

FISH PREDATION, INTERSPECIFIC PREDATION, AND THE DISTRIBUTION OF TWO *CHAOBORUS* SPECIES¹

CARL N. VON ENDE

Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115 USA

Abstract. In sampling 22 lakes in the Upper Peninsula of Michigan, I found that 2 species of *Chaoborus*, *C. punctipennis* and *C. americanus*, never co-occurred (von Ende 1975). *Chaoborus punctipennis* was found only in lakes with fish whereas *C. americanus* occurred alone in stained, bog lakes without fish. Third and 4th instar *C. americanus* lack extensive diel, vertical migratory behavior and are found near the surface waters in stained bog lakes. Adults of this species emerge in the middle of May. Third and 4th instar *C. punctipennis* exhibit diel, vertical migration. They are benthic during the day. This species emerges at the end of June.

In situ rearing experiments indicate that *Chaoborus americanus* larvae can survive in lakes with fish, when isolated from the fish. Fish (*Umbra limi*) added to a lake with *C. americanus* eliminated this *Chaoborus* species from the lake. It is concluded that the absence of *C. americanus* from lakes with *C. punctipennis* is due to fish predation on the older larvae of *C. americanus*.

Chaoborus punctipennis adults are able to disperse to lakes from which their larvae are absent. *In situ* experiments indicate *C. punctipennis* can survive on the zooplankton in a stained, fishless bog lake, but is subject to heavy predation by 3rd and 4th instar *C. americanus* larvae. It is concluded that because of early recruitment by *C. americanus*, as well as its lack of extensive vertical migration, this species excludes *C. punctipennis* from stained, fishless bog lakes.

Key words: bog lakes; *Chaoborus*; Diptera; dispersal; fish predation; Insecta; invertebrate predation; Michigan; patchy environment; vertical migration; zooplankton.

INTRODUCTION

The conditions for the regional coexistence or exclusion of species in a patchy environment have been treated theoretically by Levins and Culver (1971), Horn and MacArthur (1972), and Slatkin (1974) in models based on competition. They have considered the role of competition with respect to extinction and migration rates of species between patches of a habitat. Vandermeer (1973) applied a similar kind of model to predator-prey interactions in a patchy environment. He investigated the regional stabilization of locally unstable predator-prey relationships. Field investigations of competition in patchy environments have involved primarily intrapatch competition for space (Dayton 1971, 1975; Connell 1973; Culver 1973; Platt 1975). Field investigations of predator-prey interactions rarely have looked at regional patterns of predator and prey distribution in a patchy environment. Brooks and Dodson (1965) essentially addressed this question when they considered the patterns of distribution of herbivorous zooplankton species and planktivorous fish. However, they were dealing with a system in which migration rates of both predator and prey would be expected to be rather low. Many aquatic insects have stages of their life cycle that remain within a lake, and a stage that can migrate between lakes. This is a similar, but even better system, in which to look at competition and predation in a patchy environment.

The phantom midge larva, the predaceous larval

stage of the midge *Chaoborus*, is a common member of zooplankton and benthic communities of most lakes and ponds (Roth 1967, Hilsenhoff and Narf 1968, Hamilton 1971). It is one of the few planktonic invertebrate predators (Hutchinson 1967), and is considered to be a rather voracious predator on most other zooplankton species (Dodson 1970, Roth 1971, Sprules 1972, Allan 1973). In an initial survey of 22 lakes at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan, I found 4 *Chaoborus* species occurring in various combinations (von Ende 1975). The main characteristics of the distribution of the species were that (1) *C. americanus* was present only in lakes without fish (6 of 22); (2) *C. flavicans* and *C. punctipennis* were found only in lakes with fish, although *C. flavicans* was not present in all lakes with fish; (3) *C. trivittatus* was found in 1 of the lakes with fish, and in some of the lakes without fish. In terms of species combinations in the lakes, *C. americanus* occurred by itself or with *C. trivittatus*. *Chaoborus punctipennis* occurred alone or with *C. flavicans*, or with both *C. flavicans* and *C. trivittatus*. A similar pattern of distribution of *C. americanus* and *C. punctipennis* is reported in the surveys of Stahl (1959), Roth (1967), Hilsenhoff and Narf (1968), and Hamilton (1971). Of a total of 54 lakes sampled, *C. punctipennis* occurred in 40 and *C. americanus* in 6. They co-occurred only once. The purpose of this study was to determine why the 2 species found most commonly in the fishless and fish-lakes at UNDERC, *C. americanus* and *C. punctipennis*, respectively, never co-occur in these lakes. Also, why does *C. americanus* occur in so few lakes?

