

The impact of two *Chaoborus* species on a zooplankton community

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The responses of a zooplankton community to *Chaoborus* predation were studied in large *in situ* mesocosms in Peter Lake. *Chaoborus flavicans*, the native chaoborid, significantly reduced the density of the dominant grazer, *Daphnia pulex*, in relation to controls that lacked *Chaoborus*. *Chaoborus americanus*, a species found only in fishless bogs, reduced *Da. pulex* densities far more than the chaoborid found in Peter Lake, *C. flavicans*. *Chaoborus americanus* also significantly reduced the dominant copepod, *Diaptomus oregonensis*, in relation to both the control and the *C. flavicans* treatment. Chlorophyll *a* concentration did not differ among treatments, indicating that herbivore responses could not be explained by changes in food levels. Our results show that *Chaoborus* predation can greatly affect a zooplankton community, especially daphnids.

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Les réactions de la communauté zooplanctonique à la présence de prédateurs chaoboridés ont été étudiées *in situ* dans de grands mésocosmes, dans le lac Peter. *Chaoborus flavicans*, un chaoboridé indigène, diminue significativement la densité du brouteur dominant, *Daphnia pulex*, si l'on en juge par les populations témoins qui ne sont pas en présence de *Chaoborus*. *Chaoborus americanus*, une espèce trouvée seulement dans les tourbières sans poissons, décime encore plus les populations de *Da. pulex* que le chaoboridé du lac Peter, *C. flavicans*. Les populations du copépode dominant, *Diaptomus oregonensis*, sont aussi réduites significativement par *C. americanus*, par comparaison avec des populations témoins et avec des populations mises en présence de *C. flavicans*. La concentration de chlorophylle *a* est restée la même pour toutes les expériences, ce qui indique que les réactions des herbivores ne peuvent s'expliquer par des changements dans la quantité de nourriture disponible. Nos résultats démontrent que la prédation opérée par *Chaoborus* peut affecter considérablement la communauté du zooplancton, en particulier les daphnies.

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Introduction

Invertebrate predation is an important control mechanism in zooplankton communities when fish predation is low or absent. Large zooplankton dominate fishless assemblages where invertebrate predation structures the zooplankton community. Brooks and Dodson (1965) argued that large zooplankton are competitively superior to smaller zooplankton and thereby exclude them. Later, however, Dodson (1974) showed experimentally that invertebrate predators prey selectively upon small zooplankton and exclude the small species. Therefore, large size can be a refuge from predation by invertebrates.

Invertebrate predation is, however, potentially capable of affecting large zooplankton as well as small zooplankton. Many *Daphnia* show periods of high growth through the size classes vulnerable to *Chaoborus* predation, suggesting that life histories have been shaped by invertebrate predation (Lynch 1980). Nevertheless, *Chaoborus* spp. are capable of suppressing *Daphnia* by predation (Neill and Peacock 1980).

In an earlier study in Peter Lake, MI, bioenergetics data suggested that *Chaoborus flavicans* predation could significantly affect *Daphnia* populations (Elser *et al.* 1987). Here we test that suggestion by direct experimentation. We also compared the effects of a much larger chaoborid, *Chaoborus americanus*, on the zooplankton community. *Chaoborus americanus* is only found in fishless lakes (von Ende 1979), but it can coexist with *Daphnia* (von Ende 1982; Vanni 1988).

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Methods

Peter Lake is a small (2.4 ha), deep (19.3 m), transparent (Elser *et al.* 1986), largemouth bass dominated (Carpenter *et al.* 1987) kettle lake located in Gogebic County on the Upper Peninsula of Michigan. In late June, 1987, nine large tubular bags were filled with lake water and suspended on large wooden frames. The bags measured 1 m across and 10 m deep, penetrating the metalimnion and entering the hypolimnion. The tops of the enclosures were open to the air to allow easy gas exchange with the atmosphere and netting was attached to the frame and stretched over the bag opening to prevent fish from jumping into them.

The experimental enclosures were all stocked with ambient levels of phytoplankton and nonchaoborid zooplankton (rotifers and crustaceans). Collapsed bags were filled with lake water pumped from a depth of 1 m and passed through a 153- μ m mesh screen that removed all crustaceans and many rotifers. Because the pump killed some zooplankton, we reintroduced zooplankton to the filled bags at the same levels found in the lake. Zooplankton were collected by day (to minimize *Chaoborus* densities in the water), using vertical net (153 μ m) hauls. *Chaoborus* were removed individually using wide-mouth pipets, and the nonchaoborid zooplankton were added to the bags.

