Chaoborus populations: response to food web manipulation and potential effects on zooplankton communities

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Chaoborus populations were studied in two lakes in which fish predation was experimentally reduced, and in a reference lake. In Tuesday Lake, major reduction of fish predation led to substantial increases in density of *Chaoborus punctipennis*. Analysis of crop contents and estimates of consumption rates suggested that *C. punctipennis* caused declines of rotifer and copepod populations following the manipulations. In Peter Lake, lesser changes in fish predation caused no major change in density of *Chaoborus flavicans*, perhaps because food limitation compensated for effects of reduced predation. In both Peter Lake and the reference lake, Paul Lake, *C. flavicans* preyed heavily and selectively on *Daphnia* less than about 1.4 mm in total length. Bioenergetic calculations indicated that up to 46% of the daphnids were consumed daily. At some times of the year, certain zooplankton populations (especially noncolonial rotifers, small copepods, and small cladocerans) were strongly influenced by *Chaoborus* predation.

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Les populations de *Chaoborus* ont été suivies dans deux lacs où la prédation par les poissons a été réduite artificiellement, ainsi que dans un lac témoin. Dans le lac Tuesday, une forte réduction de la prédation par les poissons a amené des augmentations importantes des densités de *Chaoborus punctipennis*. L'analyse des contenus stomacaux et des estimations des taux de consommation indiquent que *C. punctipennis* a entraîné des réductions dans les populations de rotifères et de copépodes après la manipulation. Dans le lac Peter, des réductions moindres de la prédation des poissons n'ont occasionné aucun changement important dans la densité de *Chaoborus flavicans*, peut-être parce qu'une pénurie de nourriture a compensé les effets de la réduction de la prédation. Dans le lac Peter et dans le lac Paul (témoin), *C. flavicans* était responsable d'une prédation forte et sélective sur les *Daphnia* de taille inférieure à 1,4 mm. Des compilations bioénergétiques indiquent que jusqu'à 46% des daphnies étaient consommées chaque jour. À certaines périodes de l'année, quelques-unes des populations de zooplancton (en particulier, les rotifères non coloniaux, les petits copépodes et les petits cladocères) étaient fortement affectées par la prédation des *Chaoborus*.

[Traduit par la revue]

Introduction

Larvae of the phantom midge, *Chaoborus*, are common invertebrate predators in many lakes. They feed primarily on zooplankton, and may feed selectively on certain species. *Chaoborus* population size is regulated by both predation and food availability (von Ende 1979; Neill and Peacock 1980). Thus, changes in the trophic levels either above or below *Chaoborus* may cause changes in *Chaoborus* populations, which in turn can affect the zooplankton community structure.

Many studies have analyzed crop contents of larval *Chaoborus*, and drawn inferences about the rank order of selectivity of common food items. Lewis (1977), for example, suggests the following order: *Bosmina* > copepod copepodids and adults, *Diaphanosoma* > rotifers > nauplii, *Daphnia*. Size has a large effect on selectivity, and different *Chaoborus* species would be expected to have somewhat different preferences. Selectivity varies among instars, in part because smaller instars have difficulty handling larger zooplankton (Fedorenko 1975*a*, 1975*b*; Chimney et al. 1981). *Chaoborus* larvae grew faster on a copepod diet than on a *Daphnia* diet in laboratory studies, which implies that selective feeding on copepods is adaptive (Pastorok 1980*b*). On the other hand, *Chaoborus* appear to come into contact with *Daphnia* more frequently in their environment and as a result feed heavily on them. Fedorenko (1975*a*, 1975*b*) suggests that the diet of instar IV larvae is determined largely by spatial availability of prey, while Pastorok (1980*a*) suggests that behavioral plasticity of *Chaoborus* may also be important.

The elimination or introduction of planktivorous fish can affect *Chaoborus* populations. In some instances, introduction of predatory fish has caused a shift in dominance from one *Chaoborus* species to another (von Ende 1979). Food availability also affects *Chaoborus* survivorship, particularly in the early instars where lack of food contributes to high juvenile mortality (Neill and Peacock 1980).

During whole-lake fish manipulation experiments (Carpenter et al. 1987), we monitored the dynamics of *Chaoborus* populations and their diets. In this paper, we examine the effects of the whole-lake manipulations on *Chaoborus* population densities, feeding selectivities, and consumption rates. We also evaluate the possible effects of these changes in *Chaoborus* predation pressure on the zooplankton community.

