

Complex responses of *Chaoborus* to changes in fish populations

C. W. Ramcharan¹, N. D. Yan², D. J. McQueen³, A. Pérez-Fuentetaja⁴,
E. Demers³, and J. A. Rusak⁵

with 6 figures and 3 tables

Abstract: Larvae of the phantom midge, *Chaoborus* spp., are often the dominant invertebrate planktivore in temperate lakes. *Chaoborus* population dynamics may be influenced from the top-down by fish planktivory and in turn, may strongly influence the dynamics of their zooplankton prey. We analyzed this trophic cascade from planktivorous fish, through *Chaoborus*, to zooplankton using a seven-year study of fish biomanipulation in two oligotrophic lakes, located near Dorset, Ontario. This paper is one of a series of publications based on "The Dorset Project". Each paper focuses on different aspects of the whole-system experiment, from water chemistry to fish. Ranger Lake had a high biomass of piscivores (largemouth bass) and few planktivorous fish, while Mouse Lake with no obligate piscivores had an abundance of fish planktivores. After three years of initial study (1991–1993) the bass were removed from Ranger Lake and transferred to Mouse Lake. The entire communities of both lakes were studied for four more years (1994–1997). Before the bass transfer, total biomass of *Chaoborus* was similar in both lakes. Mouse Lake was dominated by smaller chaoborids, *C. albatius* and *C. punctipennis*, while Ranger Lake was dominated by the larger *C. flavicans* and *C. trivittatus*. After the bass transfer, planktivory was greatly reduced in Mouse Lake but did not increase as dramatically in Ranger Lake. *Chaoborus* biomass in Mouse Lake increased and there was a strong shift towards larger species. In Ranger Lake, *Chaoborus* biomass decreased somewhat, but the responses were not as strong as in Mouse Lake. Shifts in *Chaoborus* body size distributions, changes in vertical migration, and response lag times may all help weaken the trophic link between *Chaoborus* and planktivorous fish. Overall, our results suggest that responses of invertebrate predators to changes in fish planktivory are more complex than indicated by the trophic cascade hypothesis.

Introduction

The role of invertebrate predators in limnetic trophic cascades is ambiguous. In the original description of fish biomanipulation by SHAPIRO et al. (1975), invertebrate predators were ignored. In CARPENTER et al.'s (1985) trophic cascade theory, predation by planktivorous fish

Authors' addresses: ¹Dept. Biological Sciences, Louisiana State University, Baton Rouge, LA, 70808, USA. ²Dorset Research Center, The Ontario Ministry Of the Environment, PO Box 39, Dorset, Ontario, P0A 1E0, Canada. ³Dept. Biology, York University, Toronto, Ontario, M3J 1P3, Canada. ⁴Dept. Biology, State University of New York College at Fredonia, Fredonia, NY, 14063, USA. ⁵Dept. Biology, University of Regina, Regina, Saskatchewan, S4S 0A2, Canada.
Correspondence to D. J. McQueen: Department of Biology, York University, 4700 Keele St., Toronto, Ontario, Canada, M3J1P3, email NEI@island.net.

decreases the average body size of zooplankton prey and this effect was postulated to be enhanced by invertebrate predators. Under low fish planktivory, invertebrate predators should flourish. Since they are gape-limited, invertebrates should prey selectively on smaller herbivorous zooplankton. Large-bodied herbivores would thus have the double advantage of low predation from planktivorous fish and reduced competition from small-bodied herbivores that would be consumed by invertebrate predators. Under high fish planktivory, the opposite should occur. Both invertebrate predators and large herbivores should be reduced by fish, allowing small herbivores to flourish.

For a trophic cascade to function according to the model of CARPENTER et al. (1985, 1987) there must be an inverse correlation between the biomass of fish and that of invertebrate predators. Indeed, large-bodied, non-migrating chaoborids such as *Chaoborus americanus* and *C. obscuripes* are restricted to fishless lakes where they commonly reach high biomasses (VON ENDE 1979, POPE et al. 1973, STENSON 1981). However, a strong negative relationship between invertebrate predator biomass and planktivorous fish biomass is by no means assured. The effects of fish predation can be counteracted in several ways including vertical migration (e.g., LAMPERT 1989, TIOSSEM 1990), and shifts in body size and species composition. Smaller-bodied *Chaoborus* that migrate vertically to avoid fish predation are not uncommon in lakes that have planktivorous fish where they can also reach high density (e.g., POPE et al. 1973). A second requirement, if invertebrate predators are to act as facilitators of a trophic cascade, is that invertebrate predation must strongly focus on small-bodied prey. This condition is also problematic. The largest planktonic invertebrate predators such as *Chaoborus trivittatus* (e.g., PASTOROK 1981, SWIFT & FEDORENKO 1975), *C. obscuripes* (WISSEL 1997, SELL 1996), *C. americanus* (e.g., STENSON 1981), and *Leptodora kindtii* (MONAKOV 1972, BRANSTRATOR 1998) can consume the same large herbivorous zooplankters eaten by fish (BENNDORF 1995, SELL 1997, BRABAND et al. 1986, ELSER et al. 1987, MACKAY et al. 1990). If biomass of planktivorous fish is strongly reduced in a lake, large invertebrate predators can increase in abundance and exert even higher predation pressures on large zooplankton than the planktivorous fish they replaced (BENNDORF 1995, BRABAND et al. 1986, WISSEL 1997).

In this paper, we test the two requirements above that are necessary, if the invertebrate predator, *Chaoborus* spp., is to facilitate a pelagic trophic cascade. Specifically, we test whether biomass and species composition of two *Chaoborus* assemblages were affected by interannual and experimentally induced changes in biomass of planktivorous fish. We also test whether changes in *Chaoborus* biomass affected zooplankton biomass and body size in the manner predicted by trophic cascade theory (CARPENTER et al. 1985).

During a biomanipulation experiment conducted near the town of Dorset, Ontario, we studied the ecosystems of one planktivore-dominated lake (Mouse Lake) and one piscivore-dominated lake (Ranger Lake). During the pre-manipulation phase (1991–1993) of the experiment, *Chaoborus* spp. were by far the dominant invertebrate predator in these lakes in terms of biomass. From the late summer of 1993 to mid-summer 1994, the piscivores (bass, *Micropterus* spp.) were removed from Ranger Lake and transferred to Mouse Lake, and the study continued through the post-manipulation phase (1994–1997). After the bass transfer, planktivorous fish biomass quickly fell in Mouse Lake and gradually increased in Ranger Lake. If top-down effects were strong in the food webs of these lakes, then the reduced biomass of planktivorous fish in Mouse Lake should have caused an increase in *Chaoborus* biomass while the opposite should have occurred in Ranger Lake. The changes in both fish and *Chaoborus* should have

caused a shift in the herbivorous zooplankton towards larger-bodied animals in Mouse Lake and smaller-bodied animals in Ranger Lake.

Study site and experimental biomanipulation

Mouse Lake and Ranger Lake are two small (9.0 and 11.3 ha surface area, respectively), deep (4.9 and 5.6 m \bar{Z} , respectively), oligotrophic, brown-water lakes located near the town of Dorset, Ontario (RAMCHARAN et al. 1995). The lakes are both in headwaters of tertiary watersheds with geologically similar basins. Mouse Lake is approximately 5 km north of Ranger Lake. The lakes have similar basin morphometries and flushing rates.

In terms of temperature, dissolved oxygen, light penetration, chlorophyll, and most water chemistry variables, the two lakes were very similar (RAMCHARAN et al. 1995, MCQUEEN et al. 2001, DILLON et al. 2001). Both lakes developed stable summer stratification with anoxic hypolimnia. Epilimnetic total phosphorus concentrations varied from 4–7 $\mu\text{g L}^{-1}$, and dissolved organic carbon (DOC) from 4–8 mg L^{-1} in both lakes (MCQUEEN et al. 2001). In general, Ranger Lake had slightly higher levels of DOC than Mouse Lake. The most notable differences between the lakes were that Ranger Lake had a higher epilimnetic pH (about 6.5) than Mouse Lake (about 5.5) and also had higher alkalinity.

We selected Mouse and Ranger Lakes for our biomanipulation experiment because they were as similar as we could find in physico-chemical characteristics, yet were opposite in terms of their biomasses of piscivores and planktivores. For the first three years of our study (1991–1993) and for at least 30 years prior, Mouse Lake had had no obligate piscivores (RAMCHARAN et al. 1995, DEMERS 1996, DEMERS et al. 2001a). In the absence of piscivores, Mouse Lake had large populations of planktivorous fishes, primarily yellow perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), common shiner (*Notemogonus chrysoleucas*), and brown bullhead (*Ictalurus nebulosus*). In contrast, since the mid 1960's, Ranger Lake had high biomasses of piscivores comprising largemouth bass (*Micropterus salmoides*, 85%) and smallmouth bass (*Micropterus dolomieu*, 15%). Ranger Lake had the same species of planktivorous fish as Mouse Lake but their populations were much smaller.