¹ Manuscript received 12 September 1977; accepted 9 May 1978.

TABLE 1. *Chaoborus*, zooplankton, and fish species, and characteristics of the 4 bog lakes

Species	Fish present		Fish absent	
	North Gate	Hummingbird	Tender	Forest Service
<i>Chaoborus americanus</i>			×	×
<i>Chaoborus flavicans</i>		×		
<i>Chaoborus punctipennis</i>	×	×		
<i>Chaoborus trivittatus</i>		×		×
<i>Bosmina longirostris</i>	×	×		
<i>Cyclops bicuspidatus thomasi</i>	×			
<i>Daphnia catawba</i>		×		
<i>Daphnia parvula</i>		×		
<i>Daphnia pulex</i>	×		×	
<i>Diaphanosoma leuchtenbergianum</i>				×
<i>Diaptomus leptopus</i>			×	×
<i>Holopedium gibberum</i>		×		×
<i>Tropocyclops prasinus</i>		×		
<i>Perca flavescens</i>		×		
<i>Umbra limi</i>	×	×		
Lake Characteristics				
Maximum depth (m)	8.0	7.5	10.0	4.5
Secchi disk (m)	1.1	0.7	1.5	2.2
pH	4.9	5.4	4.2	4.8
Stained	Yes	Yes	Yes	No

The question of the absence of *C. punctipennis* from lakes with *C. americanus* is restricted only to those lakes in which *C. americanus* occurs alone, which are stained, fishless bog lakes. The 2 parts of this question will be discussed independently, first the absence of *C. americanus* from lakes in which *C. punctipennis* is found, and then the absence of *C. punctipennis* from lakes in which *C. americanus* is the sole species present. Often in attempting to explain the patterns of distribution of species, alternate hypotheses are not considered (Connell 1975). In this study, alternate hypotheses were tested when possible.

STUDY SITES

Of the 22 Michigan lakes sampled, I selected 4 that had representative *Chaoborus* faunas for intensive

study and experimental manipulations (Table 1). The 4 lakes are characteristic bog lakes (Table 1), are small (<0.7 ha), acid, and, except for Forest Service Bog, have stained water, and are relatively deep. Two of the lakes have fish. Generally, the zooplankton populations in the lakes without fish are dominated by larger species, whereas the species in the lakes with fish are smaller (Tables 1, 2). *Daphnia pulex* in North Gate Bog and *Holopedium gibberum* in Hummingbird Bog are exceptions. There are also size differences among the *Chaoborus* species (Table 2). *Chaoborus punctipennis* is the smallest, followed in size by *C. flavicans*. *Chaoborus americanus* is larger than *C. flavicans*, but smaller than the largest of the 4, *C. trivittatus*.

DISTRIBUTION OF *CHAOBORUS AMERICANUS*

Hypotheses

There are a number of possible explanations for the absence of *Chaoborus americanus* from the lakes in which *C. punctipennis* is found. As stated above, *C. punctipennis* occurs only in those lakes that contain fish. Fish do prey on *Chaoborus*. The 2 *Chaoborus* species found most commonly in the lakes studied with fish, *C. punctipennis* and *C. flavicans*, are noted for the diel, vertical migratory behavior of the 3rd and 4th instar larvae (Wood 1956; Stahl 1966; Roth 1968; LaRow 1968, 1969).

