Apparent Exclusion of the Cladoceran Bosmina longirostris by Invertebrate Predator Chaoborus americanus

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ABSTRACT: Zooplankton communities were sampled in 22 lakes in the Upper Peninsula of Michigan. The cladoceran *Bosmina longirostris* was present in 16 of 17 lakes with fish, but absent from the five without fish. The phantom midge larva species *Chaoborus americanus* was present only in the fishless lakes. *In situ* competition and predation experiments were conducted in a fishless lake, Tender Bog, in which *Daphnia pulex, Diaptomus leptopus* and *C. americanus* larvae were the dominant zooplankters. *Bosmina* grew well alone and when reared with *Daphnia,* but suffered significantly greater predation by *Chaoborus* larvae when offered as prey together with the other two species. From 8-12 months elapsed before *Bosmina* colonized a lake from which it had been absent. The absence of *Bosmina* from fishless lakes with the Tender Bog zooplankton community appears to be due not to local environmental conditions, or interspecific competition, but rather to low immigration rates and intense predation by *Chaoborus* larvae.

INTRODUCTION

Studies on the structure of zooplankton communities have considered the importance of vertebrate predation, competition and invertebrate predation. Vertebrate predation has been shown to be a dominant process because the visually feeding vertebrate predators prey selectively on the more visible, generally larger prey (Brooks, 1968; Hutchinson, 1971; Werner and Hall, 1974). Interspecific competition originally was hypothesized as an equally important process to explain the absence of smaller cladoceran species from lakes dominated by larger cladocerans (Brooks and Dodson, 1965); however, the significance of competition in structuring cladoceran zooplankton communities remains unresolved (Lynch, 1978, 1979; Giguere, 1979). More recently, invertebrate predation has been suggested to be a process that must be considered when discussing zooplankton community dynamics and structure (Dodson, 1974, Kerfoot, 1977; Lane, 1979; Lynch, 1979). If we are to gain a better understanding of the limits of these processes, more studies are needed in which their relative importance is investigated.

Samples from a large number of lakes at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan revealed an interesting distribution of the cladoceran *Bosmina longirostris. Bosmina* was present in most of the lakes with fish (16/17), but absent from all the lakes without fish (5/5), which are small bog lakes (von Ende, 1979). Correspondingly, *Chaoborus americanus* occurred only in the fishless lakes (von Ende, 1979). The lakes with fish had some combination of three other *Chaoborus* species: *C. flavicans, C. punctipennis* or *C. trivittatus.* The five fishless lakes were of two kinds, according to their zooplankton communities. Three of the lakes had *C. americanus, Daphnia pulex* and *Diaptomus leptopus*; the other two had *C. americanus, C. trivittatus, Holopedium gibberum, Diaptomus leptopus, Diaphanosoma leuchtenbergianum* and *Daphnia pulex.* In the latter set of lakes, *C. trivittatus* and *D. pulex* were relatively rare.

There are four obvious factors that could be operating to exclude *Bosmina* from these lakes: low dispersal rates, different environmental (physical-chemical, algal) conditions in the fishless lakes, interspecific competition and invertebrate predation. Because all the fishless lakes have lakes nearby (<1 km) with *Bosmina,* it is unlikely

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low dispersal rates alone are responsible for the pattern. However, it could be that environmental conditions in these fishless bog lakes differ sufficiently from those in the other lakes so that *Bosmina* cannot survive there. The distribution of *Daphnia* and *Chaoborus americanus,* relative to that of *Bosmina,* also suggests competition with the larger cladoceran or predation by the midge larva may be important in excluding *Bosmina* from these fishless lakes. *Chaoborus americanus* differs from the other *Chaoborus* species in that its 3rd and 4th instar larvae undergo only limited diurnal vertical migration (Fedorenko and Swift, 1972; von Ende, 1975), which would provide greater opportunity for predation because of continual spatial overlap of *Bosmina* and all larval instars. The purpose of this study was to determine experimentally the reason(s) for the absence of *Bosmina* from the set of fishless lakes having the simpler zooplankton community (*Daphnia, Diaptomus* and *C. americanus*).

