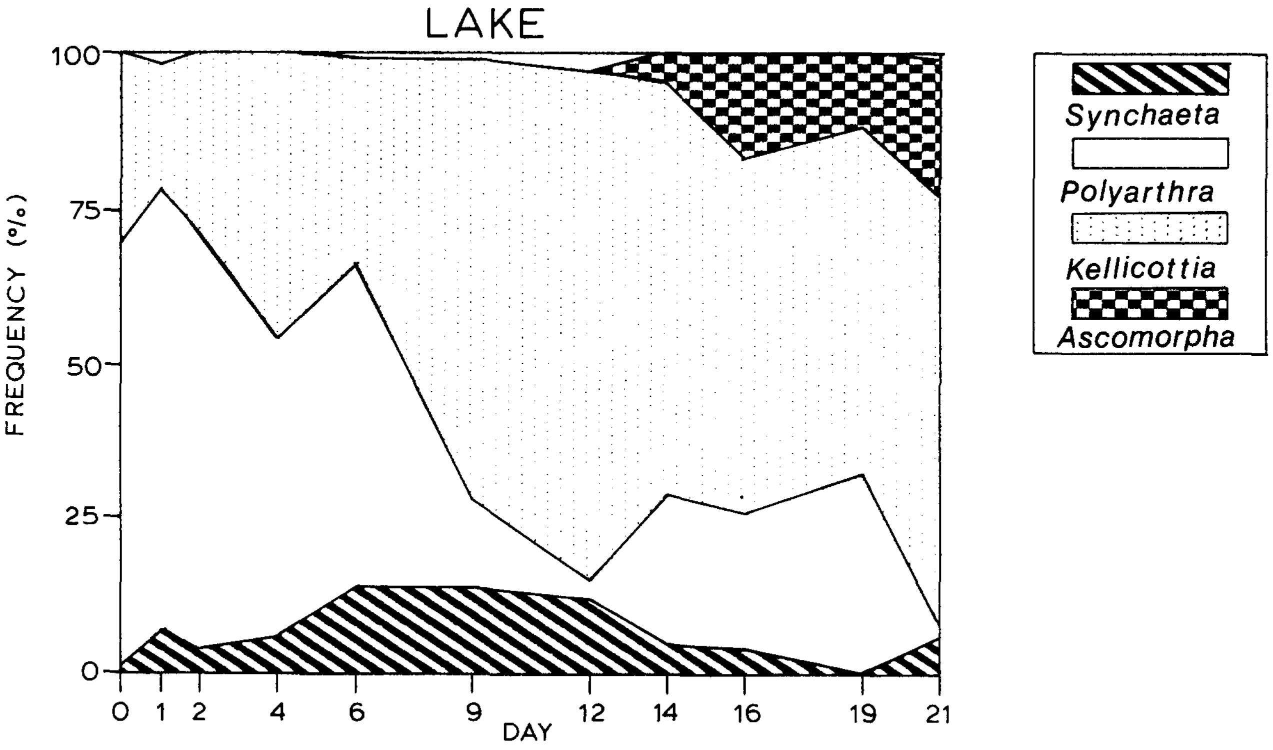
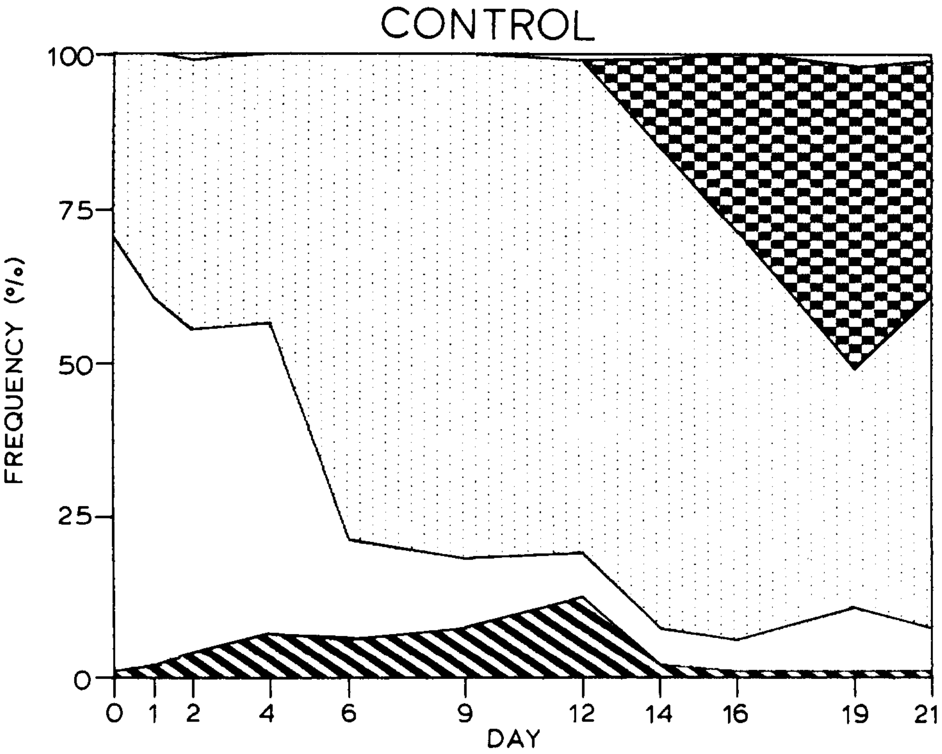