Three of the bags were stocked with the Peter Lake *Chaoborus* population at levels found in the lake. The population consists mainly of *C. flavicans*, although *Chaoborus trivittatus* is present in small numbers. Three more of the bags were stocked with *C. americanus*, which were collected from nearby fishless Tender Bog (von Ende 1982). The density of *C. americanus* used in the experiment was the density of *C. americanus* found in Tender Bog. We assume that the density of *C. americanus* in Tender Bog is representative of the typical densities attained by this species in lakes of the region. Both chaoborids were collected by vertical net hauls. Chaoborids were sorted individually using wide-mouth pipets, counted, and added to the bags. The

remaining three bags were not stocked with any *Chaoborus* species and served as the control. The bag location selected for each treatment and each replicate was determined randomly.

The bags were sampled throughout the experiment to monitor chlorophyll concentration and track changes in the zooplankton populations. Zooplankton sampling always occurred after nightfall to ensure that the *Chaoborus* had risen from the bottom of the bags. The zooplankton were initially sampled with a 12-L Schindler-Patalas trap taken every metre from 0.5 m to 9.5 m. Two days into the experiment, the bags were sampled again with duplicate 9.5-m hauls with a zooplankton net (mouth diameter, 10 cm; mesh, 80 μ m). The two methods were intercalibrated and subsequent duplicate samples were taken with the small net.

Every week between 09:00 and 10:00, water samples were taken at 0.5 m for chlorophyll analysis. Water for chlorophyll analysis was filtered through Whatman GF/F filters, which were then frozen in order to lyse the algal cells. The chlorophyll was then extracted in methanol for 24 h at 10°C and then determined by fluorometry (Strickland and Parsons 1968). Thermal profiles were taken each week; the temperatures found in the bags were always identical to those found in the lake at corresponding depths.

The zooplankton samples were preserved with 10% sucrose in buffered formalin and enumerated in a gridded dish under a dissecting microscope. Subsamples were counted until the standard error of the number of zooplankters counted per grid cell was less than 10% of the mean. Biomass estimates were computed from average lengths, using the equations of McCauley (1984).

The data were analysed over the time series by repeated measures analysis, following the procedure described by Gurevitch and Chester (1986) using the SAS statistical package (1982). Repeated measures analysis allows the use of several dates when comparing treatment effects, but does not assume that sampling dates are independent of each other, thus avoiding pseudoreplication in time (see Hurlbert, 1984; for other examples of its use, see Vanni, 1986; Cain, 1987; Fulton and Paerl, 1987; and Vanni, 1987). Since this repeated measures analysis can only use complete time series (i.e., one missing value causes a whole replicate series to be discarded), some of our bags were not included in this test. To supplement this analysis, the final densities of each common taxon in all bags were tested for significant differences between treatments using Tukey's paired comparison procedure (Box *et al.* 1978).

Results

The densities of *C. americanus* were greater than those of *C. flavicans* throughout the experiment, partly because of the different amounts stocked at the start of the study. The *C. americanus* treatments initially averaged 0.8 larvae/L, but dropped to about 0.2 larvae/L by the 3rd week, and remained at that level for the remainder of the experiment (Fig. 1). *Chaoborus flavicans* densities initially averaged 0.4 animals/L, but by the 4th week they dropped below 0.06/L and remained below that level for the remainder of the experiment (Fig. 1).

Chlorophyll levels changed during the experiment, but the changes were remarkably consistent among the *Chaoborus* treatments (Fig. 2). Repeated measures analysis revealed no chlorophyll changes between the treatments over the course of the study (Table 1). The chlorophyll values were also not significantly different between treatments at the end of the experiment when tested by Tukey's multiple comparisons procedure (Table 2).