METHODS

Tender Bog, with the simpler zooplankton community, was chosen for the experimental manipulations. The general characteristics of this lake are described by von Ende (1979). The competition experiments were planned for the same summer (1976) as the predation experiments. However, the *Daphnia pulex* population in Tender Bog disappeared for the year in early July 1976, forcing postponement of the competition experiments until 1978. The basic experimental design was to raise *Bosmina* alone and with *Daphnia* in Tender Bog. Raising *Bosmina* alone tested its ability to survive in that environment and also served as the control for the competition experiment. Competition was considered to be primarily between *Bosmina* and *Daphnia,* rather than *Bosmina* and *Diaptomus,* because *Bosmina* coexists with *Diaptomis leptopus* in other lakes at UNDERC; therefore, no attempt was made to determine the effect of *Diaptomus* alone or with *Daphnia* on *Bosmina.*

Competition experiments.—Plastic 0.95-liter containers with windows of 80 μm Nitex were used for the competition experiments. They are described in more detail by von Ende (1975). Initial densities were 16 of the respective species per container when raised alone and eight of each species when raised together. *Daphnia* was obtained from Tender Bog and *Bosmina* from nearby Beaver Bog. The animals were collected from their respective lakes the day the experiment was begun. The number of replicates was three for *Daphnia* alone, four for *Bosmina* alone and five for *Daphnia* and *Bosmina* together. Survival was monitored approximately weekly in the field with the aid of a dissection microscope while pipetting the animals from their container to a clean one. Animals were caught on the surface film only on three occasions, and only once did they constitute more than 5% of the population (11%). The experiment ran from 27 June 1978 to 6 August 1978. The average instantaneous growth rates of the *Bosmina* and *Daphnia* populations in these experiments were estimated using the equation $r = \frac{\ln N_t - \ln N_0}{t}$ (Ricklefs, 1979)

Predation experiments.—During the summer of 1976, a series of *in situ* predation cxperiments was performed to determine the intensity of predation on *Bosmina* compared to the other zooplankton species present in Tender Bog. The experimental chambers described above for the competition experiments were used and again suspended at 0.5 m in Tender Bog (Table 1).

Experiment 1 investigated predation on *Bosmina* compared to that on *Daphnia* and *Diaptomus* without regard to the size of the latter two species. *Daphnia* used were mature and larger than 1 mm; the *Diaptomus* were larger copepodids or adults. The densities of *Daphnia* and *Diaptomus* were approximately equal to their densities in Tender Bog at the end of June. Experiment 2 determined whether there was selective predation on *Bosmina* and different-sized *Daphnia* and *Diaptomus. Daphnia* were separated by eye into three size categories and *Diaptomus* into two (Table 2). For this experiment prey densities were made equal. Experiment 3 was conducted at the end of July, when *Daphnia* had transformed to ephippia; it tested survivorship of *Bosmina* in the absence of *Daphnia* as an alternative prey. The densities of prey were slightly greater in this experiment, reflecting the higher density in Tender Bog at the end of July.

By August, the *Chaoborus* population in Tender Bog was composed primarily of 3rd and 4th instar larvae (von Ende, 1975). These older instars exhibit a restricted vertical migration between the surface of 3 m (von Ende, 1975). The plankton in Tender and Beaver bogs was always concentrated in the upper 2 m. Experiment 4 determined whether the combination of some diurnal spatial separation and a large initial population size would enable *Bosmina* to coexist with *Chaoborus*; it also documented the behavior of the 3rd and 4th instar *Chaoborus* larvae in August 1976. *Chaoborus* larvae were added to each experimental container in Tender Bog at sunset. At sunrise the *Chaoborus* were removed from the experimental chambers, placed in a 19-l holding bucket, and resuspended at 3 m. The small containers were then resuspended at 0.5 m. At the next sunset the *Chaoborus* were removed from the holding chamber and again placed in the experimental containers for the night. This procedure was continued for the duration of the experiment (9 days).