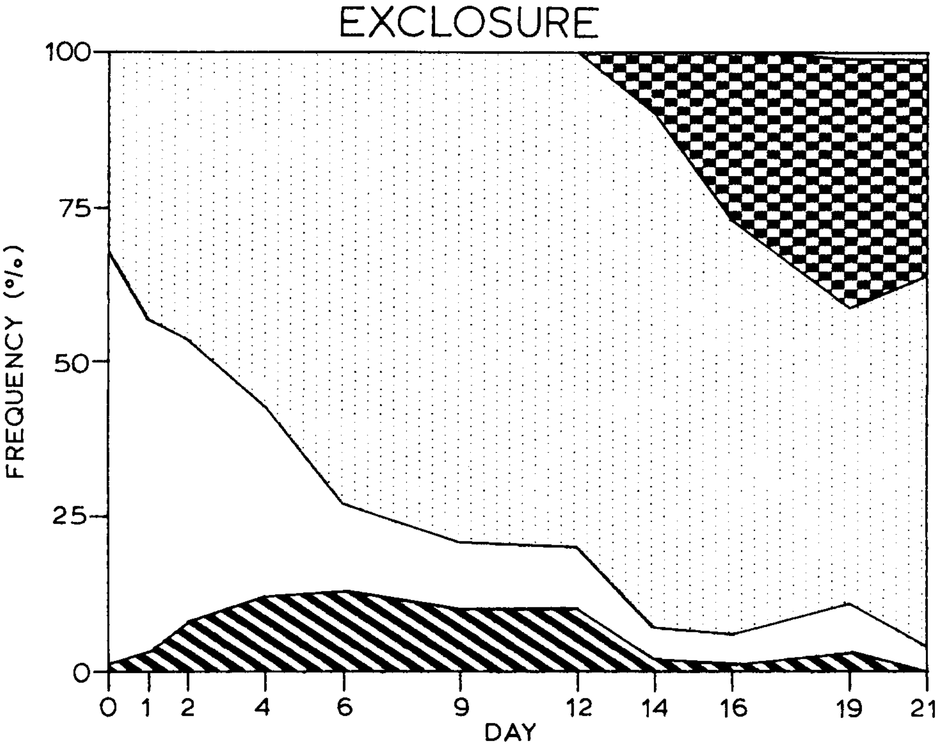