Repeated measures analysis of the common zooplankton taxa revealed few differences (Table 1). Since one day of data was lacking from one of the control treatments and many days of data were lacking from one of the *C. americanus* treatments, neither of these replicates could be considered in the repeated measures analysis, leaving only two replicates of both the control and the *C. americanus* treatment. The effect of this

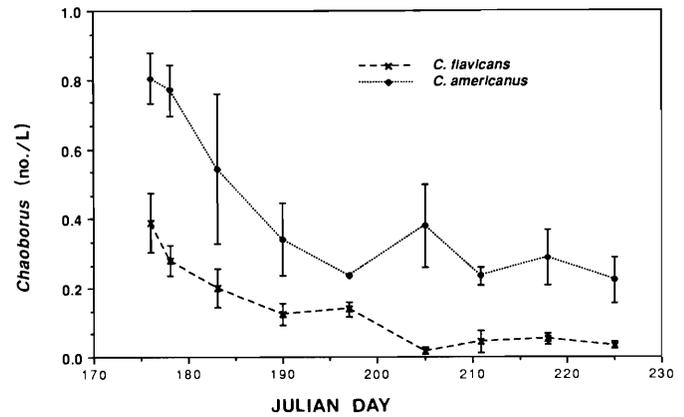


FIG. 1. Mean *Chaoborus* density over time. The error bars represent 1 standard deviation.

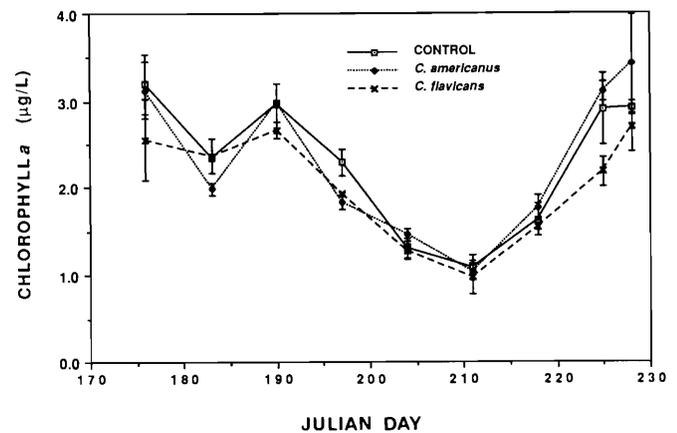


FIG. 2. Chlorophyll measurements over time. The error bars represent 1 standard deviation.

TABLE 1. Repeated measures analysis results

Taxon	<i>P</i> value
<i>Daphnia pulex</i>	ns
<i>Daphnia rosea</i>	ns
Total <i>Daphnia</i>	0.040
<i>Diaptomus oregonensis</i>	0.027
<i>Tropocyclops prasinus</i>	ns
Copepodites	ns
Nauplii	ns
<i>Keratella cochlearis</i>	0.064
<i>Kellicottia longispina</i>	ns
<i>Conochilus unicornis</i>	0.080
<i>Holopedium gibberum</i>	ns
Chlorophyll <i>a</i>	ns

NOTE: ns, $p > 0.10$.

deletion was a decrease in the error degrees of freedom, resulting in a more conservative test. Total *Daphnia* ($p < 0.04$) and *Diaptomus oregonensis* ($p < 0.027$) (Fig. 4) were the only two taxa that exhibited significant differences at the $p < 0.05$ level.

All common zooplankters were tested for differences between treatments using their final experimental densities in Tukey's test (Table 2). *Daphnia pulex*, the dominant zooplankter (by biomass) in Peter Lake (Carpenter *et al.* 1987), showed

TABLE 2. Tukey's paired comparisons

Taxon	Control	<i>C. flavicans</i>	<i>C. americanus</i>	Range
<i>Daphnia pulex</i>	4.54a	1.02b	0.09c	0.84
<i>Daphnia rosea</i>	0.44a	0.13a	0.03a	0.51
<i>Holopedium gibberum</i>	0.33a	0.0a	0.09a	0.56
<i>Tropocyclops prasinus</i>	0.72a	0.64a	0.50a	1.45
<i>Diaptomus oregonensis</i>	1.56a	1.42a	0.21b	0.80
Total adult copepods	2.26a	2.06a	0.96a	1.82
Copepodites	5.42a	10.32a	4.81a	8.36
Nauplii	3.01a	8.58a	7.66a	6.53
Chlorophyll	2.91a	2.79a	3.42a	1.21

NOTE: The first three columns are mean final densities (no./L) of each of the taxa for each treatment. The last column is a statistically determined range at the $p < 0.05$ significance level. If the difference of two final density values is greater than the range, then the difference is significant. Within each taxon, significantly different means are marked with different letters.