To determine the vertical migratory pattern of *Chaoborus,* samples were collected on 3 August 1976 at 3-hr intervals for 24 hr with a 30.4-l Patalas-Schindler plankton trap. Two samples were taken at each depth from the surface to 6 m at 1-m intervals. The density of instars of *Chaoborus* larvae used in the predation experiments corresponded approximately to those in Tender Bog at the time of the experiments.

TABLE 1.—Details of predation experiments with 2nd, 3rd and 4th instar *C. americanus*

Experiment	Replicates	Prey	Initial number/ container	*Chaoborus* (Instar-No.)	Duration of experiment	Date of experiment
1	4	*Bosmina*	6	2nd-2	48 hr	12-13 July
		Daphnia	6	3rd-1		
		Diaptomus	2			
2	5	*Daphnia* (large)	6			
		Daphnia (medium)	6			
		Daphnia (small)	6	2nd-2	24 hr	20 July
		Diaptomus (adult)	6	3rd-1		
		Diaptomus (copepodid)	6			
		Bosmina	6			
3	6	*Diaptomus* (adult)	10	3rd-3	48 hr	30-31 July
		Diaptomus (copepodid)	10			
		Bosmina	10			
4	3	*Bosmina*	30/50/70	3rd-1 4th-1	9 days	10-18 Aug.

TABLE 2.—Size classes of prey in Experiment 4

Prey	Size range (mm)
Daphnia (large)	1.25-1.82
Daphnia (medium)	0.83-1.16
Daphnia (small)	0.50-0.79
Diaptomus (adult)	1.73-2.08
Diaptomus (copepodid)	0.46-1.48
Bosmina	0.23-0.56

Chaoborus and zooplankton densities in Tender Bog were monitored throughout the summer of 1976. Predation experiments 1-3 were analyzed by X^2 contingency table analysis. The number of prey remaining in the control containers (without *Chaoborus*) were compared with the experimental containers (with *Chaoborus*). All replicates were tested for homogeneity before combining. For experiments 2 and 3, the contingency tables were subdivided to determine the class responsible for the significant difference (Zar, 1974). Experiment 4 was analyzed by a two-way analysis of variance.

A crude estimate of the colonization rate of *Bosmina* was obtained during a previous study (von Ende, 1979), when fish were added to a bog lake (North Bog) with the same zooplankton fauna as Tender Bog. In fact, the densities of *Chaoborus americanus* in the two lakes were comparable (von Ende, 1979). North Bog was sampled in August, September and October 1973, and in October in 1974 and 1975 (*see* von Ende, 1979, for sampling details). The fish (*Umbra limi*) were added in September 1973.

RESULTS

Competition experiments.—The growth of *Bosmina* in the control containers of the competition experiment demonstrates that it was not inhibited by the general conditions in Tender Bog. (Table 3). The mean density in the containers at the end of the experiment ($\overline{X}=490.2$) was greater than twice the maximum density recorded for the natural population of *Bosmina* in Beaver Bog during the summer of 1976 (Dempsey, 1978). The same results were obtained in the summer of 1976 for an equivalent set of containers in which *Bosmina* was grown by itself in Tender Bog (Dempsey, 1978).

Bosmina also grew well in the experimental containers with *Daphnia* in 1978 (Table 3). The small size of the containers should have maximized the potential for interaction between the two species. However, although the patterns of population growth for *Bosmina* in the experimental and control containers were not exactly parallel, the final density of *Bosmina* in the experimental containers was about one-half that in the control containers. Except for the 3rd week, the mean instantaneous growth rates were very close in the experimental and control containers (Table 4).