After three years of initial study (1991–1993, pre-manipulation), we began in the fall of 1993 to remove both species of bass from Ranger Lake and by the summer of 1994 had transferred 85% of the bass to Mouse Lake. In the post-manipulation years of our study (1994–1997), bass biomass in Mouse Lake increased dramatically and remained high (Table 1). Within a year of the manipulation, planktivore biomass dropped just as dramatically and remained low. In Ranger Lake, bass biomass was severely reduced by the transfer and was kept low by removal of remaining fish and destruction of bass nests. Estimates of consumption showed that the residual bass biomass caused only small losses to planktivo-

Table 1. Biomasses (kg ha^{-1}) of benthivorous, piscivorous, and planktivorous fish in Mouse and Ranger Lakes from 1991 to 1997 (DEMERS et al. 2001a).

Lake	Fish Type	Pre-Manipulation			Post-Manipulation			
		1991	1992	1993	1994	1995	1996	1997
Mouse Lake	Benthivores	7.70	10.14	11.67	10.10	5.80	9.39	9.69
	Piscivores	0.00	0.00	0.00	8.76	5.67	4.28	3.41
	Planktivores	4.10	4.85	4.90	3.46	1.53	1.29	0.48
Ranger Lake	Benthivores	17.05	20.10	19.30	16.03	14.33	11.86	19.95
	Piscivores	3.35	2.20	2.70	0.76	0.59	0.27	0.25
	Planktivores	1.76	0.51	1.54	0.68	0.87	1.38	2.71

rous fish (DEMERS et al. 2001b). Planktivore biomass increased gradually but did not quite reach the high biomass found in Mouse Lake before the manipulation.

Benthivorous fishes, primarily white sucker (*Catostomus commersonii*) (Table 1), composed the major fish biomass both before and after the bass manipulation in both lakes (DEMERS et al. 2001a).

Methods

From 1991 to 1997, *Chaoborus* populations were sampled in both lakes approximately every two weeks from mid-April to early September. In each lake, we sampled six stations distributed along the lake's major axis (RAMCHARAN et al. 1995). Samples were collected at night (2300–0200) with a single tow of a conical (5:1 aspect ratio), 250 μm mesh tow-net with a square mouth opening (30 x 30 cm) (FILION 1991). A flow meter (Rigosha Corp. Model 2503) was used with each tow (MCQUEEN & YAN 1993, YAN et al. 1992). Net filtration efficiency was usually around 100%.

Chaoborus were examined using a dissecting microscope and data were recorded using ZEBRA2 enumeration software (DataBase Microcomputing, Kingston Ont., ALLEN et al. 1994). Only samples from the two deepest stations in each lake were enumerated (LimnoServices, Kingston, Ont.). In 1991, *Chaoborus* were not identified to either species or instar; all animals in the samples were counted for each sample date. For all other years, *Chaoborus* were identified to species and instar (based on head-capsule length, McEACHERN 1986) whenever possible. Initially we enumerated samples from all six stations within each lake. Comparisons among the samples from 1991 indicated that enumerating only samples from the two deepest stations would be sufficient to characterize the *Chaoborus* populations. Thereafter, we attempted to count at least 30 *Chaoborus* of each species, processing either one or both of the deep station samples to reach this goal.

We used a video imaging system and digital calipers (SPRULES et al. 1981) to measure standard length (shortest distance between anterior and posterior air bladders), which was then increased by 8% to compensate for shrinkage caused by preservation in 4% sugar-saturated, buffered formalin (LASENBY et al. 1994). Dry mass was estimated using length-weight regressions developed by LASENBY et al. (1994). The regression model for *C. americanus* (dry mass (μg) = 1.425 x length (mm)^{3.599}) was applied to the similarly-shaped *C. trivittatus*; the model for *C. punctipennis* (dry mass (μg) = 0.64 x length (mm)^{3.794}) was also applied to both *C. albatus* and *C. flavicans*.

As with *Chaoborus*, zooplankton samples were enumerated and measured (LimnoServices, Kingston, Ont.) using the ZEBRA2 system, video imaging, and digital calipers. All animals were identified to species whenever possible. For each lake and sample date, we enumerated just one sample that was a volume-weighted composite of sub-samples taken from each of the six stations (YAN et al. 2001, RAMCHARAN et al. 1995).

The statistical significance of all experimental effects on biomass, density, and body size of different species and size groups was evaluated using Randomized Intervention Analysis (RIA) (STEWART-OATEN et al. 1986, CARPENTER et al. 1989, BOX & TIAO 1975, MCQUEEN et al. 2001). In RIA, the absolute value of the average difference between two time series (\bar{D}) before the manipulation minus the average difference between the time series after the manipulation ($|\bar{D}_{\text{pre}} - \bar{D}_{\text{post}}|$) is an indication of the strength of an experimental effect ($\bar{D}_{\text{observed}}$). By randomizing the data within each lake's time series and repeatedly recalculating the absolute value of $|\bar{D}_{\text{pre}} - \bar{D}_{\text{post}}|$, we create a frequency distribution of expected values ($\bar{D}_{\text{predicted}}$). The percent area of this curve that falls above $\bar{D}_{\text{observed}}$ is used as a P-value to test the null hypothesis of no difference between pre- and post-manipulation values. RIA does not detect absolute changes, only relative changes (divergence or convergence) in the experimental time series. The time-series plots must be examined to determine if one or both lakes changed and the direction of change. In our case, we re-calculated $\bar{D}_{\text{predicted}}$ 10,000 times (using Visual Basic macros in Microsoft Excel version 7.0), and used an a value of 0.05 for statistical tests. In some cases, the data were log-transformed to reduce the effects of extreme values on the outcome of the RIA tests. No other data transformations, such as auto-regressive integrated averaging (CARPENTER et al. 1989), were employed.

We used correlation analysis to study the relative strengths of top-down (fish biomass) and bottom-up (zooplankton biomass) effects on *Chaoborus* biomass. Details of fish sampling and data analysis are

presented elsewhere in this series (DEMERS 1996, DEMERS et al. 2001a). In brief, we used multiple mark-recapture to estimate biomasses of each of several fish species in both lakes in the early spring of 1991 and 1992, and in both the spring and early fall from 1993 to 1997. Details of zooplankton sampling (in this paper we refer to all non-*Chaoborus* zooplankters as simply zooplankton) and data analysis are presented elsewhere (YAN et al. 2001). Zooplankton were sampled similarly to *Chaoborus*, except that a 40 μm mesh tow-net was used and was deployed during the day. Net filtration efficiency varied from 22% to 90%.

Pearson product-moment correlations (Statistica Version 5.0, Statsoft Inc., Tulsa, OK) were estimated between the biomasses of planktivorous fish and *Chaoborus*. Stomach contents were used to distinguish planktivores from other fishes (DEMERS 1996, DEMERS et al. 2001b). In our correlation analyses, we created two functional groups of *Chaoborus* in terms of vulnerability to fish planktivory, based on the large differences in body size between the small (*C. albatus* and *C. punctipennis*) and large (*C. flavicans* and *C. trivittatus*) species. Body size does appear to affect vulnerability to fish predation in our lakes, since in Ranger Lake the extent of vertical migration in *C. punctipennis* was less than for the large chaoborids (TSALKITZIS et al. 1993). Our correlations were based on annual mean biomasses, therefore sample sizes were low and overall trends are more illustrative than the occasional statistically significant result.

Bottom-up effects of resource (prey) supply on *Chaoborus* biomass were also studied using correlation. Since large zooplankters are difficult for invertebrate predators to ingest, we attempted to correlate *Chaoborus* biomass with only the vulnerable portion of zooplankton biomass. Prey that are small enough in minimum dimension (width) to fit the mouth gape of *Chaoborus* should be the most readily ingested (e.g., SWIFT & FEDORENKO 1975, PASTOROK 1981). *C. punctipennis* has too small a mouth to consume most meso-zooplankton, and this species feeds primarily on rotifers and occasionally on small bosminids (e.g., MOORE et al. 1994). *C. flavicans* and *C. trivittatus* have mouth gapes of approximately 0.6 mm and 0.8 mm, respectively, and can feed on a wide range of prey sizes (SELL 1996, 1997, SWIFT & FEDORENKO 1975, WISSEL 1997). Based on a published relationship between *Daphnia* size and consumption by *Chaoborus* (PASTOROK 1981), RAMCHARAN et al. (2001) developed a size-based function that estimates vulnerability of different species of prey to *C. flavicans* and *C. trivittatus* predation. In this paper, we use the function of RAMCHARAN et al. (2001) to define the size of the zooplankton prey species vulnerable to predation by the large chaoborids (*C. flavicans* and *C. trivittatus*). We then estimated the correlation across years of the biomass of each *Chaoborus* species (and of the large species combined) with the annual average biomass of vulnerable prey.

Results

Chaoborus populations

We estimated average annual biomass of a species or group as the mean biomass among sample days within a season. The number of sample days in a year ranged from seven to ten per season.

Before the fish manipulation, average annual biomass of all *Chaoborus* species was about the same in both lakes in 1991 and 1992 but was higher in Mouse Lake in 1993 (Fig. 1). A more important difference between the two lakes was in the species composition of their *Chaoborus* assemblages. Before the manipulation, Mouse Lake was dominated by small-bodied species, primarily *C. punctipennis*. *C. albatus*, the smallest chaoborid in our lakes, appeared very occasionally (Fig. 2). The two largest species in our study, *C. flavicans* and *C. trivittatus*, were the biomass dominants in Ranger Lake. Density of *Chaoborus* showed similar patterns to biomass (Fig. 3). Mouse Lake had higher densities of small-bodied species compared to Ranger Lake.