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Materials and methods

Study sites

Paul, Peter, and Tuesday lakes lie within 0.5 km of each other in the same moraine (sec. 36, tp. 45 N, rge. 42 W, Gogebic County, MI) within the University of Notre Dame's Environmental Research Center. All three lakes are small but relatively deep (Paul Lake, area = 1.2 ha, max depth = 12.2 m; Peter Lake, area = 2.4 ha, max depth = 19.3 m; Tuesday Lake, area = 0.8 ha, max depth = 18.5 m). Further limnological descriptions are given by Carpenter et al. (1986).

Experimental manipulation

Fish manipulations are fully described by Carpenter et al. (1987) and are summarized briefly below. Before manipulation, Paul and Peter lakes contained only largemouth bass (*Micropterus salmoides*). Planktivorous fishes have been absent from these lakes since the late 1970s (Elser et al. 1986*b*). Tuesday Lake frequently becomes anoxic in winter, and contained winterkill-tolerant planktivorous minnows (predominantly redbelly dace, *Phoxinus eos*). *Chaoborus* is a prominent item in the diets of all these fishes (Carpenter et al. 1987; Hodgson and Kitchell 1987). In May 1985, fish were exchanged between Peter and Tuesday lakes; 90% of the adult bass in Peter Lake were moved to Tuesday Lake, and 90% of the minnows in Tuesday Lake were moved to Peter Lake. No changes were made in Paul Lake. In Tuesday Lake, bass survivorship was high and by mid-July 1985 the introduced bass had almost completely eliminated the minnow population (Carpenter et al. 1987). In Peter Lake, minnows were eliminated in less than 1 month by the remaining adult bass, while recruitment of young of the year bass was high (Carpenter et al. 1987). Bass fed inshore through most of 1985; consequently, planktivory by fish was reduced. Overall, planktivory by fish in both manipulated lakes was less in 1985 than in 1984.

Zooplankton and phytoplankton collection and analysis

Zooplankton samples were collected weekly between 09:00 and 10:00 from mid-May to mid-September in 1984 and 1985 using vertical hauls of an 80 μm mesh Nitex net. Single hauls were made in 1984 and duplicate hauls were pooled in 1985. Zooplankton were identified, counted, and measured under a dissecting microscope. Length was converted to mass using the equations of Downing and Rigler (1984). Biomass of *Holopedium gibberum* was calculated from a general zooplankter equation (Peters and Downing 1984).

Biomass and density estimates for *Glenodinium* sp. were made from weekly epilimnetic water samples. *Glenodinium* cell volume was calculated from measurements of cell dimensions (Elser et al. 1986*a*) and converted to dry weight using the equation of Reynolds (1984).

Chaoborus collection and analysis

Chaoborus were sampled after dusk at biweekly intervals from 31 May to 18 September 1985 and from 1 July to 30 September 1984. Three to nine 3-m vertical hauls were made with a 202 μm mesh net and samples were preserved in 5% formalin. Although head capsules of instar I larvae are 140–150 μm across and could possibly pass through the net, we believe that instar I larvae generally encountered the net lengthwise and were adequately represented in the samples. In 1985 only, samples for *Chaoborus* crop analysis were collected at the same time with an 80 μm mesh net. Initially, we preserved samples following the method outlined by Swift and Fedorenko (1973), but then we switched to preserving the samples with Lugol's solution (Lewis 1977). These methods worked equally well in preventing eversion of the *Chaoborus* crop and preserving food items in the crop.

Crop contents were analyzed according to methods outlined by Swift and Fedorenko (1973). Only crops of instar III and IV *Chaoborus* were examined. For each sample, we attempted to obtain data from at least 10 animals with full crops. The number of individuals dissected ranged from 12 to 80. The number of prey items per crop depended on the type of prey eaten; smaller prey were more abundant in the crops than larger prey. The number of prey per full crop ranged from 1 to 14. Masses of individual zooplankters found in the crop were estimated from the average masses of each corresponding species in the water column. Whole *Daphnia* were measured when possible. Otherwise, *Daphnia* postabdominal claws were measured and converted into *Daphnia* length following the equations of Kitchell and Kitchell (1980). The selectivity of *Chaoborus* for each prey species was calculated using the electivity coefficient recommended by Jacobs (1974):

$$[1] \qquad D = (r - p)/(r + p - (2rp))$$

where r is the proportion of the given prey species in the diet and p is the proportion of that species in the environment. Values range from 0 to +1 for positive selection and from −1 to 0 for negative selection.