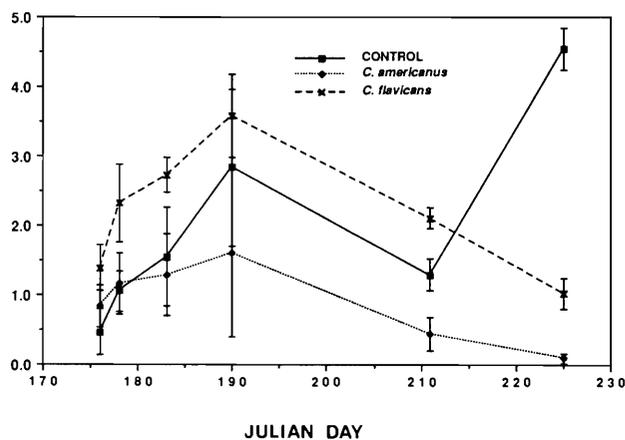


FIG. 3. *Daphnia pulex* density over time. The error bars indicate 1 standard deviation.

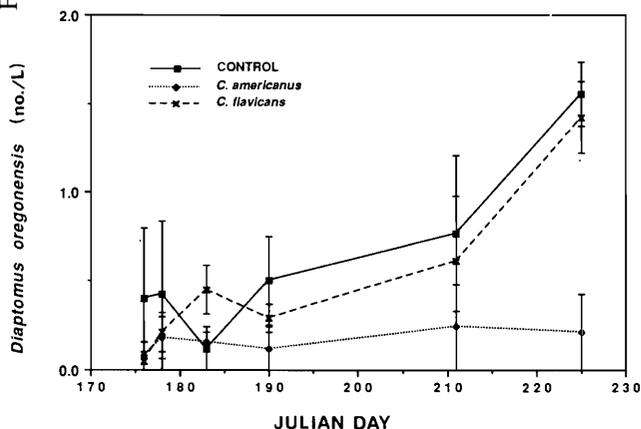


FIG. 4. *Diaptomus oregonensis* density over time. The error bars indicate 1 standard deviation.

the strongest trend (Fig. 3). Each of the three treatment means was statistically different (Table 2). *Chaoborus americanus* kept *Da. pulex* densities low from 2 weeks into the study, whereas *C. flavicans* did not elicit any response in *Daphnia* population size until the final sampling effort 7 weeks into the experiment (Fig. 3).

Diaptomus oregonensis, the dominant copepod in Peter Lake (Carpenter *et al.* 1987), also showed a response to the *C. americanus* treatment. Both the control and the *C. flavicans* treatment means were statistically different from the *C. americ-*

anus mean value (Table 2). *Diaptomus oregonensis* numbers were low throughout the experiment in the *C. americanus* treatment, whereas they rose steadily in both the control and the *C. flavicans* treatments (Fig. 4). No other zooplankton taxa showed significant results using Tukey's test.

Discussion

Chaoborus have been shown to be important invertebrate predators in some systems (Allan 1973; Fedorenko 1975; von Ende 1975; Neill 1978; Elser *et al.* 1987) and of little predatory significance in others (Dodson 1972; Neill and Peacock 1980; Neill 1985). The most devastating effects of *Chaoborus* predation always occur when the midges are in their final instar (Elser *et al.* 1987), but sometimes too few chaoborids survive to that instar to affect the zooplankton population (Neill and Peacock 1980). All of the *Chaoborus* in our study were either 3rd or 4th instar, which means that the midges had previously passed through their life history bottleneck (Neill and Peacock 1980). These *Chaoborus* were large enough to handle at least young *Daphnia* (Pastorok 1980), if not adults (Lynch 1980; Elser *et al.* 1987; Vanni 1988). Many studies have shown that *Daphnia*, especially adults, are not preferred prey (Sikorowa 1968; Lewis 1977; Pastorok 1978, 1980; Spitze 1985). Therefore, *Daphnia* population size would appear to be a relatively insensitive indicator of *Chaoborus* predation pressure. In this study, however, both species of *Chaoborus* greatly affected the zooplankton population.