TABLE 3.—Mean densities per container ± 95% confidence limits (except for 6/27) for *Daphnia* and *Bosmina* competition experiment in 1978

Experimental condition	Date 6/27	7/4	7/11	7/19	7/27	8/6
Daphnia alone	16.0	50.7	87.7	102.0	168.0	153.0
n=3		±27.7	± 40.7	± 59.8	±111.4	± 92.6
Bosmina alone	16.0	53.2	115.8	189.2	362.8	409.2
n=4		±13.0	± 19.2	± 24.7	± 20.3	±177.1
Daphnia + *Bosmina*						
n=5						
Daphnia	8.0	31.2	52.6	80.4	127.0	114.0
		±13.9	± 17.5	± 30.1	± 33.4	± 28.0
Bosmina	8.0	25.0	52.2	63.2	138.2	192.6
		± 3.3	± 9.5	± 24.2	± 74.0	± 91.0

TABLE 4.—Mean instantaneous growth rates of *Bosmina* and *Daphnia* in control and experimental containers

Experimental condition	Period (days) 1-7	8-14	15-22	23-30	30-40
Bosmina alone	0.16	0.12	0.06	0.08	0.01
Bosmina with *Daphnia*	0.16	0.11	0.02	0.10	0.03
Daphnia alone	0.16	0.08	0.02	0.06	−0.01
Daphnia with *Bosmina*	0.16	0.07	0.05	0.06	−0.01

Therefore, the effect of *Daphnia* on *Bosmina* appeared to be about equivalent to the effect of *Bosmina* on itself.

Predation experiments.—The overall results of the predation experiments show that *Bosmina* can be subject to heavy predation by *Chaoborus americanus.* In Experiment 1, in which the size of the three prey species was not controlled, *Bosmina* was consumed at a significantly greater rate ($X^2=14.086$, $P<0.001$) than the other two species (Table 5). When *Daphnia* and *Diaptomus* were separated into size classes (Experiment 2), *Bosmina* still suffered a significantly greater predation rate ($X^2=11.675$, $P<0.05$; Table 6). Subdivision of the contingency table showed the difference between the experimental and control conditions was due to the difference in the number of *Bosmina.* When only *Diaptomus* was offered as an alternative prey (Experiment 3), *Bosmina* again had significantly greater mortality ($X^2=36.965$, $P<0.001$; Table 7). Subdivision of the contingency table proved the difference was due to *Bosmina.* The vertical migratory behavioı of the 3rd and 4th instar *C. americanus* larvae (Fig. 1) shows there could be some temporal spatial separation of the older instars and *Bosmina,* if *Bosmina* were restricted to the upper meter. However, in the experimental situation (Table 8), the reduced exposure time and large initial population sizes did not confer an advantage on the *Bosmina* in the experimental containers. Analysis of variance shows both the predation effect ($F=425.9$, $P<0.001$) and the *Bosmina* density effect ($F=23.6$, $P<0.001$) were significant. Also, the interaction was significant ($F=23.8$, $P<0.001$) because the final densities of the control populations reflected the initial densities, whereas the experimental populations were essentially the same at the end of the experiment.

The addition of fish to North Bog in September 1973 produced several dramatic changes. First, the fish eliminated *Chaoborus americanus* by October 1974. It was replaced by *C. punctipennis,* although the latter was rare in 1974 and 1975. Secondly, there was a gradual shift from a Tender Bog-type community (*Daphnia*

TABLE 5.—Results of predation Experiment 1. Mean number of prey remaining per container at 48 hr

Prey	Control	Experimental
Bosmina	6.0	0.5
Daphnia	6.0	6.0
Diaptomus	2.0	2.0
		$X^2 = 14.086$, $P<0.001$

TABLE 6.—Results of predation Experiment 2. Mean number of prey remaining per container at 24 hr

Prey	Control	Experimental
Daphnia (large)	6.0	6.0
Daphnia (medium)	6.0	6.2
Daphnia (small)	8.0	6.8
Diaptomus (adult)	6.0	6.0
Diaptomus (copepodid)	6.6	5.2
Bosmina	6.0	2.0
		$X^2 = 11.675$, $P<0.05$