Typically, the larvae are in or near the benthos during the day, but migrate to the surface waters at nighttime. I found this also to be the case for these species in North Gate and Hummingbird bogs (von Ende 1975). In contrast, *C. americanus* does not undergo extensive vertical migration in Tender and Forest Service bogs (von Ende 1975). In Tender Bog, 3rd and 4th instar larvae are continuously concentrated in the

TABLE 2. Mean (\bar{x}) and standard error (SE) of cladoceran (adults), copepod (adults), and *Chaoborus* (4th instar larvae) species in the 4 bog lakes (n = 30)

Taxa	Body length		Head capsule length	
	\bar{x}	SE	\bar{x}	SE
<i>Chaoborus americanus</i>	12.42	0.47	1.57	0.06
<i>C. flavicans</i>	10.78	0.29	1.35	0.04
<i>C. punctipennis</i>	9.29	0.47	1.07	0.04
<i>C. trivittatus</i>	12.79	0.69	1.96	0.09
<i>Bosmina</i>	0.38	0.04		
<i>Cyclops</i>	0.78	0.02		
<i>Daphnia catawba</i>	1.22	0.14		
<i>D. parvula</i>	0.93	0.12		
<i>D. pulex</i>	1.39	0.04		
<i>Diaphanosoma</i>	0.70	0.05		
<i>Diaptomus</i>	2.12	0.12		
<i>Holopedium</i> (carapace)	0.85	0.11		
<i>Holopedium</i> (sheath)	1.72	0.14		
<i>Tropocyclops</i>	0.53	0.02		