Following the bass transfer, total *Chaoborus* biomass generally increased in Mouse Lake, although there was considerable inter-annual variability (Fig. 1 and 2, Table 2, RIA P= 0.011). The three highest average annual values for biomass recorded in Mouse Lake were in the post-manipulation years 1994, 1995, and 1997. However, the second-lowest average annual bio-

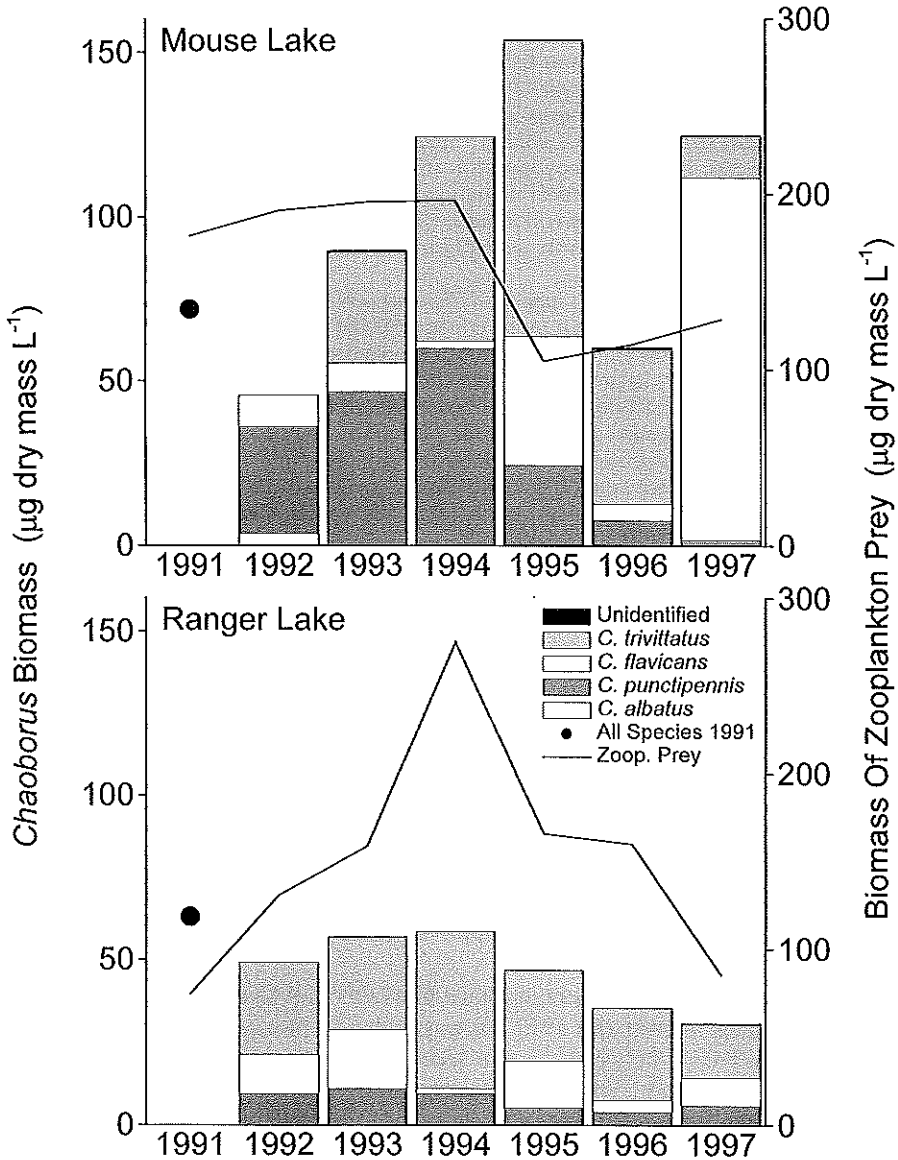


Fig 1. Average annual biomasses of *Chaoborus* species found in Mouse (upper panel) and Ranger (lower panel) lakes from 1992 to 1997. For 1991, only total *Chaoborus* biomass was available. The solid line shows average annual biomasses of zooplankton prey (see Methods) plotted against the right y-axis.

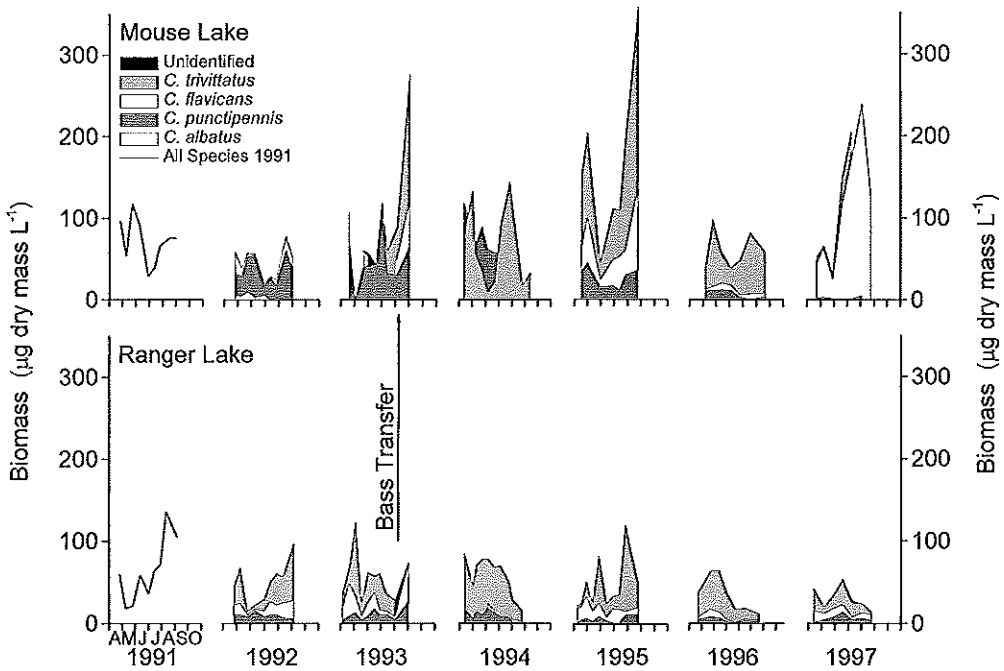


Fig 2. Biomass of *Chaoborus* species found in Mouse and Ranger Lakes from 1991 to 1997. In 1991, chaborids were not identified to species. The Unidentified category comprises 1st and 2nd instar animals that sometimes could not be identified to species. *Chaoborus* species are plotted in increasing order of body size from *C. albatu* to *C. trivittatus*.

mass was also found in a post-manipulation year, 1996. In Ranger Lake, average annual biomass decreased steadily between 1994 and 1997, but this change was not as marked as the biomass increase in Mouse Lake. Total *Chaoborus* density showed the same trends as biomass: An increase in Mouse Lake with little change in Ranger Lake, but in this case the divergence of the two lakes was not statistically significant (Fig. 3, Table 2, RIA $P = 0.326$).

Species composition of the *Chaoborus* assemblage was dramatically affected by the fish manipulation but only in Mouse Lake (Fig. 1 and 2). In this lake the bass transfer seemed to initiate large interannual oscillations in species composition but with a general progression towards domination by larger species. The small-bodied *C. punctipennis* initially increased in 1994, then declined to near extinction by 1997 (Fig. 2 and 3). Perhaps because of this large interannual variability, RIA did not detect a statistically significant difference between the lakes in either their biomass ($P = 0.233$) or density ($P = 0.126$) time series for *C. punctipennis*, even though both biomass and density of this species steadily declined in Mouse Lake following the manipulation (Fig. 2 and 3). As *C. punctipennis* declined, large-bodied species became both numerical and biomass dominants in Mouse Lake. *C. flavicans* increased in 1995, decreased in 1996, then increased again in 1997 to comprise by far the major component of *Chaoborus* biomass. The largest chaoborid, *C. trivittatus*, increased in 1994, remained high in 1995 and 1996, but fell to pre-manipulation levels in 1997.

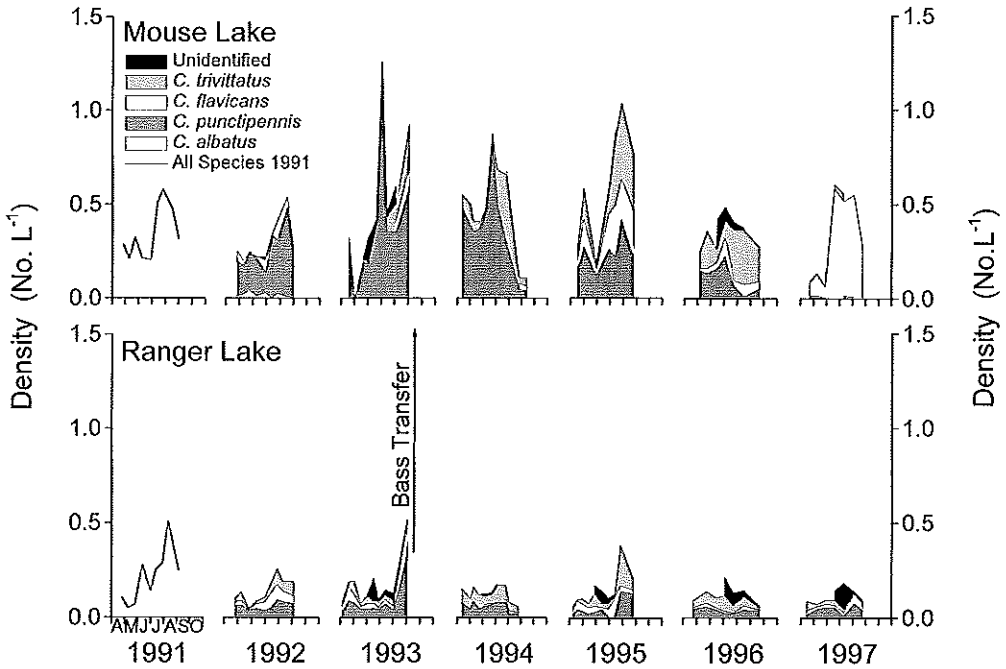


Fig 3. Density of *Chaoborus* species found in Mouse and Ranger Lakes from 1991 to 1997. In 1991, chaborids were not identified to species. The Unidentified category comprises 1st and 2nd instar animals that sometimes could not be identified to species. *Chaoborus* species are plotted in increasing order of body size from *C. albatulus* to *C. trivittatus*.