Estimates of food consumption by instar III and IV larvae of *Chaoborus* were made using the bioenergetics approach of Swift (1976). Consumption (C) in milligrams of dry mass per animal in a day was given by:

$$[2] \qquad C = (P + R)/E$$

where P is growth in milligrams grown per animal each day, E is efficiency of assimilation (we used $E = 0.67$, as calculated by Swift (1976)), and R is respiration in milligrams respired per animal each day, calculated from body size and temperature using the regression equations of Swift (1976), assuming that 1 μL O_2 is equivalent to 9.13×10^{-4} mg dry mass (Peters 1983). We calculated the lower limit assuming that larvae spent 6 h d^{-1} in the epilimnion and 18 h d^{-1} in the hypolimnion; for the upper limit we assumed larvae spent 9 h d^{-1} in the epilimnion and 15 h d^{-1} in the hypolimnion. These assumptions were based on reported vertical migration patterns of *Chaoborus* (Saether 1970). In most cases, P could not be calculated directly because continuous recruitment made it impossible to distinguish cohorts. Therefore, we assumed that $P = 0$ when change in biomass was zero or negative, and that P equalled the change in biomass when it was positive. This assumption underestimates P by the amount of secondary net production that does not appear as a net positive biomass increment. The assumption was tested by calculating productivity and its error by Allen curve methods (Carpenter 1984) during one time interval when cohorts could be defined. Once C was calculated (eq. 2), we estimated how much of any particular food item (i) was eaten by *Chaoborus*:

$$[3] \qquad C_i = Cf_i$$

where f_i is proportion by mass of food item i in the crop and C is the consumption rate. First-order error analysis (Meyer 1975) was used to calculate 95% confidence intervals for C_i from the errors in P and R. Like all propagated errors, these confidence intervals are minimum estimates because they do not include unknown sources of variance.

Results

In the reference lake, Paul Lake, densities of instar IV *Chaoborus flavicans* were similar in September 1984 and 1985 (Fig. 1). In Peter Lake, effects of bass removal on the *C. flavicans* population was slight. Both *C. punctipennis* and *C. trivittatus* occurred in small numbers in Paul and Peter lakes. *C. flavicans* densities were generally higher in Paul Lake than in Peter Lake, but this difference was unrelated to the fish manipulations.

In Tuesday Lake, *Chaoborus* populations were larger following the addition of bass and removal of minnows (Fig. 1). In both years, *C. punctipennis* was the dominant chaoborid, although *C. flavicans* and *C. trivittatus* were also present. In 1985, *C. punctipennis* emerged 2–3 weeks earlier than in 1984. Increased densities of all instars of *C. punctipennis* after emergence in 1985 could have resulted from increased recruitment and (or) increased survivorship. Because pre-emergence densities of instar IV larvae were similar in 1984 and 1985, increased survivorship probably accounted for greater densities in 1985. The absence of nearby lakes with large *C. punctipennis*