Fig. 4. Percent of total zooplankton abundances due to the various dominant species (those accounting for > 1% of total abundance) in the lake and treatments during the *in situ* mesocosm experiment.


CONTROL
100
75
50
25
0
FREQUENCY (%)
0
1
2
4
6
9
12
14
16
19
21
DAY


EXCLOSURE
100
75
50
25
0
FREQUENCY (%)
0
1
2
4
6
9
12
14
16
19
21
DAY

ments, this same succession occurred. The only difference was a more rapid increase in *K. bostoniensis* dominance in the bags, and greater *A. ecaudis* importance than in the lake after day 16. The latter was probably due to the increasingly littoral conditions of the bags after day 16, when clumps of algae became common. This would favor the proliferation of *A. ecaudis* and other littoral species. In fact, on day 21, a few *Chydorus sphaericus* individuals were also found in the bags of both treatments. *C. sphaericus* is common in the littoral of this lake.

The most noteworthy feature of Fig. 4 is the almost identical rotifer succession seen in the Control (where *Chaoborus* densities were high) and in the *Chaoborus*-free Exclosure treatment during this experiment.

Discussion

Chaoborus larvae are 'ambush predators' (Riessen *et al.*, 1984), which lie motionless in the water column, and strike quickly at prey as they pass by. Because larger zooplankton are difficult to capture and ingest, *Chaoborus* prey heavily on small species (Fedorenko, 1975a, 1975b; Stenson, 1976; Vinyard & Menger, 1980; Chimney *et al.*, 1981), which are more likely to be captured once contact is made (Swift & Fedorenko, 1975), and which require a shorter handling time for ingestion (Pastorok, 1981). Because *Chaoborus* larvae have a high feeding rate (Riessen *et al.*, 1984), they can significantly affect crustacean zooplankton community structure when they are abundant (Kajak & Rybak, 1979), resulting in dominance by the most resistant prey species (Sprules, 1972). *Chaoborus* predation can also induce the development of morphological devices like enlarged capsules in *Holopedium* (Stenson, 1987) and elongated helmets, spines and neck teeth in *Daphnia* (Kreuger & Dodson, 1981; Dodson, 1988, 1989), which deter *Chaoborus* predation.

Rotifers are the major food source for early *Chaoborus* instars (Neill & Peacock, 1980). However, only Moore & Gilbert (1987) have examined the interaction between *Chaoborus* and various rotifer prey. They showed that soft-bodied rotifers are more susceptable to *Chaoborus* predation than loricate ones.