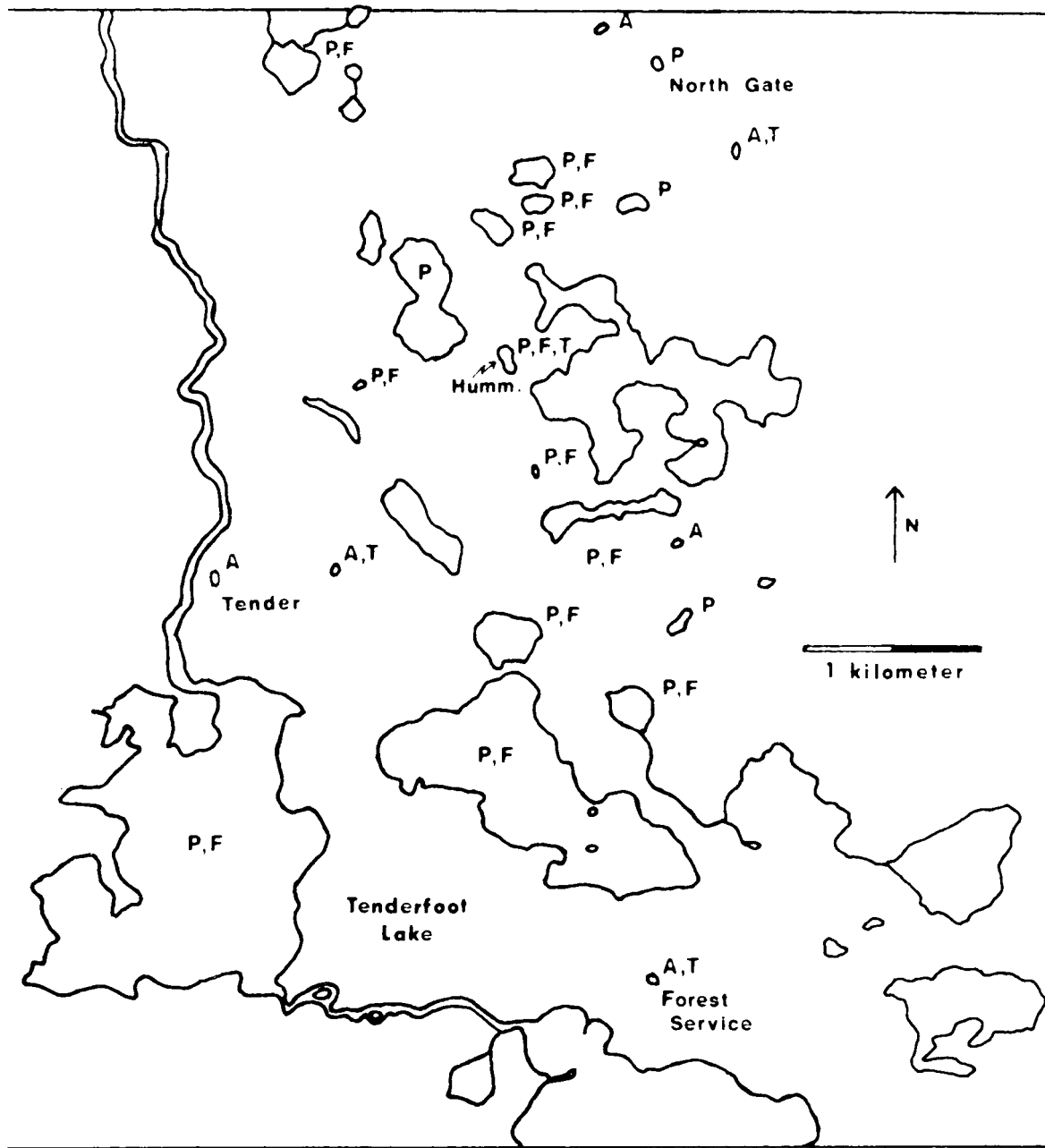


FIG. 1. Map of University of Notre Dame Environmental Research Center showing distribution of *Chaoborus* species among the lakes. A = *C. americanus*, F = *C. flavicans*, P = *C. punctipennis*, T = *C. trivittatus*

upper 3 m. In Forest Service Bog they are generally at 3 m during the day and evenly distributed at night. Therefore, a first hypothesis is that because *C. americanus* is continually near the surface waters and is a relatively large species, it may be subject to predation by planktivorous fish sufficient to exclude it from lakes with fish.

An alternate hypothesis is that the environmental conditions and/or the food resources associated with these lakes are responsible for the absence of *C.*

americanus. That is, can *C. americanus* live in these lakes on the prey available when isolated from fish? As noted above, the zooplankton in the lakes with fish generally are smaller. The *Daphnia pulex* population in North Gate Bog lasts only a short time in the spring (J. Koenings, *personal communication*). Because *C. americanus* is a larger species, it may be unable to utilize the smaller prey in the lakes with fish. Although not as likely, perhaps the environmental conditions in the lakes with fish restrict the distribution of *C. ameri-*

TABLE 3. Mean number of *Chaoborus americanus* for 1.5-m vertical tows (238 l) in Tender Bog and North Bog, Michigan. $N = 2$ except for 12 October 1974 and 24 October 1975 when $N = 3$. Fish added to North Bog 23 August 1973

Lake	Instar	1973					1974	1975
		22 Aug	23 Aug	31 Aug	8 Sep	6 Oct	12 Oct	24 Oct
Tender	4th	273.5	238.5	234.0	449.0	527.5	281.3	159.3
	3rd	67.0	52.5	6.0	2.5	0	0.3	0
	2nd	3.5	1.0	0.5	0	0	0	0
North	4th	249.0	264.0	305.0	195.5	90.5	0	0
	3rd	26.5	52.0	15.5	23.5	0.5	0	0
	2nd	3.0	2.5	2.5	3.0	0	0	0

canus. In this study, I did not attempt to separate the effects of these 2 factors.

A 3rd possible explanation is that *C. americanus* is unable to disperse sufficiently to reach the lakes from which it is absent. It was not possible to test this hypothesis directly. However, Hilsenhoff (1971) showed that *Chaoborus albatrus*, *C. flavicans*, and *C. punctipennis* were able to recolonize a lake 4 yr after it had been defaunated. The immigrants probably came from populations in 7 lakes within 3.2 km, the closest being 0.4 km. From the distribution of the lakes studied containing *C. americanus* (Fig. 1), it seems that over time, some of the lakes with *C. punctipennis* would have been colonized by *C. americanus*. Its absence does not seem to be due to inability to disperse.

Methods

To test the fish predation hypothesis, 340 fish (*Umbra limi*) were added to another bog lake, North Bog, on 23 August 1973. The lake is similar in size and morphometry to Tender Bog. *Chaoborus americanus* was the sole *Chaoborus* species present, and it was abundant. I collected plankton samples in North Bog and Tender Bog (used as a control) before and after the fish were added to North Bog. On each sampling date in 1973, I took 2 1.5-m vertical tows (238 l each) with a plankton net with a 53 cm mouth diameter. Three vertical tows were taken in each lake when sampled in 1974 and 1975. All samples were collected between 2330 h and 0130 h.