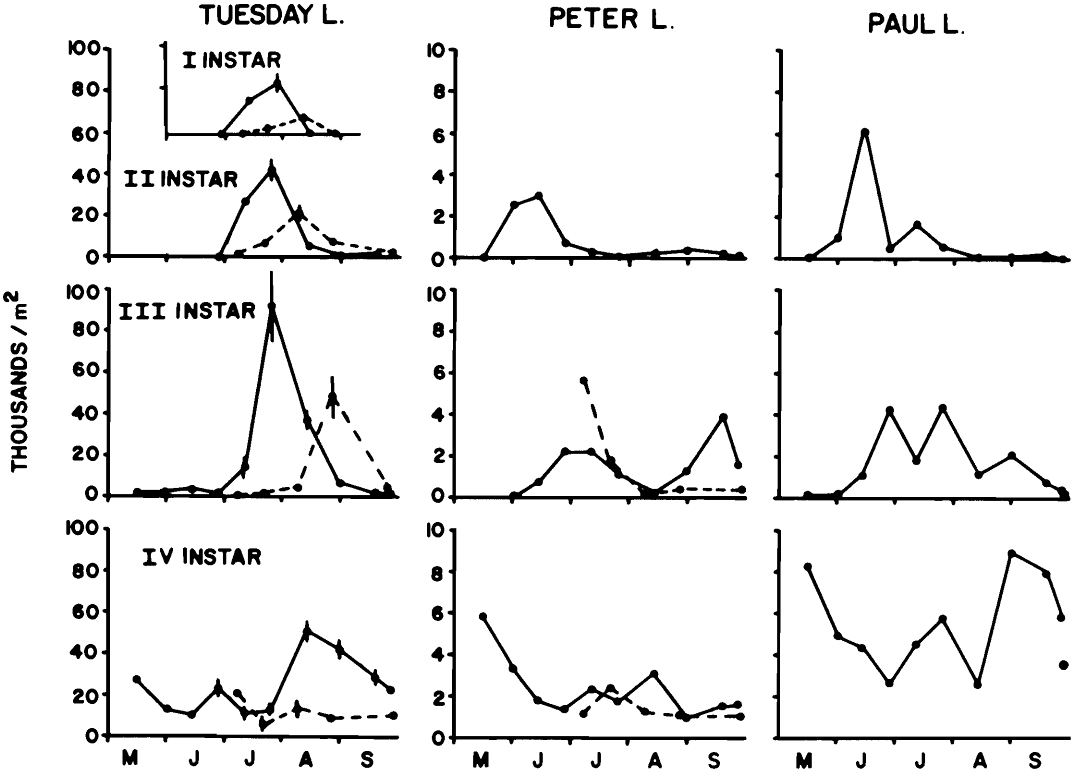

FIG. 1. Density of instars of *C. punctipennis* in Tuesday Lake and *C. flavicans* in Paul and Peter lakes (May–September) vs. time for 1984 (- - -) and 1985 (—). The single data point in September in Paul Lake is for 1984. Vertical bars show standard errors of six samples.

populations made it unlikely that increased densities resulted from oviposition by immigrating adults.

Changes in the diet of *C. punctipennis* in Tuesday Lake during 1985 (Fig. 2) corresponded to temporal changes in the zooplankton community (Fig. 3). During most of the summer, copepods (primarily adults and copepodids of *Tropocyclops prasinus*) dominated the biomass of food in *C. punctipennis* crops. *Bosmina longirostris* and *Diaphanosoma leuchtenbergianum* were consumed in May and early June, but contributed less than 3% to the total biomass of consumed prey. *Diaphnia pulex, D. rosea,* and *Holopedium gibberum* were eaten in August and September and contributed substantially (>90%) to the biomass of the crop contents. *Chaoborus punctipennis* consumed rotifers throughout most of the summer until the end of August. Rotifers identified in the crops included *Keratella cochlearis, Kellicottia bostoniensis, Polyarthra vulgaris, Conochiloides dossuarius,* and *Trichocerca multicrinis*. Rotifers accounted for only a small portion of the biomass in the crops, except in early August (Fig. 2), when only rotifers and the dinoflagellate *Glenodinium* were found in the crops. *Glenodinium* was present in *C. punctipennis* crops during most of the summer, but contributed only a very small amount of food biomass except in early August (Fig. 2).

The percentage of *C. punctipennis* found with full crops declined over the summer of 1985 in Tuesday Lake (Fig. 4). This decline corresponded to declining densities of rotifers and *Tropocyclops* (Fig. 3). *Bosmina* was never abundant in 1985 (Fig. 3). The decline in chaoborids with full crops in 1985 corresponded to an increase in mean zooplankter size (Fig. 4) due to increasing dominance of the large cladocerans *Daphnia* and *Holopedium*.

In Tuesday Lake in 1985, *C. punctipennis* selected for cladocerans in early and late summer (Fig. 5). In early summer, *Bosmina* and *Diaphanosoma* were selected, while in late summer, *Daphnia* and *Holopedium* were preferred. Although *Daphnia* and *Holopedium* were present in small numbers throughout the summer, *C. punctipennis* did not select for them until the copepod and rotifer assemblages had declined dramatically (cf. Figs. 2, 3, and 5). *C. punctipennis* selected for copepods at three dates before the copepod decline in August, but did not select for them on the two dates corresponding to the copepod biomass maxima. *Chaoborus punctipennis* did not select for rotifers as a group, although large numbers of certain taxa (*Keratella, Kellicottia, Conochiloides,* and *Trichocerca*) were consumed.

The diets of *C. flavicans* in Paul and Peter lakes were similar (Table 1). Most of the biomass in the crops came from *Daphnia* (both *D. rosea* and *D. pulex*). The electivity indices indicated that *C. flavicans* in Peter and Paul lakes always selected for cladocerans but never for copepods (Fig. 5). *Chaoborus flavicans* in Peter Lake selectively consumed rotifers in early summer.

Chaoborus flavicans did not consume *Daphnia* size classes in proportion to their abundance (Fig. 6). Rather, *Daphnia* less than about 1.4 mm were consumed preferentially by *C. flavicans* in both Paul and Peter lakes.

In our calculations of consumption rate, no serious error resulted from estimating P from the biomass increment. In Tuesday Lake during 25 July – 13 August, cohorts could be discerned, and P (with 95% confidence interval) was 3440 ± 580 mg m^{-2}. Over the same period, the biomass increase (with 95% confidence interval) was 3070 ± 450 mg m^{-2}. These numbers are not significantly different.