TABLE 7.—Results of predation Experiment 3. Mean number of prey remaining per container at 48 hr

Prey	Control	Experimental
Bosmina	12.8	1.8
Diaptomus (adult)	10.0	10.0
Diaptomus (copepodid)	10.0	9.6
		$X^2 = 36.965$, $P<0.001$

pulex, Diaptomus leptopus) to a Beaver Bog-type community (*Bosmina, Diaphanosoma leuchtenbergianum, Ceriodaphnia reticulata* and *D. leptopus*). In October 1973 the Tender Bog type still was present, whereas in October 1974 the zooplankton consisted of *D. leptopus* and rotifers. By October 1975 *Bosmina, Ceriodaphnia, Diaphanosoma* and *D. pulex* were present, in addition to *D. leptopus.* Except for the presence of *D. pulex,* the community had shifted to that of Beaver Bog. The presence of *Bosmina* in October 1975 indicates it took 8-12 months for it to colonize the lake successfully.

Discussion

The answer to the original question of the reason(s) for the absence of *Bosmina* from Tender Bog lies in the relative rates of three factors: the immigration rate of *Bosmina,* the population growth rate of *Bosmina* and the predation rate of *Chaoborus. Bosmina* can disperse to lakes from which it is absent; but its dispersal rate is low. Environmental conditions and *Daphnia pulex* did not inhibit the growth of *Bosmina* in Tender Bog. In contrast, Lynch (1978) found, in a competition experiment in August and September, that *D. pulex* did significantly affect the density of *B. longirostris* but did not drive it to extinction. In a competition experiment at the same time of the year between these two species in Frains Lake, Michigan, Dempsey (1978) found *Bosmina* went extinct in three of four experimental containers with *Daphnia,* and the density was low in the fourth. *Daphnia* was not native to Frains Lake.

The difference in outcome between these two sets of experiments and our experiment may be due to a seasonal shift in competitive balance as Lynch (1978) observed between *Daphnia pulex* and *Ceriodaphnia,* or to the different environment of the bog lake habitat. We think it is the latter. Neill (1978) found food limitation and

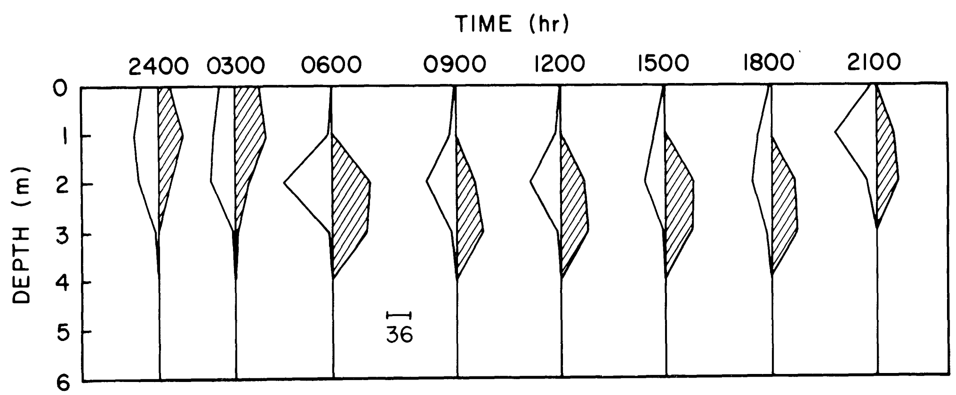

Fig. 1.—Vertical distribution in Tender Bog of 3rd and 4th instar (hatched) *C. americanus* larvae over 24-hr period. Bar shows number of larvae/30.4-1 trap

TABLE 8.—Results of predation Experiment 4. Mean number of prey remaining per container at 9 days