In Ranger Lake, the biomasses and densities of different *Chaoborus* species fluctuated from year to year, however, overall changes in species composition in response to the fish manipulation were not as evident as in Mouse Lake (Fig. 1, 2, and 3). The large chaborids, *C. flavicans* and *C. trivittatus* remained dominant throughout the six years for which we have species-specific data. The large divergences between Mouse and Ranger Lakes in their time series for biomass and density of *C. flavicans*, *C. trivittatus*, and both species together were found to be statistically significant by RIA (Table 2).

The apparent difference between the lakes in their range of interannual variation in *Chaoborus* biomass was analyzed using Levene's test for homogeneity of variances (Statistica Version 5.0, Statsoft Inc., Tulsa, OK). We compared the variance of average annual biomass (log-transformed) of each *Chaoborus* species, small species, large species, and total biomass between Mouse and Ranger Lakes (a separate test for each variable). For each chaborid species and for the biomass of small species, interannual variation was higher in Mouse Lake compared to Ranger Lake (P values from 0.030 to 0.002). No significant difference was found between the lakes for interannual variation in either large species biomass ($P = 0.087$) or total *Chaoborus* biomass ($P = 0.070$).

Average *Chaoborus* body length varied seasonally, interannually, and as a result of the fish manipulation. Typically, average body length showed a seasonal, mid-summer decrease caused

Table 2. Results of Randomized Intervention Analyses for biomasses, densities, and body lengths of several different species and size categories of *Chaoborus*. N is number of observations. \bar{D} is the average difference between values for Mouse Lake and Ranger Lake. Pre and Post refer to pre- and post-manipulation data, respectively. $\bar{D}_{pre} - \bar{D}_{post}$ is the difference between the average pre- and post-manipulation \bar{D} values. Observed is the value found in our data. Predicted is the value found by repeated (10,000 times) data randomization. P is the frequency with which the observed $\bar{D}_{pre} - \bar{D}_{post}$ exceeds the predicted $\bar{D}_{pre} - \bar{D}_{post}$, and is a measure of the statistical significance of the difference between Observed and Predicted. Small Species is the summed biomass of *C. albatus* and *C. punctipennis*; Large Species is the biomass of *C. flavicans* and *C. trivittatus*. Zooplankton prey is the biomass of zooplankton with body widths of less than 0.85 mm.

		N		\bar{D}		$\bar{D}_{pre} - \bar{D}_{post}$		
		Pre	Post	Pre	Post	Observed	Predicted	P
<i>Chaoborus</i>	Total*	28	36	10.11	57.98	47.87	15.35	0.011
Biomass	<i>C. punctipennis</i>	19	36	27.33	17.17	10.16	6.72	0.233
	<i>C. flavicans</i>	19	31	-6.34	27.68	34.02	11.38	0.008
	<i>C. trivittatus</i>	19	36	-11.96	17.06	29.02	11.81	0.049
	Small Species	19	36	28.94	17.15	11.79	6.80	0.164
	Large Species	19	36	-18.14	40.83	58.97	16.32	0.002
<i>Chaoborus</i>	Total*	28	36	0.19	0.26	0.07	0.05	0.326
Density	<i>C. punctipennis</i>	19	36	0.22	0.12	0.09	0.05	0.126
	<i>C. flavicans</i>	19	31	-0.01	0.09	0.11	0.03	0.005
	<i>C. trivittatus</i>	19	36	-0.01	0.06	0.06	0.02	0.041
	Small Species	19	36	0.23	0.12	0.16	0.01	0.096
	Large Species	19	36	-0.02	0.14	0.08	0.00	0.002
<i>Chaoborus</i>	Total	18	29	-0.77	0.05	0.82	0.33	0.037
Length	<i>C. punctipennis</i>	18	27	-0.26	0.02	0.28	0.31	0.485
	<i>C. flavicans</i>	6	28	-0.57	-0.11	0.46	0.42	0.389
	<i>C. trivittatus</i>	12	21	-0.57	-0.34	0.23	0.47	0.710
<i>Chaoborus</i> 4 th	Total	18	29	-0.87	-0.36	0.51	0.31	0.169
Instar Length	<i>C. punctipennis</i>	7	11	-0.41	-0.70	0.29	0.51	0.671
	<i>C. flavicans</i>	7	12	-1.58	-1.78	0.20	1.04	0.869
	<i>C. trivittatus</i>	7	18	-3.61	-2.69	0.92	1.04	0.501
Zooplankton Prey		37	37	-4.61	3.03	7.64	6.43	0.345

*Total *Chaoborus* biomass and density, and zooplankton biomass include pre-manipulation data for 1991–1993; the other data sets include 1992–1993.

by *Chaoborus* phenology (Fig. 4). From April to June, overwintering animals were emerging while new recruits were hatching and growing from May to October. New fourth instars were found from mid-July to mid-September. The fish manipulation likely caused an increase in average body length of the total *Chaoborus* assemblage in Mouse Lake and a decrease in Ranger Lake (RIA P = 0.037) (Fig. 5, Table 2). Annual average body length changed primarily as a result of shifts in the relative densities of small and large chaoborids, and not due to

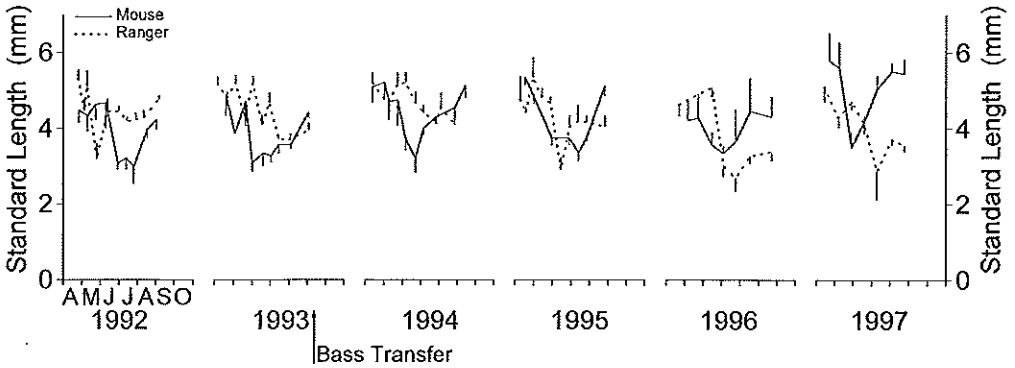


Fig 4. Standard length (nearest distance between air bladders) of all *Chaoborus* species in Mouse (solid line) and Ranger (broken line) from 1992 to 1997. All values are average lengths weighted by the densities of species and instars. Error bars are one standard deviation and are drawn in only one direction for clarity.

changes in the body length of each individual species (Fig. 5). Body lengths of the three most abundant species (*C. punctipennis*, *C. flavicans*, and *C. trivittatus*) were unaffected by the manipulation (Table 2). Interestingly, there was some interannual covariance between the two lakes in the body sizes of the three abundant *Chaoborus* species. Except for *C. flavicans* in Ranger Lake, body sizes of the other chaoborid populations in both lakes decreased between 1994 and 1995, dropped again between 1995 and 1996, and then rose from 1996 to 1997 (Fig. 5).

Fish-*Chaoborus* interactions

Only one value in the correlations between fish and *Chaoborus* biomass was statistically significant, and this may be a spurious result due to multiple pairwise comparisons. As stated in the Methods, interpreting overall patterns of correlations may be more useful than focusing on the occasional significant value.

In Mouse Lake, small-bodied *C. punctipennis*, which would have been less vulnerable to fish predation, was positively associated with the biomass of planktivorous fish (Table 3). The larger, more vulnerable chaoborids, were either negatively or only weakly correlated with fish biomass. In Ranger Lake, biomass of all the *Chaoborus* species were either negatively or weakly correlated to fish biomass. When the data for both lakes were combined, the biomass of *C. punctipennis* was positively related to fish biomass, while biomass of the other chaoborids showed only very weak negative correlations (Table 3, Fig. 6).