Estimated consumption rates indicated that *Chaoborus* predation could have significant effects on certain taxa at certain times (Fig. 7). In Paul Lake, *C. flavicans* had minimal effects

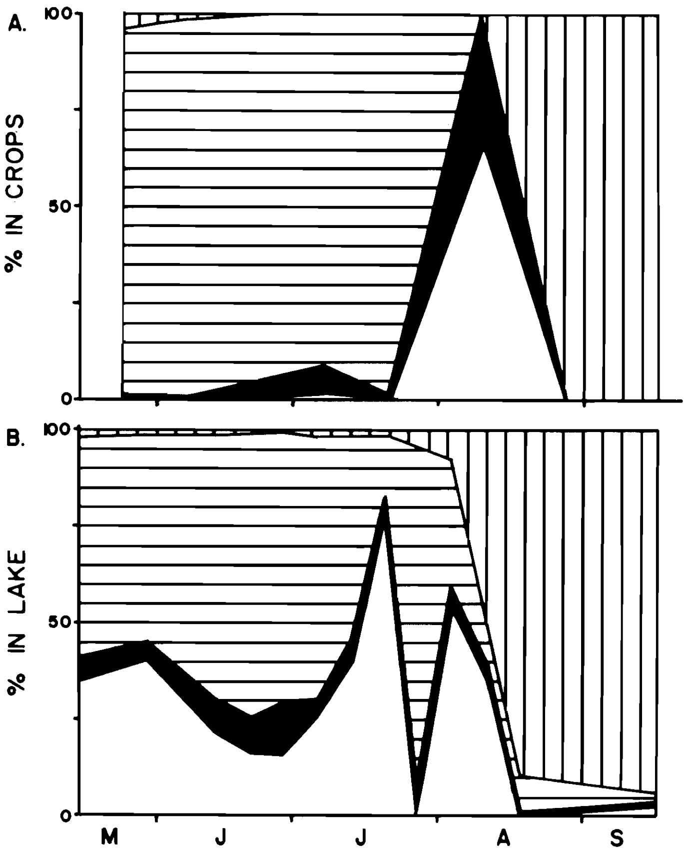

FIG. 2. Diet of *C. punctipennis* (A) and standing stock of zooplankton and the alga *Glenodinium* (B) in Tuesday Lake in 1985. Values are expressed as the percent contribution by biomass to the crop contents (A) and the standing stock (B). Organisms are grouped as cladocerans (vertical hatching), copepods (horizontal hatching), rotifers (black), and *Glenodinium* (white).

on rotifers and copepods, but could potentially consume up to 21% of the cladoceran biomass in a day. In Peter Lake, *C. flavicans* had minimal effects on copepods, but could consume up to 20% of the rotifer biomass in a day. In Peter Lake, predation on *Daphnia* by *C. flavicans* in May was severe.

The potential impact of *Chaoborus* predation was greatest in Tuesday Lake (Fig. 7). Heavy predation on rotifers and copepods (predominantly *Tropocyclops*) during June and July (Fig. 7) contributed to declining biomasses of these zooplankters (Fig. 2B). Predation by *C. punctipennis* on *Bosmina* (the only cladoceran present) in May and early June (Fig. 7) contributed to low cladoceran biomass during this period (Fig. 2). The considerable decline in these prey populations during the summer of 1985 contrasts with seasonal trends in 1984 (Fig. 3). However, predation by *C. punctipennis* had only a minor effect on the dense populations of *Daphnia* and *Holopedium* that developed in Tuesday Lake in August and September (cf. Figs. 2 and 7). Even though cladocerans were the most important food item in the crops in August and September (Fig. 2), most *Chaoborus* had empty crops (Fig. 4), and total consumption of cladocerans was therefore low (Fig. 7).

Discussion

The cascading trophic interactions hypothesis postulates that a decline in planktivory by fishes leads to increased planktivory by invertebrates such as *Chaoborus* (Carpenter et al. 1985). The increased densities of *Chaoborus* following the fish manipulation in Tuesday Lake support this hypothesis. Survivorship of larval instars I and II depends strongly on the supply of food, principally rotifers (Fedorenko 1975*a*, 1975*b*; Neill and Peacock 1980; Chimney et al. 1981). During June and July 1985, rotifer densities in Tuesday Lake were similar to those of June and July 1984 (Fig. 3), suggesting that food availability for instar I and II larvae was similar in the 2 years. Therefore, we attribute the increased density of *Chaoborus* instars III and IV in 1985 to decreased predation coupled with adequate food supplies for younger larvae.