Initial *Bosmina* density	Final *Bosmina* density: Control	Final *Bosmina* density: Experimental
30	63.3	1.0
50	109.5	0.3
70	151.0	0.8

water quality appeared to be important in limiting the invasion of montane lakes in British Columbia by *D. pulex.* Stained bog lakes such as Tender Bog are noted for their low planktonic primary production (Wetzel, 1975). Apparently *D. pulex* does not have a competitive advantage in these bog lakes. Furthermore, the early disappearance of *Daphnia* in 1976 in Tender Bog indicates the potential for competition between *Bosmina* and *Daphnia* in Tender Bog may not always exist throughout the summer in any given year. However, because the *Daphnia* population in Ed's Bog, another lake at UNDERC with the same fauna as Tender Bog, generally is longer-lived during the summer, this phenomenon may be peculiar to Tender Bog.

In spite of differences in instars (consequently, size) between experiments, *Bosmina* definitely was more heavily preyed upon than the other two prey species. Usually daphnid cladocerans are less preferred prey for *Chaoborus* than copepods (Sprules, 1972; Swüste *et al.,* 1973), although predation experiments with small nondaphnid cladoceran species as alternative prey have not been done previously. In a review of the literature on *Chaoborus* predation, Lewis (1977) concluded *Bosmina* generally is the zooplankter most highly selected by *Chaoborus;* he described *Chaoborus* selectively in general as depending on the prey size, and the visibility and behavior. Similarly, Pastorok (1978) defined the vulnerability of the prey as the product of the encounter rate between predator and prey and the capture success of the predator. If *Bosmina* is considered in terms of these parameters, a possible explanation of the higher predation rates follows.

First, Swift and Fedorenko (1975) and Pastorok (1978) found, in predation studies with *Chaoborus americanus* and *C. trivittatus* and a number of zooplankton species, that handling time and strike efficiency decreased with increased prey size. Second, from our observations in the competition and predation experiments, it is obvious *Bosmina* was much more active than *Daphnia.* As Swift and Fedorenko (1975) observed, *Bosmina* constantly scurried jerkily about the containers. *Bosmina* appeared generally to be more active than *Diaptomus leptopus,* although the latter had a very rapid escape response. Swift and Fedorenko (1975) found *Bosmina* had a swimming speed about equal to that of *Diaptomus kenai* juveniles, less than *D. kenai* adults, and greater than *D. tyrelli* adults. Equally important, however, *Bosmina*'s escape response to predaceous copepods and probably *Chaoborus,* is to sink passively (Kerfoot, 1975), whereas *D. kenai* moves at a rate of 147 $cm \cdot s^{-1}$ when disturbed (Swift and Fedorenko, 1975). Because *D. leptopus* adults are only slightly smaller than *D. kenai* adults (von Ende, 1979), the former should have a similar escape capability. Therefore, it would appear that the high predation rate on *Bosmina* is the result of its high vulnerability. Because it moves frequently, it has a much greater chance of encountering the predator. A model of zooplankton prey selection by Gerritsen and Strickler (1977) predicts an ambush predator such as *Chaoborus* is most efficient on fast-moving prey. Then given that *Bosmina* has encountered the predator, its chances of being captured are high because of its small size and its passive escape response. The low predation rate of *C. americanus* on *D. leptopus* in our experiments probably is the result of using 2nd and 3rd instar larvae. Swift and Fedorenko (1975) found 3rd instar *C. americanus* larvae could not handle the large *D. kenai* adults.

Because the predation experiments were done in small containers, there is the question of the potential intensity of *Chaoborus* predation on *Bosmina* on a larger scale. Lynch's (1979) results provide some insight. The data cited below are estimated from his Figure 3. In experiments in plastic bags (1.0 m x 1.8 m) with several zooplankton species, he found an inverse relationship between *C. americanus* densities and *Bosmina* densities. *Bosmina* was barely detectable in bags with mean *Chaoborus* densities of 500-2000/m^2, whereas at the same time *Bosmina* reached mean densities ranging from about 2 x 10^5 to 2 x $10^6/m^2$ in bags with no *Chaoborus*. *Bosmina* was not detectable in the pond (0.25 ha, max. depth 2.5 m) at this time, where mean *Chaoborus* densities were $6500/m^2$. Thus the greater predation *Bosmina* suffers in prey selection experiments is likely to be reflected at the population level as population decline, if *Chaoborus* densities are high.