Chaoborus americanus had a far greater effect on *Da. pulex* than did *C. flavicans* (Fig. 3). This effect could be attributed to several factors. *Chaoborus americanus* was initially stocked at double the density of *C. flavicans* (Fig. 1), because of the higher density of *C. americanus* found in Tender Bog (von Ende 1982). Also, *C. americanus* is an incomplete migrator (von Ende 1982), whereas most *Chaoborus* (including *C. flavicans*) migrate by day into the hypolimnion and some even burrow into the sediments (Teraguchi and Northcote 1966; Roth 1968; Hrbacek 1977). Fedorenko and Swift (1972) found that even 4th instar *C. americanus* were found above the thermocline in Eunice Lake. Since *C. americanus* larvae live a much larger portion of their life in relatively warm water, their metabolism would also be expected to be higher than the hypolimnetic *C. flavicans*, possibly leading to higher activity and elevated consumption rates (Elser *et al.* 1987). Furthermore, the incomplete migrator *C. americanus* is exposed to its zooplankton food throughout the diel cycle, whereas *C. flavicans* spends the daylight hours in the food-poor hypolimnion. Finally,

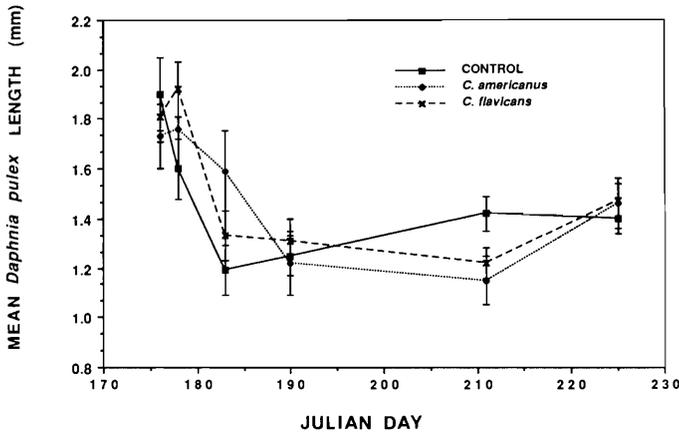


FIG. 5. *Daphnia pulex* mean length over time.

C. americanus is an exotic predator to Peter Lake, so the zooplankters present may not have previously developed any defenses against it.

The fact that chlorophyll concentrations were very similar in the bags indicates that predation, not food supply, caused the differences observed. Since the average size of *Daphnia* did not change across treatments or over the course of the experiment (Fig. 5), it appears that the effect was not solely caused by predation upon young *Daphnia*.

Diaptomus oregonensis, a calanoid copepod, was unaffected by *C. flavicans*, although *C. americanus* kept the *Di. oregonensis* population low throughout the experiment (Tables 1 and 2, Fig. 4). *Chaoborus* was found to be highly selective for copepods in other studies (Lewis 1977). Among copepods, *Chaoborus* selects calanoids over cyclopoids (Anderson and Raasveldt 1974). Therefore, it is surprising that the *Di. oregonensis* densities were similar in both the control and the *C. flavicans* treatment. Low initial densities of *Di. oregonensis* made it difficult to detect statistically the effects of *C. flavicans*.

Most of the zooplankton taxa tested showed no differences between treatments. It is possible that low densities made detection of responses difficult, or that complex responses occurred. For example, although most rotifers did not respond to the varying levels of predation pressure, perhaps there was a trade-off between increased predation and reduced competition. Neill (1984) found that rotifers had a higher survivorship in the presence of *C. trivittatus* because of lessened competition with cladocerans for food. Our results indicated no difference in chlorophyll levels between treatments, but perhaps there was lesser quality phytoplankton available in the treatment where heavy grazing by *Daphnia* occurred. Cladocerans can also control rotifer populations by accidentally wounding them, so the presence of cladocerans is detrimental to rotifers even when food is abundant (Gilbert and Stemberger 1985).

In summary, our results show that *Chaoborus* predation can directly control populations of *Daphnia pulex*, which is often the most important herbivore in trophic cascades that regulate phytoplankton (Carpenter 1988). Our results raise the possibility that *Chaoborus* can, in some circumstances, limit the success of *Da. pulex* when planktivorous fishes are absent or scarce. Strong interactions between *Daphnia* and *Chaoborus* are known from highly oligotrophic lakes (Neill and Peacock 1980; Neill 1984), but our results show direct control of *Daphnia* by *Chaoborus* in more productive systems. We suggest that the interactions of *Chaoborus* with planktivorous fish and *Daphnia* merit more detailed study in mesotrophic and eutrophic lakes.

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