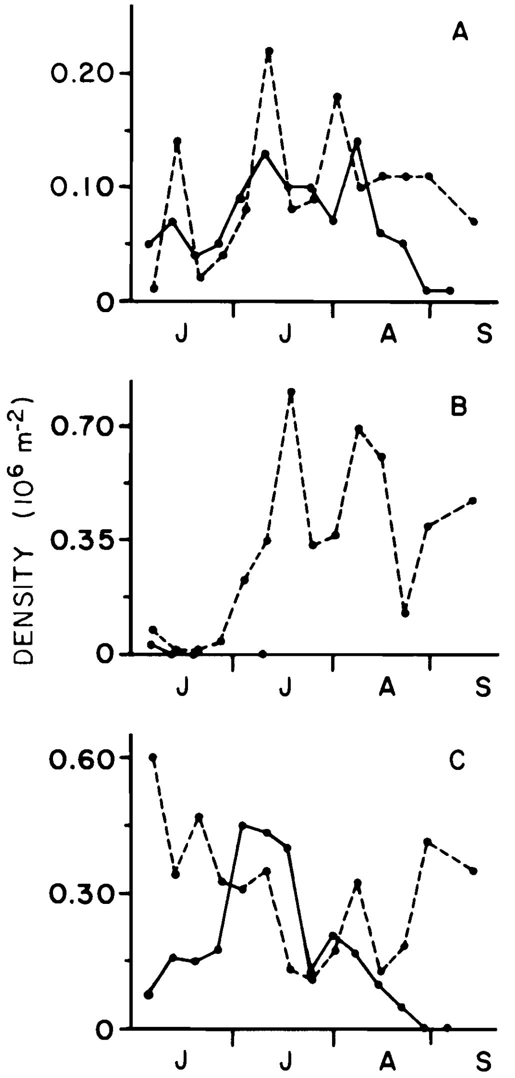

FIG. 3. Density of selected prey items in Tuesday Lake during 1984 (- - -) and 1985 (—). (A) *Tropocyclops prasinus*; (B) *Bosmina longirostris*; (C) total rotifers.

There was little net change in the *Chaoborus* population of Peter Lake following the manipulation. Although zooplankton biomass changed after the fish manipulation (Carpenter et al. 1987), it is difficult to relate these changes conclusively to the stability of the *Chaoborus* population.

The responses of zooplankton prey are most sensitive to changes in instar IV populations of *Chaoborus*, because about three-quarters of the growth and food consumption occurs during this stage. For example, Neill and Peacock (1980) found that increased densities of *Chaoborus* instars III and IV in enclosures had catastrophic effects on the zooplankton. Our results suggest that *Chaoborus punctipennis* had similarly

TABLE 1. Diet of *C. flavicans* and zooplankton abundance in Paul and Peter lakes in 1985; food items and zooplankton are expressed as percent contribution by biomass to the crop content and to the standing stock, respectively

	Crop contents, %			Standing stock, %		
	Cladocerans	*Copepods*	*Rotifers*	*Cladocerans*	*Copepods*	*Rotifers*
Paul Lake						
85-5-31	99.99	0.0	0.01	83.76	12.60	3.63
85-6-27	100.00	0.0	0.0	41.33	54.94	3.73
85-7-25	99.99	0.0	0.01	66.90	31.82	1.68
85-8-30	100.00	0.0	0.0	76.45	22.97	0.58
Peter Lake						
85-5-31	94.29	5.37	0.34	72.22	25.11	2.66
85-6-13	78.1	21.79	0.11	67.27	32.16	0.55
85-6-27	97.95	2.03	0.02	78.30	21.47	0.23
85-7-11	81.36	18.62	0.01	78.11	21.45	0.44
85-7-25	91.07	8.93	0.0	79.57	19.22	1.21
85-8-13	99.98	0.0	0.02	54.62	42.59	2.80
85-8-30	80.64	19.28	0.07	67.68	25.15	6.19