Triangle Lake represented the ideal situation in which to further examine this important predator-prey interaction. I was especially interested in determining whether selective predation on soft-bodied rotifers could control dominance in a natural community. Triangle Lake is dominated year-round by rotifers (Havens, 1989), and *Chaoborus* is the only significant planktonic predator. Dense rotifer populations are common in precipitation-acidified lakes (Yan & Geirling, 1985) and in naturally acidic bog lakes (Stoneburger & Smock, 1980) in North America, as well as in eutrophic non-acid waters (Neill, 1985). *Chaoborus* densities in Triangle Lake (which peaked at over 800 m^{-3}) were high relative to those recorded in the literature (Pope *et al.*, 1973; Stenson *et al.*, 1978; Yan *et al.*, 1985). Such high densities are likely the result of the abundant rotifer prey, which can exert a bottom-up control of *Chaoborus* populations (Neill & Peacock, 1980). During May to July, I found a highly significant positive relationship between *Kellicottia bostoniensis* dominance and *Chaoborus* densities. Also, the predation experiments showed that *Chaoborus* II and III larvae were feeding preferentially on the soft-bodied *Synchaeta oblonga*, showing negative selection for the loricate species *Kellicottia bostoniensis*. These results are consistent with those of Moore & Gilbert (1987) who compared selectivity for *S. oblonga* versus *Keratella*. They suggested that soft-bodied species are more vulnerable because they are easily deformed and packed into the crop, allowing more rapid feeding than on loricate species. It is unclear whether the long spines of *K. bostoniensis* hinder ingestion by *Chaoborus*, since it was the only loricate species used in this study. *Chaoborus* larvae are known to align loricate rotifers and ingest them lengthwise, and Moore & Gilbert (1987) suggested that only lateral spines, such as those of *Keratella taurocephala*, are an effective deterrent to *Chaoborus* predation. However, their conclusion is based upon a comparison of predation rates on *Keratella* morphs, where spine length is considerably shorter than in *Kellicottia*. Future research should compare predation rates on *Kellicottia* versus *Keratella* of similar lorica size (not including spines). In the predation experiments, I also found selectivity for *Polyarthra vulgaris* to be intermediate between that for *S. oblonga* and *K. bostoniensis*. This suggests that the escape tactics of *P. vulgaris* (Stemberger & Gilbert, 1987) are moderately effective in preventing capture by *Chaoborus* larvae, but not as effective as a hard lorica. It is not surprising that the rapidly-attacking *Chaoborus* larvae captured a substantial number of *P. vulgaris* in the experiments. Gilbert & Williamson (1978) found that *Polyarthra* could effectively escape predation by *Asplanchna*, but not the more rapidly-attacking *Mesocyclops*. It is likely that the ambush predator *Chaoborus* captures some *P. vulgaris* individuals before they are able to utilize their escape maneuvers.

Taken together, the significant positive relationship between *K. bostoniensis* dominance and *Chaoborus* densities in the lake, and the demonstration of selective predation on soft-bodied rotifers suggested *Chaoborus* control of zooplankton community structure. However, exclosure of the predators from mesocosms resulted in no significant changes in the species dominance or in the succession observed in the lake. This was despite the fact that the 21 day duration of the experiment was several times the generation time of rotifers at 20 °C (Lindstrom, 1983; Walz, 1983). Two important conclusions can be drawn from these results:

First, the existance of selective predation does not necessarily imply that a predator significantly impacts prey populations in nature. Future predation experiments should be coupled with whole-community biomanipulations, involving either mesocosms, as done herein, or the whole-lake approach. In previous studies (Kajak & Ryback, 1979; Smyly, 1980; Winner & Greber, 1980; Chimney *et al.*, 1981; Riessen *et al.*, 1984; Moore & Gilbert, 1987) this has not been done, and hence, the extent to which the demonstrated selective predation affects the prey in nature is unclear.

Second, the results suggest that the effect of *Chaoborus* predation on rotifers is minimal, compared to that on crustacean prey. At the typical mid-summer water temperatures of temperate eutrophic lakes, the intense reproductive output of planktonic rotifers may greatly exceed losses due to *Chaoborus* predation. In contrast, because crustacean zooplankton have markedly longer generation times than rotifers (Gannon & Stemberger, 1978), they are impacted to a greater extent by *Chaoborus* predation. In fact, intense *Chaoborus* predation in Triangle Lake may exclude *Ceriodaphnia* (which is abundant in the littoral) from the limnetic zone. Future research should examine the *Chaoborus*-rotifer interaction in lakes of lesser productivity, to determine the extent to which this statement can be generalized.

If *K. bostoniensis* dominance during summer is not the result of selective predation, then what is the controlling factor? This question cannot be answered conclusively without further research. However, it is likely the result of competition. During spring, cryptomonads dominated the phytoplankton of Triangle Lake. They were replaced by *Gonyostomum semen* in summer. During the *Gonyostomum* bloom, bacteria represent the major food source for the zooplankton. *K. bostoniensis* may be better able to utilize bacteria than *P. vulgaris*, and hence, replaces it as the dominant species in mid-summer. This hypothesis is consistent with the results of Bogdan & Gilbert (1984), who found that *Polyarthra* specializes on small flagellates such as *Cryptomonas*, and the results of Sanders *et al.* (1989), who found that *Kellicottia* is a bacterivore but *Polyarthra* is not. *Kellicottia*'s long spines may also give it a hydrodynamic advantage (Stemberger & Gilbert, 1987), such that less energy expenditure is required for maintaining its position in the water column during summer, when edible algal biovolume (and perhaps food availability in general) in Triangle Lake is low.