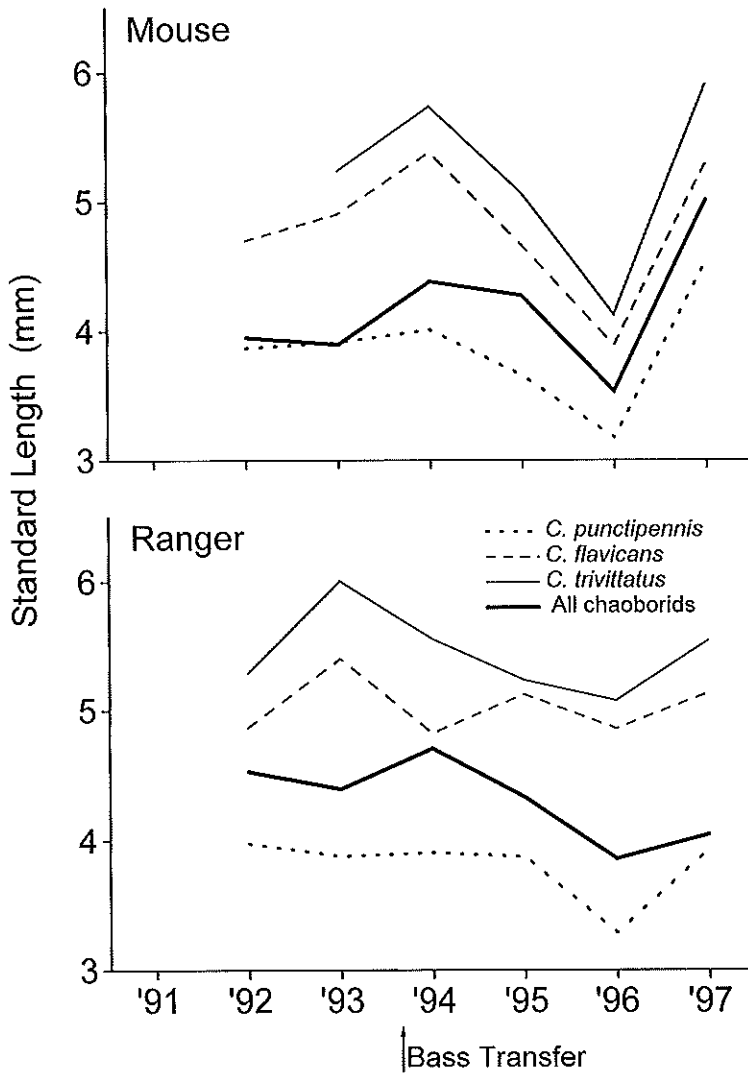


Fig. 5. Average annual standard length (nearest distance between air bladders) of the three most common *Chaoborus* species in Mouse Lake (upper panel) and Ranger Lake (lower panel). *C. punctipennis* is represented by the dotted line, *C. flavicans* by the dashed line, *C. trivittatus* by the thin solid line, and the total chaoborid community by the thick solid line.

Chaoborus-zooplankton interactions

Before the fish manipulation, the average annual biomass of total zooplankton was higher in Mouse Lake than Ranger Lake (Fig. 6, YAN et al. 2001). Although species compositions of the two lakes were very similar, Mouse Lake had a higher proportion of small bodied zooplankters

Table 3. Pearson's correlation coefficients between annual average biomasses of planktivorous fish, zooplankton, and *Chaoborus* species. "Large Species" is the combined biomass of *C. flavicans* and *C. trivittatus*. Total *Chaoborus* includes occasional occurrences of *C. albatius* and unidentifiable animals. "Zooplankton Prey" is the average annual biomass of animals that were highly vulnerable to predation from large *Chaoborus* (see Methods). Numbers in parentheses are n values, and statistically significant ($p < 0.05$) correlation coefficients are in bold.

	<i>C. punctipennis</i>	<i>C. flavicans</i>	<i>C. trivittatus</i>	Large Species	Total <i>Chaoborus</i>
Planktivores					
Mouse Lake	0.773 (6)	-0.440 (6)	0.075 (5)	-0.472 (7)	-0.009 (7)
Ranger Lake	-0.529 (6)	-0.191 (6)	-0.692 (6)	-0.806 (7)	-0.790 (7)
Both Lakes	0.607 (12)	-0.235 (12)	0.032 (11)	-0.185 (14)	-0.084 (14)
Zooplankton Prey					
Mouse Lake	0.801 (6)	-0.471 (6)	-0.396 (6)	-0.670 (6)	0.371 (7)
Ranger Lake	0.306 (6)	-0.456 (6)	0.979 (6)	0.776 (6)	0.251 (7)
Both Lakes	0.350 (12)	-0.327 (12)	0.001 (12)	-0.272 (12)	0.040 (14)

than Ranger Lake. After the bass transfer, total zooplankton biomass in the two lakes showed no statistically significant responses. However, in both lakes body size and species composition changed (YAN et al. 2001). With decreased fish planktivore biomass, the proportion of large animals (mostly cladocerans such as *Daphnia* and *Holopedium*) increased in Mouse Lake while the proportion of small zooplankton decreased. In Ranger Lake, the opposite happened; the zooplankton assemblage shifted from large-bodied to small-bodied species.

Biomass of zooplankton prey was positively correlated with biomass of *C. punctipennis* in both Mouse and Ranger Lakes and also in both lakes together (Table 3). Zooplankton prey was negatively correlated with biomass of *C. flavicans*, again in either lake and also in both lakes together. In Mouse Lake, biomass of zooplankton prey was negatively correlated with biomass of *C. trivittatus* and total biomass of large chaoborids, but in Ranger Lake the same comparisons had strong positive correlations. All other correlations showed either weak or inconsistent patterns indicating that more detailed food web analyses may be required to determine the trophic relationships between *Chaoborus* and their prey (RAMCHARAN et al. 2001).

Discussion

Overall, the density (Fig. 3) and biomass (Fig. 1 and 2) of *Chaoborus* found in our study lakes were somewhat high for oligotrophic lakes (YAN et al. 1985). In Mouse Lake, 95% of *Chaoborus* density fell within the range of 352.7 to 497.4 animals m^3 (1722.5 to 2428.7 animals m^2), while in Ranger Lake, density ranged from 119.5 to 162.6 animals m^3 (671.2 to 913.7 animals m^2). POPE et al. (1973) report density values ranging from approximately 10 to 500 animals m^3 in lakes with fish. MACKAY et al. (1990) report a density of approximately 300 to 1200 animals m^3 in the more productive Peter Lake, and YAN et al. (1991) found a density of 100–300 animals m^3 in Swan Lake. Perhaps *Chaoborus* biomass was high in our study lakes because high levels of dissolved organic carbon (MCQUEEN et al. 2001, DILLON et al. 2001) had reduced

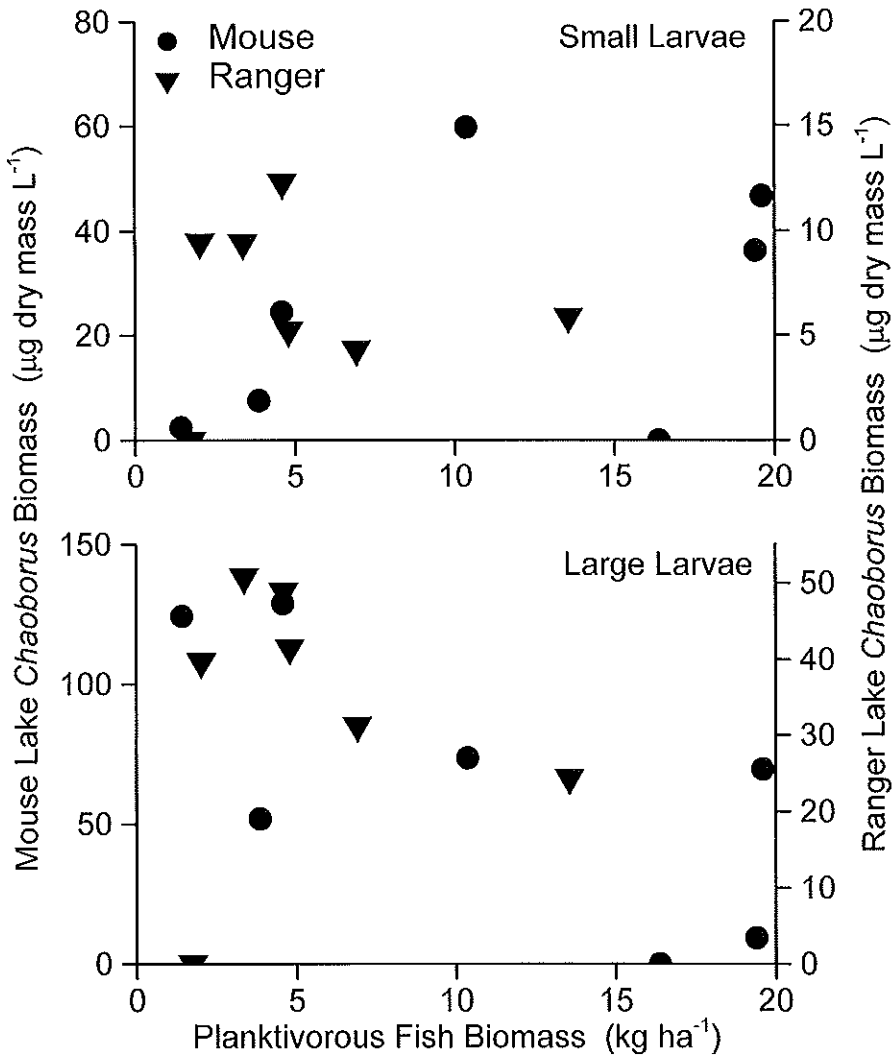


Fig. 6. Relationships between the biomasses of planktivorous fish and *Chaoborus* in Mouse Lake (closed symbols, left Y-axis) and Ranger Lake (open symbols, right Y-axis). Note the differences in scale of the Y-axis for the two lakes.

water clarity and interfered with fish feeding, and also because the anoxic hypolimnia (MCQUEEN et al. 2001) provided a refuge from fish.