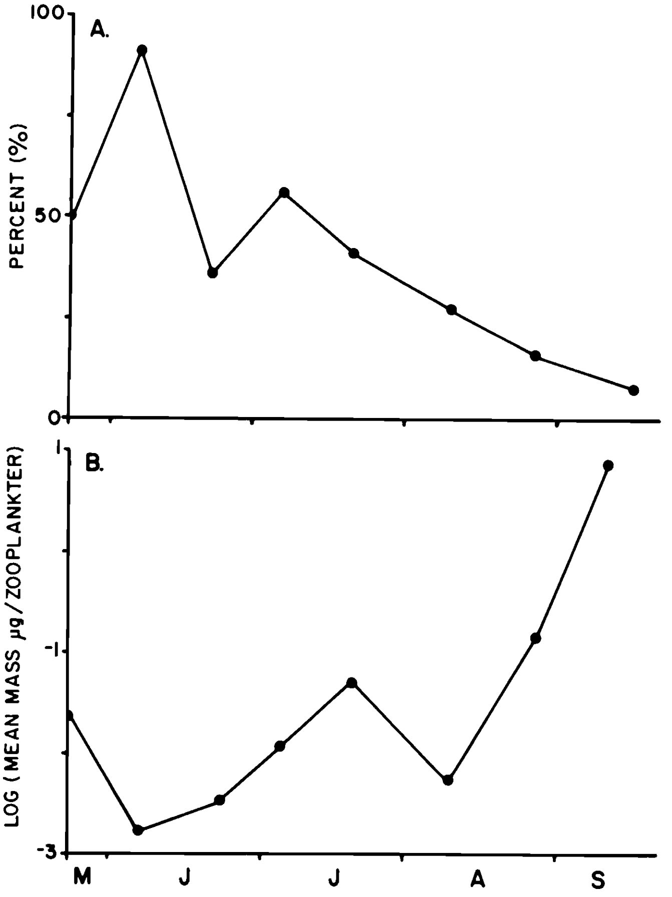

FIG. 4. Percentage of *C. punctipennis* with full crops (A) and log of mean mass (μg) per zooplankter (B) for May–September.

strong effects on certain zooplankton populations in Tuesday Lake.

Increased *Chaoborus* density in Tuesday Lake in 1985 had negative effects on populations of rotifers and copepods, and possibly *Bosmina*. The declines in rotifer and copepod densities during August 1985 corresponded to maximal densities of instar IV *C. punctipennis* (Fig. 1) and consumption rates large enough

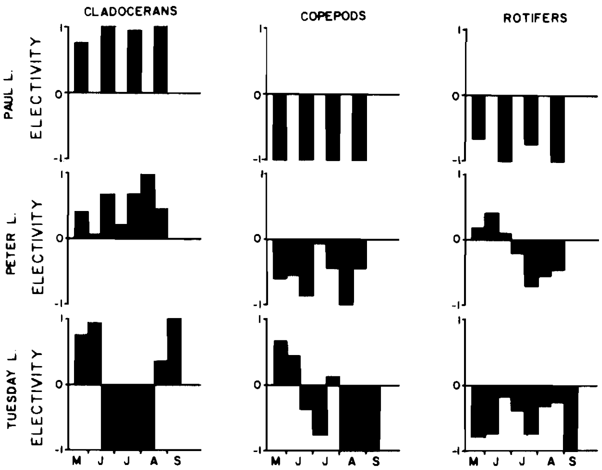

FIG. 5. Electivity indices for May–September, grouped by food item and lake. The indices are for *C. punctipennis* in Tuesday Lake and *C. flavicans* in Paul and Peter lakes.

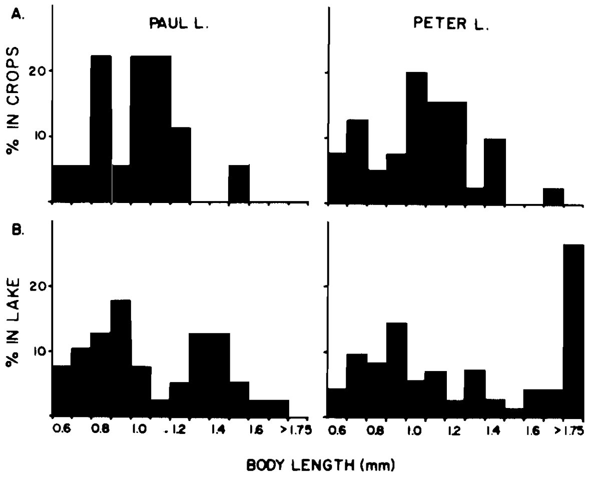

FIG. 6. Body length distribution of *Daphnia* in *C. flavicans* crops (A) and in the lakes (B), for Paul and Peter lakes. Values are expressed as percentage of *Daphnia* contributing to a particular size range.