The high density of *Chaoborus* in Tender Bog presents the potential for high predation rates. Predation may be even more intense on *Bosmina* because of the lower diversity of alternative prey, and the dominance of the smaller 2nd and 3rd instar *Chaoborus* throughout most of the summer. Lynch (1979) estimated the mean instantaneous death rate of *Bosmina* in his control bags with a mean *Chaoborus* density of ca. $1000/m^2$ (estimated from his Fig. 3) to be 0.18. *Chaoborus* density in Tender Bog on 5 September 1976, for a combined depth of Patalas-Schindler plankton trap samples of 1.8 m, was $1188/m^2$. Because Lynch's bags were 1.8 m deep, these values are comparable. Therefore, 0.18 can be used as a crude estimate of the death rate of *Bosmina* in Tender Bog in August and September, although this is a conservative estimate for June and July when the *Chaoborus* density is greater. Obviously, *Chaoborus* predation is considered the major source of *Bosmina* mortality. A high predation rate could be balanced by a high immigration rate, or high reproductive rate, or both. Our results suggest immigration rates may be rather low for *Bosmina* in these bog lakes. Goulden *et al.* (1978) concluded, from laboratory studies that *Bosmina* usually has a lower r_{max} than large *Daphnia* species because of its smaller clutch size, although they predicted *Bosmina* should have a higher r at low food densities. In our experiment, the *Bosmina* controls had instantaneous growth rates equal to or greater than *Daphnia* alone, which may confirm Goulden *et al.*'s (1978) conclusion. Because *Bosmina* had reproductive rates comparable to those of *Daphnia,* but does not survive in the lake, it must be because it is more vulnerable to predation. A comparison of *Bosmina*'s estimated death rate with its growth rate in our experiment (Table 4) supports this conclusion. Finally, both the absence of *Bosmina* from Tender Bog, because of *Chaoborus* predation, and the species composition of this bog lake, fit the high-intensity *Chaoborus*-predation scenario Lynch (1979) described for his Pleasant Pond community, except that *Daphnia-Bosmina* interactions are less important in Tender Bog.

Although this study has examined the importance of *Chaoborus* predation in fishless lakes, the effect should be considered also in lakes with fish. *Chaoborus* densities usually are lower in lakes with fish, but in some instances they can become high (Juday, 1921; Eggleton, 1931). Northcote and Clarotto (1975) in studying the zooplankton communities of eight lakes in British Columbia with and without fish reported *Bosmina* was present in all of the lakes except one, Lake Placid. This was the one lake, of the eight, with the greatest concentration of *Chaoborus.* In Lake Placid *C. flavicans* reached densities of over 30/100-1 in the near-surface waters at night. These results, as well as ours, suggest that if *Chaoborus* densities are sufficiently high, they may have a significant impact on *Bosmina* populations even though overlap of predator and prey is not continuous in time.

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LITERATURE CITED

BROOKS, J. L. 1968. The effects of prey size selection by lake planktivores. *Syst. Zool.,* **17**:272-291.

——— AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science,* **150**:28-35.

DEMPSEY, D. O. 1978. Zooplankton community structure: Factors affecting the distribution of *Bosmina longirostris*. M.S. Thesis, Northern Ill. Univ., DeKalb. 117 p.

DODSON, S. I. 1974. Zooplankton competition and predation: An experimental test of the size efficiency hypothesis. *Ecology*, **55**:605-613.

EGGLETON, F. E. 1931. A limnological study of the profundal bottom fauna of certain freshwater lakes. *Ecol. Monogr.*, **1**:231-332.