If the food webs of our study lakes were structured as described by the trophic cascade hypothesis, then a low biomass of bass should have resulted in a high biomass of planktivorous fish, as well as low biomasses of both small *Chaoborus* and small zooplankton (CARPENTER et al. 1987). Conversely, a high biomass of bass should have caused a low biomass of planktivorous fish and high biomass of both large *Chaoborus* and large zooplankton. Overall,

our results indicate that limnetic food web interactions are more complex than the simple cascade model suggests. In general, fish planktivory seemed to have a detectable effect on the biomass and species composition of the *Chaoborus* assemblage. On the other hand, in only a few cases did the *Chaoborus* community have an effect on the zooplankton assemblage in the manner predicted by the cascade model. Factors such as time lags in population responses, prey defenses, and interannual variability all seemed to play important roles in the community structure of our lakes. Here we discuss the trophic interactions in our study lakes from the top, down.

In terms of changing the fish communities, the biomanipulation was quite effective (Table 1). Increasing piscivore biomass strongly reduced planktivorous fish biomass in Mouse Lake. Release from piscivory allowed planktivore biomass to increase in Ranger Lake, but over a long time period of four years (DEMERS et al. 2001a). In several other studies, for example in Paul and Tuesday Lakes studied by CARPENTER & KITCHELL (1993), a tighter negative relationship between piscivorous and planktivorous fish biomasses had been found.

As fish planktivory fluctuates, responses in total biomass and species composition of macroinvertebrates are commonly found (e.g., NORTHCOTE et al. 1978, CARPENTER & KITCHELL 1993, GULATI et al. 1990). In our case, the effects of the fish manipulation on total *Chaoborus* biomass were not strongly evident during the pre-manipulation period but were clearer after the bass transfer. Before the manipulation, *Chaoborus* biomass was actually slightly lower in Ranger Lake in two of the three pre-manipulation years (Fig. 1) (RAMCHARAN et al. 1995) despite the lower fish planktivory compared to Mouse Lake (DEMERS et al. 2001b). Perhaps other factors such as juvenile survival (NEILL 1985) or system productivity (SAUNDERS & LEWIS 1988) kept *Chaoborus* populations in Ranger Lake low relative to Mouse Lake in the pre-manipulation years.

Following the bass transfer, total *Chaoborus* biomass strongly increased in Mouse Lake but did not decrease in Ranger Lake either as much or as dramatically. In Ranger Lake, the response of planktivorous fish to the removal of the bass was delayed. This may in turn have delayed responses of *Chaoborus*. Although the bass were removed in the fall of 1993, planktivorous fish biomass did not increase notably in Ranger Lake until 1996, and did not reach high levels until 1997, the last year of our study (DEMERS et al. 2001a). Therefore, there were only two post-manipulation years (1996 and 1997) with high levels of planktivorous fish in Ranger Lake.

Even though the responses of the *Chaoborus* assemblage to the fish manipulation seemed to be more closely coupled in Mouse Lake, there were still years with unexpected patterns. In the three pre-manipulation years, planktivorous fish biomass in Mouse Lake was much higher than in Ranger Lake, yet as noted above, average annual *Chaoborus* biomass was actually about 25% higher, rather than lower (Fig. 1 and 2) (RAMCHARAN et al. 1995). Moreover, in the summer of 1993, just before the bass transfer, and also in 1994, the first post-manipulation year, total *Chaoborus* biomass in Mouse Lake were the highest found in this study, yet these were the two years of highest planktivorous fish biomass (DEMERS et al. 2001a). The opposite pattern was also found. *Chaoborus* in Mouse Lake failed to reach high biomass in 1996, even though planktivorous fish had been greatly reduced by the manipulation.

There are several reasons why total *Chaoborus* biomass may not be tightly coupled to planktivorous fish biomass. Some well-known possibilities are that *Chaoborus* may be able to avoid fish predation. Factors other than fish predation may be driving *Chaoborus* abundance.

And, populations of invertebrates may respond to changes in fish planktivory, but with a considerable lag time of several years (HE et al. 1994, BENNDORF 1995, SELL 1997).

In our lakes, *Chaoborus* assemblages may have been able to counteract fish predation by changes in community size structure. Smaller chaoborids are less vulnerable to fish than larger species (e.g., POPE et al. 1973). Before the manipulation, when planktivorous fish biomass in Mouse Lake was still high, the *Chaoborus* assemblage was dominated by the small species, *C. albatus* and *C. punctipennis*. We originally thought *C. trivittatus* to be absent from Mouse Lake (RAMCHARAN et al. 1995), but this species appeared in 1993. In the years following the manipulation, as the planktivorous fish in Mouse Lake were reduced, the smaller chaoborids declined while the larger chaoborids, *C. flavicans* and *C. trivittatus*, flourished. Dominance seemed to switch from one to the other large *Chaoborus* species from year to year.

Low vulnerability to planktivory may explain the dominance of small chaoborids when the biomass of planktivorous fish was high, but why are larger chaoborids favored when fish planktivory is low? The dynamics of *Chaoborus* populations must be affected by factors other than fish planktivory. One likely factor is inter-specific competition for zooplankton prey. Since *Chaoborus* ingest their prey whole, they are gape-limited predators (e.g., SWIFT & FEDORENKO 1975, PASTOROK 1981). Mouth diameter is a major determinant of the maximum size of prey that can be ingested (SWIFT & FEDORENKO 1975). The smaller species in our lakes, *C. albatus* and *C. punctipennis*, ingest mostly smaller zooplankters such as rotifers (MOORE et al. 1994), while larger chaoborids can eat a wide range of prey sizes (e.g., SELL 1996, 1997, SWIFT & FEDORENKO 1975, WISSEL 1997). Occasionally, the largest prey in our lakes may even have been so large as to be difficult for the largest chaoborids to ingest. The sudden decline in *Chaoborus* biomass in Mouse Lake in 1996 (Fig. 1) was associated with a large increase in the biomass of *Holopedium* (YAN et al. 2001). This large, sheathed zooplankter has a low vulnerability to *Chaoborus* (ALLAN 1973), thus predator biomass may have been food-limited in 1996.

The difference in diet ranges between small and large chaoborids may partially explain their population dynamics, at least in Mouse Lake. When fish planktivory was high in Mouse Lake, smaller zooplankton formed the major biomass (Fig. 5, YAN et al. 2001). Small chaoborids would have enjoyed lower fish predation than their larger congeners, and also abundant prey. When the biomass of planktivorous fish declined in Mouse Lake, larger species comprised an increasing fraction of the total zooplankton biomass. Unable to ingest these larger prey (e.g., MOORE et al. 1994), smaller chaoborids may have been out-competed by the larger species. In Ranger Lake, larger *Chaoborus* species were always the biomass dominants, and larger-bodied zooplankton were fairly abundant throughout the seven years of the experiment (YAN et al. 2001).

Besides shifts in size distribution, another very effective device that *Chaoborus* can use to reduce predation is vertical migration. Before the manipulation, *Chaoborus* populations in Mouse Lake had a pronounced diurnal vertical migration (TSALKITZIS et al. 1993). During the day, the largest chaoborids migrated through the anoxic hypolimnion and down to the sediment. At night they would swim up to the epilimnion. In Ranger Lake, *Chaoborus* had only a small (about 2 m) diurnal vertical migration, remaining just below the metalimnion during the day. After the fish manipulation, once the biomass of planktivorous fish had decreased, the extent of vertical migration was considerably reduced in Mouse Lake but did not change much in Ranger Lake (MCQUEEN et al. 1999). Changes in vertical migration patterns of zooplankton

are a common result of both natural and experimental changes in fish planktivory (LUECKE 1986, DINI & CARPENTER 1991, HORPPILA 1997) and can be mediated by chemical exudates released by fish (DAWIDOWICZ et al. 1990). In Ranger Lake, fish planktivory may not have reached a level sufficient to trigger a strong vertical migration response in *Chaoborus* (MCQUEEN et al. 1999).