Acknowledgements

This study was supported by a grant from the Research Council of Kent State University.

References

Bogdan, K. G. & J. J. Gilbert, 1984. Body size and food size in freshwater zooplankton. Proc. nat. Acad. Sci. 81: 6427–6431.

Chimney, M. J., R. W. Winner & S. K. Seiklop, 1981. Prey utilization by *Chaoborus punctipennis* in a small, eutrophic reservoir. Hydrobiologia 85: 193–199.

Cotner, J. B., 1984. Significance of dissolved phosphorus in an acid bog lake. M.S. Thesis, Kent State Univ., Ohio, USA.

Cronberg, G., 1988. Mass development of the flagellate *Gonyostomum semen* in Swedish forest lakes – an effect of acidification? Hydrobiologia 161: 217–236.

Dodson, S. I., 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55: 605–613.

Dodson, S. I., 1988. Cyclomorphosis in *Daphnia galeata mendotae* Birge and *D. retrocurva* Forbes as a predator-induced response. Freshwat. Biol. 19: 109–114.

Dodson, S. I., 1989. The ecological role of chemical stimuli for the zooplankton: predator-induced morphology in *Daphnia*. Oecologia 78: 361–367.

Fedorenko, A. Y., 1975a. Instar and species-specific diets in two species of *Chaoborus*. Limnol. Oceanogr. 20: 238–249.

Fedorenko, A. Y., 1975b. Feeding characteristics and predation impact of *Chaoborus* larvae in a small lake. Limnol. Oceanogr. 20: 250–258.

Gannon, J. E. & R. S. Stemberger, 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. Trans. am. microsc. Soc. 97: 16–35.

Gilbert, J. J. & C. E. Williamson, 1978. Predator-prey behavior and its effect on rotifer survival in associations of *Mesocyclops edax*, *Asplanchna girodi*, *Polyarthra vulgaris*, and *Keratella cochlearis*. Oecologia 37: 13–22.

Havens, K. E., 1989. Seasonal succession in the plankton of a naturally acidic, highly humic lake in Northeastern Ohio, USA. J. Plankton Res. 11. In press.

Hillbricht-Ilkowska, A., Z. Kajak, J. Ejsmont-Karabin, A. Karabin & J. Ryback, 1975. Ecosystem of the Mikolajskie Lake. The utilization of the consumers production by invertebrate predators in pelagic and profundal zones. Pol. Arch. Hydrobiol. 22: 53–64.

Kajak, Z. & J. Rybak, 1979. The feeding of *Chaoborus flavicans* and its predation on lake zooplankton. Int. Revue ges. Hydrobiol. 64: 361–378.

Kreuger, D. A. & S. I. Dodson, 1981. Embryological induction and predation ecology in *Daphnia pulex*. Limnol. Oceanogr. 26: 219–223.

Lewis, W. M., Jr., 1977. Feeding selectivity of a tropical *Chaoborus* population. Freshwat. Biol. 7: 311–325.

Lindstrom, K., 1983. Changes in growth and size of *Keratella cochlearis* in relation to some environmental factors in cultures. Hydrobiologia 104: 325–328.

Moore, M. V. & J. J. Gilbert, 1987. Age-specific *Chaoborus* predation on rotifer prey. Freshwat. Biol. 17: 223–236.

Neill, W. E., 1985. The effects of herbivore competition upon the dynamics of *Chaoborus* predation. Arch. Hydrobiol. 21: 483–491.