FEDORENKO, A. Y. AND M. C. SWIFT. 1972. Comparative biology of *Chaoborus americanus* and *Chaoborus trivittatus* in Eunice Lake, British Columbia. *Limnol. Oceanogr.*, **17**:721-730.

GERRITSEN, J. AND J. R. STRICKLER. 1977. Encounter probabilities and community structure and zooplankton: A mathematical model. *J. Fish. Res. Board Can.*, **34**:73-82.

GIGUERE, L. 1979. An experimental test of Dodson's hypothesis that *Ambystoma* (a salamander) and *Chaoborus* (a phantom midge) have complementary feeding niches. *Can. J. Zool.*, **57**:1091-1097.

GOULDEN, C. E., L. HORNIG AND C. WILSON. 1978. Why do large zooplankton species dominate? *Verh. Int. Ver. Limnol.*, **20**:2457-2461.

HUTCHINSON, B. P. 1971. The effect of fish predation on the zooplankton of ten Adirondack Lakes, with particular reference to the alewife, *Alosa pseudohargenus*. *Trans. Am. Fish. Soc.*, **100**:325-335.

JUDAY, C. 1921. Observations on the biology of *Corethra punctipennis* Say. *Biol. Bull.*, **40**:271-286.

KERFOOT, W. C. 1975. The divergence of adjacent populations. *Ecology*, **56**:1298-1313.

———. 1977. Implications of copepod predation. *Limnol. Oceanogr.*, **22**:316-325.

LANE, P. A. 1979. Vertebrate and invertebrate predation intensity on freshwater zooplankton communities. *Nature*, **280**:391-393.

LEWIS, W. M. 1977. Feeding selectivity of a tropical *Chaoborus* population. *Freshwater Biol.*, **7**:311-326.

LYNCH, M. 1978. Complex interactions between natural coexploiters—*Daphnia* and *Ceriodaphnia*. *Ecology*, **59**:552-564.

———. 1979. Predation, competition, and zooplankton community structure: An experimental study. *Limnol. Oceanogr.*, **24**:253-272.

NEILL, W. E. 1978. Experimental studies on factors limiting colonization by *Daphnia pulex* Leydig of coastal montane lakes in British Columbia. *Can. J. Zool.*, **56**:2498-2507.

NORTHCOTE, T. G. AND R. CLAROTTO. 1975. Limnetic macrozooplankton and fish predation in some coastal British Columbia lakes. *Verh. Int. Ver. Limnol.*, **19**:2378-2393.

PASTOROK, R. A. 1978. Predation by *Chaoborus* larvae and its impact on the zooplankton community. Ph.D. Dissertation, Univ. Washington, Seattle. 238 p.

RICKLEFS, R. E. 1979. Ecology. Chiron Press, New York, New York. 966 p.

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

SWIFT, M. C. AND A. Y. FEDORENKO. 1975. Some aspects of prey capture by *Chaoborus* larvae. *Limnol. Oceanogr.*, **20**:418-426.

SWÜSTE, H. F., R. CREMER AND S. PARMA. 1973. Selective predation by larvae of *Chaoborus flavicans* (Diptera, Chaoboridae) *Verh. Int. Ver. Limnol.*, **28**:1559-1563.

VON ENDE, C. N. 1975. Organization of bog lake zooplankton communities: Factors affecting the distribution of four *Chaoborus* species (Diptera:Chaoboridae). Ph.D. Dissertation, Univ. Notre Dame, Notre Dame, Indiana. 107 p.

———. 1979. Fish predation, interspecific predation, and the distribution of two *Chaoborus* species. *Ecology*, **60**:119-128.

WERNER, E. E. AND D. J. HALL. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish *(Lepomis macrochirus)*. *Ibid.*, **55**:1042-1052.

WETZEL, R. 1975. Limnology. W. B. Saunders Co., Philadelphia, Pa. 743 p.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 620 p.

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