An important consideration in any food web experiment is response lag time. Organisms with short generation times such as most mesozooplankton can respond more quickly to changes in fish planktivory than macrozooplankton that have longer generation times (WIENS et al. 1986, HE et al. 1994, SCHINDLER et al. 1975). The dispersal ability of adult *Chaoborus* may also confound the trophic links between *Chaoborus*, their predators, and their prey. Populations of *Chaoborus* within a single lake are more properly thought of as sub-populations within a much larger local population. Even with high fish planktivory, *Chaoborus* biomass may not be strongly reduced, if dispersal of adults from nearby lakes is also high. For example, when high biomass of planktivorous cutthroat trout were introduced to Eunice Lake, British Columbia, it took two years for *C. trivittatus* to be completely eliminated (NORTHCOTE et al. 1978). Similarly, stocking with cutthroat trout took six years to reduce the biomass of *C. flavicans* (LUECKE 1986). Conversely, when fish planktivory is reduced in a lake, it may take several years for new *Chaoborus* species to arrive from local populations. When planktivorous fish were eliminated from a quarry near Gräfenhain, Germany, it took 5–10 years for the biomass of *C. flavicans* to reach high levels (BENNDORF 1995, BENNDORF et al. 1988). A larger species, *C. obscuripes*, which eventually became the dominant planktivore did not appear until 11 years following the fish removal. Within the time scale of our study, the *Chaoborus* assemblage in Mouse Lake showed stronger responses to decreases in planktivory than the one in Ranger Lake showed to increased planktivory. Lake communities tend to move along different trajectories in response to fish additions and removals (HE et al. 1994). Perhaps the chaoborid populations of Ranger Lake simply take a longer time to fully respond.

Our results emphasize the importance of a long-term data set in evaluating the results of whole-system experiments (MCQUEEN et al. 1989, 1992, MILLS et al. 1987, DEMELO et al. 1992). Both *Chaoborus* and fish are univoltine predators. While seasonal population dynamics are informative, a single experimental observation for these predators essentially spans a year. Each year is only one more n . If the interannual variability that we have found was typical, and there is no reason to believe that it was unusual, then only in data sets of several years length can the effects of trophic interactions be detected with confidence. For example, biomass of planktivorous fish in Mouse Lake were high from 1991 to 1994, and low from 1995 to 1997, and these time periods were typified by low and high *Chaoborus* biomass, respectively. Yet, within the high planktivory period there were two years (1993 and 1994) of quite high *Chaoborus* biomass and within the low planktivory period there was a year (1995) of quite low *Chaoborus* biomass. Similar *Chaoborus* population dynamics were found in Peter, Paul, and Tuesday Lakes from 1984 to 1990 by SORANNO et al. (1993), and in Little Rock Lake from 1985 to 1993 by FISCHER & FROST (1997). Without long-term data sets, it would be impossible to place purported effects of an experimental manipulation in the proper context of normal inter-annual variability (RUSAK et al. 2001).

In summary, as a result of our manipulation of piscivorous fish, the biomass of planktivorous fish in Mouse Lake decreased dramatically, while that in Ranger Lake increased but not as strongly. The wide range in fish planktivory induced in our two study lakes over the exper-

imental period seemed to produce responses in the total biomass and species composition of *Chaoborus* assemblages. Years with high planktivorous fish biomass were typified by low *Chaoborus* biomass and the dominance of smaller species. In years with low fish biomass, *Chaoborus* biomass was higher and was shifted towards larger species. Ranger Lake had less variation in the biomass of planktivorous fish compared to Mouse Lake and did not as strongly show the same responses in *Chaoborus*. Interannual variability was considerable especially in Mouse Lake where total *Chaoborus* biomass could be high despite high fish biomass and low even with low fish biomass. The dominance of smaller zooplankton under high fish planktivory probably was an advantage for smaller-bodied chaoborids in addition to their lower vulnerability to fish predation. As a whole, the *Chaoborus* assemblages in our lakes were able to maintain a surprisingly high biomass, despite a high biomass of planktivorous fish. Shifts in body size and changes in diurnal vertical migration patterns were compensatory mechanisms that allowed *Chaoborus* to somewhat ameliorate the effects of fish predation.

Acknowledgements

We gratefully thank our crew chief, Stanley Sutey, and the many technicians who helped collect these data for their considerable efforts and dedication to this project. We are equally grateful to both Dr. William Geiling and Dee Geiling (LimnoServices, Kingston, Ontario) for enumerating our *Chaoborus* samples. They continued to work hard under very difficult circumstances. This paper is dedicated to the memory of Dr. William Geiling.

References

- ALLAN, J.D. (1973): Competition and the relative abundances of two cladocerans. – *Ecology* **54**: 484–496.
- ALLEN, G., YAN, N.D. & GEILING, W.T. (1994): ZEBRA2 Zooplankton enumeration and biomass routines for APIOS: A semi-automated sample processing system for zooplankton ecologists. – The Ontario Ministry Of the Environment. PIBS 2872. Queen's Printer for Ontario.
- BENNDORF, J. (1995): Possibilities and limits for controlling eutrophication by biomanipulation. – *Int. Rev. ges. Hydrobiol.* **80**: 519–534.
- BORKENT, A. (1981): The distribution and habitat preferences of the Chaoboridae (Culicomorpha: Diptera) of the Holarctic Region. – *Can. J. Zool.* **59**: 122–133.
- BOX, G.E.P. & TIAO, G.C. (1975): Intervention analysis with applications to economic and environmental problems. – *J. Amer. Statis. Assoc.* **70**: 70–79.
- BENNDORF, J., SCHULTZ, H., BENNDORF, A., UNGER, R., PENZ, E., KNESCHKE, H., KOSSATZ, K., DUMKE, R., HORNIG, U., KRUSPE, R. & REICHEL, S. (1988): Food web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypertrophic Bautzen reservoir. – *Limnol.* **19**: 97–110.
- BRABAND, Å, FAAFENG, B. & NILSEN, J.P.M. (1986): Juvenile roach and invertebrate predators: delaying the recovery phase of eutrophic lakes by suppression of efficient filter-feeders. – *J. Fish. Biol.* **29**: 99–106.
- BRANSTRATOR, D.K. (1998): Predicting diet composition from body length in the zooplankton predator *Leptodora kindtii*. – *Limnol. Oceanogr.* **43**: 530–535.
- CARPENTER, S.R., FROST, T.M., HEISEY, D. & KRATZ, T.K. (1989): Randomized intervention analysis and the interpretation of whole-ecosystem experiments. – *Ecology* **70**: 1142–1152.
- CARPENTER, S.R. & KITCHELL, J.F. (eds) (1993): *The trophic cascade in lakes*. – Cambridge University Press.

- CARPENTER, S.R., KITCHELL, J.F. & HODGSON, J.R. (1985): Cascading trophic interactions and lake productivity. – *BioScience* **35**: 634–639.
- CARPENTER, S.R., KITCHELL, J.F., HODGSON, J.R., COCHRAN, P.A., ELSER, J.J., ELSER, M.M., LODGE, D.M., KRETCHMER, D., HE, X. & VON ENDE, C.N. (1987): Regulation of lake primary productivity by food web structure. – *Ecology* **68**: 1863–1876.
- DAWIDOWICZ, P., PIJANOWSKA, J. & CIECHOMSKI, K. (1990): Vertical migration of *Chaoborus* is induced by the presence of fish. – *Limnol. Oceanogr.* **35**: 1631–1637.
- DEMELO, R., FRANCE, R. & MCQUEEN, D.J. (1992): Biomanipulation: Hit or myth? – *Limnol. Oceanogr.* **37**: 192–207.
- DEMERS, E. (1996): Role of predation in structuring the fish communities of two small, oligotrophic lakes. – PhD. thesis, York University, Toronto, Ontario.
- DEMERS, E., MCQUEEN, D.J., POPIEL, S.A., ROCCHI, A.M., RAMCHARAN, C.W. & PÉREZ-FUENTETAJA, A. (2001a): Changes in the fish community structure. – *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **56**: 23–48.
- DEMERS, E., MCQUEEN, D.J., RAMCHARAN, C.W. & PÉREZ-FUENTETAJA, A. (2001b): Did piscivores regulate changes in fish community structure? – *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **56**: 49–80.
- DILLON, P.J., MCQUEEN, D.J., RAMCHARAN, C.W., YAN, N.D., DEMERS, E. & HUDSON, J.J. (2001): Changes in nutrient and ion chemistry. – *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **56**: 227–255.
- DINI, M.J. & CARPENTER, S.R. (1991): The effect of whole-lake community manipulations on *Daphnia* migratory behavior. – *Limnol. Oceanogr.* **36**: 370–377.
- ELSER, M.M., VON ENDE, C.N., SORANNO, P. & CARPENTER, S.R. (1987): *Chaoborus* populations: response to food web manipulation and potential effects on zooplankton communities. – *Can. J. Zool.* **65**: 2846–2852.
- FILION, J.-M. (1991): Improving plankton samplers with simple electronics. – *Limnol. Oceanogr.* **36**: 204–210.
- FISCHER, J.M. & FROST, T.M. (1997): Indirect impacts of lake acidification on *Chaoborus* population dynamics: the role of food limitation and predation. – *Can. J. Fish. Aquat. Sci.* **54**: 637–646.
- GULATI, R.D., LAMMENS, E.H.R.R., MEIJER, M.-L. & VAN DONK, E. (eds.) (1990): Biomanipulation. Tool for water management. – *Hydrobiol.* **200/201**, Kluwer.
- HE, X., SCHEURELL, M.D., SORANNO, P.A. & WRIGHT, R.A. (1994): Recurrent response patterns of a zooplankton community to whole-lake fish manipulation. – *Freshwat. Biol.* **32**: 61–72.
- HORPPILA, J. (1997): Diurnal changes in the vertical distribution of cladocerans in a biomanipulated lake. – *Hydrobiol.* **345**: 215–220.
- LASENBY, D.C., YAN, N.D., FUTTER, M.N. (1994): Changes in body dimensions of larval *Chaoborus* in ethanol and formalin. – *J. Plank. Res.* **16**: 1601–1608.
- LAMPERT, W. (1989): The adaptive significance of diel vertical migration of zooplankton. – *Funct. Ecol.* **3**: 21–27.
- LUECKE, C. (1986): A change in the vertical migration of *Chaoborus flavicans* after the introduction of trout. – *J. Plank. Res.* **8**: 649–657.
- MACKAY, N.A., CARPENTER, S.R. & SORANNO, P.A. (1990): The impact of two *Chaoborus* species on a zooplankton community. – *Can. J. Zool.* **68**: 981–985.
- MCEACHERN, L.J. (1986): Diet and vertical distribution of three coexisting species of *Chaoborus* (Diptera; Chaoboridae) larvae in Chub Lake, Ontario. – MSc. Thesis, Trent University, Peterborough, Ontario.
- MCQUEEN, D.J., JOHANNES, M.R.S. & POST, J.R. (1989): Bottom-up and top-down impacts on freshwater pelagic community structure. – *Ecol. Monogr.* **59**: 289–309.
- MCQUEEN, D.J., MILLS, E.L., FORNEY, J.L., JOHANNES, M.R.S. & POST, J.R. (1992): Trophic level relationships in pelagic food webs: comparisons derived from long-term data sets for Oneida Lake, New York (USA), and Lake St. George, Ontario (Canada). – *Can. J. Fish. Aquat. Sci.* **49**: 1588–1596.
- MCQUEEN, D.J., RAMCHARAN, C.W., YAN, N.D., DEMERS, E., PÉREZ-FUENTETAJA, A. & DILLON, P.J. (2001): Objectives, methods, the physical-chemical setting. – *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **56**: 1–21.