Neill, W. E. & A. Peacock, 1980. Breaking the bottleneck: interactions of nutrients and invertebrate predators in oligotrophic lakes. In W. C. Kerfoot (ed), Ecology and evolution of zooplankton communities. University Press of New England, Hanover, NH, USA.

Pastorok, R. A., 1980. The effects of predator hunger and food abundance on prey selection by *Chaoborus* larvae. Limnol. Oceanogr. 25: 910–921.

Pastorok, R. A., 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 65: 1311–1324.

Pope, G. F., J. C. H. Carter & G. Power, 1973. The influence of fish on the distribution of *Chaoborus* spp. and density of larvae in the Matamek River System, Quebec. Trans. am. Fish. Soc. 102: 707–714.

Riessen, H. P., W. J. O'Brien & B. Loveless, 1984. An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. Ecology 65: 514–522.

Sanders, R. W., K. G. Porter, S. J. Bennett & A. E. DeBiase, 1989. Seasonal patterns of bactivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. Limnol. Oceanogr. 34: 673–678.

SAS Institute, 1985. SAS users guide: Statistics. Version 5 Edition. SAS Institute, Inc. Cary, NC, USA.

Smyly, W. J. P., 1980. Food and feeding of aquatic larvae of the midge *Chaoborus flavicans* in the laboratory. Hydrobiologia 70: 179–188.

Sprules, W. G., 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375–386.

Stemberger, R. S. & J. J. Gilbert, 1987. Defenses of planktonic rotifers against predators. In W. C. Kerfoot & A. Sih (eds), Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH, USA.

Stenson, J. A. E., 1976. Significance of predator influence on composition of *Bosmina* sp. populations. Limnol. Oceanogr. 21: 814–822.

Stenson, J. A. E., 1987. Variation in capsule size of *Holopedium gibberum*: a response to invertebrate predation. Ecology 68: 928–934.

Stenson, J. A. E., T. Bohlin, L. Henrikson, B. I. Nilsson, H. G. Nyman, H. G. Oscarson & P. Larsson, 1978. Effects of fish removal from a small lake. Verh. int. Ver. Limnol. 20: 794–801.

Stoneburger, D. L. & L. A. Smock, 1980. Plankton communities of an acidic, polymictic brownwater lake. Hydrobiologia 69: 131–138.

Swift, M. C. & A. Y. Fedorenko, 1975. Some aspects of prey capture by *Chaoborus* larvae. Limnol. Oceanogr. 20: 418–425.

Vanderploeg, H. A. & D. Scavia, 1979. Two electivity indices for feeding with special reference to zooplankton grazing. J. Fish. Res. Bd Can. 36: 362–365.

Vanni, M. J., 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. Can. J. Fish. aquat. Sci. 45: 1758–1770.

Vinyard, G. L. & R. A. Menger, 1980. *Chaoborus americanus* predation on various zooplankters: functional response and behavioral observations. Oecologia 45: 90–93.

Walz, N., 1983. Individual culture and experimental population dynamics of *Keratella cochlearis*. Hydrobiologia 107: 35–45.

Winner, R. W. & J. S. Greber, 1980. Prey selection by *Chaoborus punctipennis* under laboratory conditions. Hydrobiologia 68: 231–233.

Yan, N. D. & W. Geirling, 1985. Elevated planktonic rotifer biomass in acidified metal-contaminated lakes near Sudbury, Ontario. Hydrobiologia 120: 199–205.

Yan, N. D., C. J. Lafrance & G. G. Hitchin, 1982. Planktonic fluctuations in a fertilized, acidic lake: the role of invertebrate predators. In R. E. Johnson (ed.), Acid Rain and Fisheries, American Fisheries Society, MD, USA.

Yan, N. D., R. W. Nero, W. Keller & D. C. Lasenby, 1985. Are *Chaoborus* larvae more abundant in acidified than in non-acidified lakes in Central Canada? Holarc. Ecol. 8: 93–99.