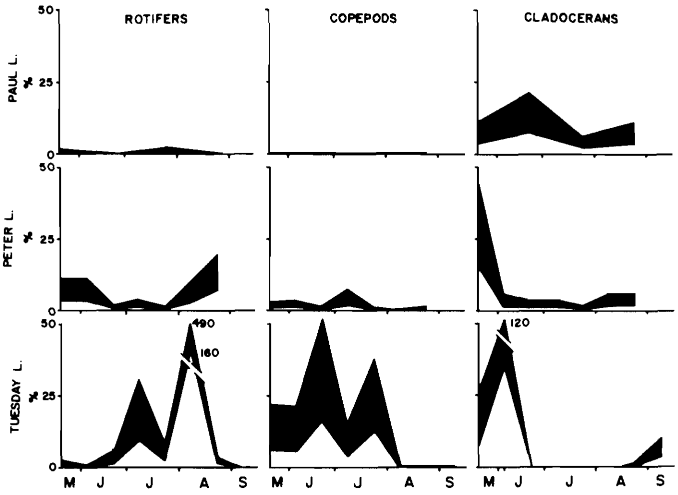

FIG. 7. Percentage of zooplankton standing crop potentially consumed by *Chaoborus* in 1 day for May–September 1985, arranged by lake and food item. Height of the black band denotes a 95% confidence interval for mean consumption.

to remove the entire rotifer population in a day (Fig. 7). No comparable declines in rotifer and copepod populations occurred in 1984 (Fig. 3). Neill (1981) noted that under certain conditions copepods cannot reproduce rapidly enough to compensate for losses to predation by *Chaoborus*. Consumption estimates indicate that *Chaoborus* affected copepod populations in 1985, especially as many of the copepods found in the crops were adults. The estimated loss rates to *Chaoborus* predation of 10–50% of the population per day could have strong negative effects on copepod populations with relatively long turnover times. In 1984, *Bosmina* were common in Tuesday Lake and constituted over 90% of the biomass in the crops of *C. punctipennis* in a sample taken in August (P. Soranno, personal observation). In late May 1985, *C. punctipennis* did select for *Bosmina*; consumption rates indicated that effects on the *Bosmina* population were severe and could explain the very low densities of *Bosmina* observed throughout 1985. Our conclusion is corroborated by von Ende and Dempsey (1981), who found that high densities of *C. americanus* were responsible for the absence of *Bosmina* from a fishless lake.

In contrast to its potential effects on rotifers and copepods, *C. punctipennis* had little effect on populations of *Daphnia* and *Holopedium* in Tuesday Lake. By reducing densities of rotifers and copepods, high *Chaoborus* predation may have facilitated the increase in populations of large cladocerans. Once established, the *Daphnia* and *Holopedium* populations may have further contributed to the declining densities of rotifers and copepods through interference and competition for algal food (Neill 1984; Gilbert and Stemberger 1985). Increased densities of large cladocerans were accompanied by an increase in the number of *Chaoborus* with empty crops. In early August 1985, when instar III and IV populations were maximal, only rotifers and algae were found in *C. punctipennis* crops. Starvation may have caused the decline in the *C. punctipennis* population during September 1985.

The most striking result from Paul and Peter lakes was the potentially strong impact of *Chaoborus flavicans* predation on *Daphnia pulex* and *D. rosea*. *Chaoborus flavicans* (instar IV head capsule length = 1.34 mm) is larger than *C. punctipennis* (instar IV head capsule length = 1.04 mm). This size difference may explain the more effective predation by *C. flavicans* on daphnids. In both Paul and Peter lakes, *C. flavicans* had positive electivities for *Daphnia*. Some studies have shown that *Daphnia* is not a preferred food of *Chaoborus* (Lewis 1977; Pastorok 1980*b*), although Sardella and Carter (1983) also found large numbers of *Daphnia* in *C. flavicans* crops. High encounter rates between *C. flavicans* and *Daphnia* may account for this high selectivity (Fedorenko 1975*a*, 1975*b*; Pastorok 1980*b*).

In our lakes, *Chaoborus* fed on pre-reproductive *Daphnia* less than about 1.4 mm in length. Spitze (1985) found that attack rates by *Chaoborus* on *Daphnia* declined for prey larger than about 1.1–1.4 mm, which is consistent with our results. Neck teeth, which interfere with predation by *Chaoborus* (Krueger and Dodson 1981), were commonly observed on small *Daphnia*, but we did not measure frequencies of individuals with and without neck teeth. Our consumption estimates are similar to those of other authors (Fedorenko 1975*a*, 1975*b*; Lewis 1977), and we agree with Allan (1973) that *Chaoborus* predation can significantly limit the growth of *Daphnia* populations. Dodson (1972) also found that *Chaoborus* eat small, nonreproductive daphnids and are significant predators on *D. rosea*. *Chaoborus* predation would select for daphnid life histories that minimized mortality between birth and attainment of about 1.4 mm in length (Lynch 1980). High neonate production coupled with fast body growth (Neill 1981) or large body size at birth may account for the persistence of *Daphnia* populations despite high predation rates by *Chaoborus* in Paul and Peter lakes.

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