- MCQUEEN, D.J., RAMCHARAN, C.W., DEMERS, E., YAN, N.D., CONFORTI, L. & PÉREZ-FUENTETAJAM, A. (1999): *Chaoborus* behavioral responses to changes in fish density. – Arch. Hydrobiol. **145**: 165–179.
- MCQUEEN, D.J. & YAN, N.D. (1993): Metering filtration efficiency of freshwater zooplankton hauls: reminders from the past. – J. Plank. Res. **15**: 57–65.
- MILLS, E.L., FORNEY, J.L. & WAGNER, K.J. (1987): Fish predation and its cascading effect on the Oneida Lake food chain. – In: KERFOOT, W.C. & SHI, A. (eds.): Predation. Direct and indirect impacts on aquatic communities. – University Press of New England, pp. 118–131.
- MOORE, M.V., YAN, N.D. & PAWSON, T. (1994): Omnivory of the larval phantom midge (*Chaoborus* spp.) and its potential significance for freshwater planktonic food webs. – Can. J. Zool. **72**: 2055–2065.
- MONAKOV, A.V. (1972): Review of studies on feeding of aquatic invertebrates conducted at the Institute of Biology of Inland Waters, Academy of Sciences, USSR. – J. Fish. Res. Bd. Can. **29**: 363–383.
- NEILL, W.E. (1985) The effects of herbivore competition upon the dynamics of *Chaoborus* predation. – Arch. Hydrobiol. Beih. Ergeb. Limnol. **21**: 483–491.
- NORTHCOTE, T.G., WALTERS, C.J. & HUME, J.M.M. (1978): Initial impacts of experimental fish introductions on the macrozooplankton of small oligotrophic lakes. – Verh. Internat. Verein Limnol. **20**: 2003–2012.
- PASTOROK, R.A. (1981): Selection of prey by *Chaoborus* larvae: A review and new evidence for behavioral flexibility. – In: KERFOOT, W.C. (ed): Evolution and ecology of zooplankton communities. – Univ. Press of New England, pp. 538–554.
- POPE, G.F., CARTER, J.C.H. & POWER, G. (1973): The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River System, Québec. – Trans. Amer. Fish. Soc. **4**: 707–714.
- RAMCHARAN, C.W., MCQUEEN D.J., DEMERS, E., POPIEL, S.A., ROCCHI, A.M., YAN N.D., WONG, A.H. & HUGHES, K.D. (1995): A comparative approach to determining the role of fish predation in structuring limnetic ecosystems. – Arch. Hydrobiol. **133**: 389–416.
- RAMCHARAN, C.W., MCQUEEN, D.J., PÉREZ-FUENTETAJAM, A., YAN, N.D., DEMERS, E. & RUSAK, J.A. (2001): Analysis of lake food webs using individual-based models to estimate *Chaoborus* production and consumption. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **56**: 101–126.
- RUSAK, J.A., YAN, N.D., SOMERS, K.M., MCQUEEN, D.J. & RAMCHARAN, C.W. (2001): Differences in the variability of crustacean zooplankton communities between manipulated and reference lakes. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **56**: 171–186.
- SAUNDERS, J.F., III & W.M. LEWIS, JR. (1988) Dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). – Ecol. Monogr. **58**: 337–353.
- SCHINDLER, D.W., MILLS, K.H., MALLEY, D.F., FINDLAY, D.L., SHEARER, J.A., DAVIES, I.J., TURNER, M.A., LINSLEY, G.A. & CRUIKSHANK, D.R. (1975): Long-term ecosystem stress: The effects of years of experimental acidification on a small lake. – Science **228**: 1395–1401.
- SELL, A. (1996): Reaktionen der Zooplanktongemeinschaft auf eine extreme Biomanipulation: Die Rolle des invertebraten Räubers *Chaoborus*. – PhD. Thesis, Institut für Hydrobiologie, Dresden, Germany.
- SELL, A. (2001): Long-term effects of planktivore removal: results from a manipulated and a reference lake. – Verh. Internat. Verein. Limnol. **27**.
- SHAPIRO, J., LAMARRA, V. & LYNCH, M. (1975): Biomanipulation: an ecosystem approach to lake restoration. – In: BREZONIK, P.L. & FOX, J.L. (eds.): Water quality management through biological control. C Rep. No. ENV-07-75-1, University of Florida.
- SORANNO, P.A., CARPENTER, S.R. & MOEGENBURG, S.M. (1993): Dynamics of the phantom midge: implications for zooplankton. – In: CARPENTER, S.R. & KITCHELL, J.F. (eds): The trophic cascade in lakes. – Cambridge University Press, pp. 103–115.
- SPRULES, W.G., HOLTBY, L.B. & GRIGGS, G. (1981): A microcomputer-based measuring device for biological research. – Can. J. Zool. **59**: 1611–1614.
- STENSON, J.A.E. (1981): The role of predation in the evolution of morphology, behavior and life history of two species of *Chaoborus*. – Oikos **37**: 323–327.
- STEWART-OATEN, A., MURDOCH, W. & PARKER, K. (1986): Environmental impact assessment: "Pseudoreplication" in time? – Ecology **67**: 929–940.

- SWIFT, M.C. & FEDORENKO, A. (1975): Some aspects of prey capture by *Chaoborus* larvae. – *Limnol. Oceanogr.* **20**: 418–425.
- TJOSSEM, S.F. (1990): Effects of fish chemical cues on vertical migration behavior of *Chaoborus*. – *Limnol. Oceanogr.* **35**: 1456–1468.
- TSALKITZIS, E., YAN, N.D., MCQUEEN, D.J., POPIEL, S.A. & DEMIERS, E. (1993): Habitat separation among three temperate *Chaoborus* species. – *Arch. Hydrobiol.* **129**: 385–403.
- VON ENDE, C.N. (1979) Fish predation, interspecific competition, and the distribution of two *Chaoborus* species. – *Ecology* **60**: 119–128.
- WIENS, J.A., ADDICOTT, J.F., CASE, T.J. & DIAMOND, J. (1986): Overview: The importance of spatial and temporal scale in ecological investigations. – In: DIAMOND, J. & CASE, T.J. (eds.): *Community ecology*. – Harper and Row, pp. 145–153.
- WISSEL, B. (1997): Planktonstruktur und Primärproduktion in zwei Ganz-Seen-Experimenten mit drastischen Unterschieden in der Fischbesiedlung. – Diploma Thesis, Institut für Hydrobiologie, Dresden, Germany.
- YAN, N.D., NERO, R.W., KELLER, W., LASENBY, D.C. (1985). Are *Chaoborus* larvae more abundant in acidified than in non-acidified lakes in central Canada? – *Holarctic Ecology* **8**: 93–99.
- YAN, N.D., KELLER, W., MACISAAC, H.J. & McEACHERN, L.J. (1991): Regulation of zooplankton community structure of an acidified lake by *Chaoborus*. – *Ecol. Appl.* **1**: 52–65.
- YAN, N.D., MCQUEEN, D.J., PAWSON, T.W., GIRARD, R. & VISMAN, V. (1992): Measuring zooplankton net filtration efficiency in Dorset lakes. – The Ontario Ministry of the Environment and Energy. PIBS 2049E. Queen's Printer for Ontario.
- YAN, N.D., PÉREZ-FUENTETAJA, A., RAMCHARAN, C.W., MCQUEEN, D.J. (2001): Changes in the crustacean zooplankton communities of Mouse and Ranger Lakes. – *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **56**: 127–150.