To evaluate the 2nd hypothesis, I tried to raise early instars of *C. americanus in situ* in North Gate and Hummingbird bogs. Because of the difficulty of ver-

tical migration in the older instars of *C. punctipennis* and *C. flavicans*, I raised the *C. americanus* larvae by themselves. Therefore, I was not testing whether *C. americanus*' absence was due to competition with the resident *Chaoborus* species, but whether *C. americanus* could survive in the lakes under the environmental conditions and on the prey available.

To raise *C. americanus in situ*, I constructed small chambers from round, polyethylene refrigerator containers (0.95 l), with tightly sealing tops. Two rhomboidal "windows" were cut in the sides, and a circular window in the cover. Nitex (80 μ m) was glued over the windows with Testor's cement. The screened windows allowed for circulation of water and food for the prey into the containers. I placed 10, 1st instar *C. americanus* from Tender Bog in each container. If there were an optimum size prey that had to be above a threshold density for *C. americanus* to survive, this could be detected by raising the larvae at different prey densities. Therefore, the experiments were conducted at 2 different prey densities, hereafter referred to as low prey density and high prey density. I assumed that if a threshold density of an optimum prey existed, then it was between the levels of the prey density treatment that I chose. The densities were determined in the following manner to duplicate prey densities (including day to day variation) as closely as possible.

I collected a sample of zooplankton with a 30-l plexiglas plankton trap equipped with an 80 μ m Nitex net (Schindler 1969). I concentrated the sample to 300 ml and took a 10-ml sample for the low prey density treatment level. This aliquot was essentially equivalent to the actual number of prey/litre found in the lake. The

TABLE 4. Chi-square contingency table analysis of survivorship and instar distribution of *Chaoborus americanus* in Hummingbird Bog, Michigan, on day 52

	Low prey	High prey	χ^2
Survived	24	18	
Died	6	12	
			1.984 ($P = .159$)
3rd instar	18	2	
4th instar	6	16	
			17.832 ($P < .001$)

TABLE 5. Chi-square contingency table analysis of survivorship and instar distribution of *Chaoborus americanus* in North Gate Bog on day 60

	Low prey	High prey	χ^2
Survived	27	21	
Died	3	9	
			2.604 ($P = .107$)
3rd instar	21	0	
4th instar	6	21	
			29.037 ($P < .001$)

high prey density treatment level was 3 times the density of the low prey density. I gave containers receiving the high prey density treatment level a 30 ml aliquot of the concentrated plankton sample. Three replicates of each of the prey densities were run simultaneously in Hummingbird and North Gate bogs. I began the experiments on 30 May 1973 and they ran at least 52 days. I suspended the containers at 0.5 m depth and changed the prey every other day. In the statistical analysis of the experiments, I pooled the results of the replicates and analyzed larval survivorship and relative growth rates by chi-square contingency table analysis (Sokal and Rohlf 1969).

Results

The results of adding fish to North Bog (Table 3) show that predation by the mudminnows was sufficient to eliminate *Chaoborus americanus* from the lake, or at least to drive the population to a level undetectable by my sampling method. Although Tender and North bogs had comparable densities of *C. americanus* larvae before the fish were added, several months later there were already fewer larvae in North Bog. (Five of 7 fish collected from North Bog 1 week after the introduction were feeding on 4th instar *C. americanus*.) One year later, no *C. americanus* larvae were found in North Bog, although a few *C. punctipennis* larvae were found. Similar results were obtained in an unrelated study, when mudminnows were introduced into another bog lake at the study area that contained *C. americanus*, but no fish (E. Brady, personal communication).

Chaoborus americanus survived and grew in both Hummingbird and North Gate bogs (Tables 4, 5). Average survivorship for the 2 treatment levels was 70% in North Gate Bog and 80% in Hummingbird Bog. Although not significantly different ($\alpha = .05$), survivorship was slightly higher at the lower prey density. Observations during the experiment suggest there may have been some cannibalism at the higher food level. In both rearing experiments, the growth rates of the larvae were greater at the higher prey density. There were significantly ($P < .001$) more larvae in the 4th instar at the higher prey density than at the lower prey density (Tables 4, 5).

Discussion

The results of the rearing experiments and the fish introduction confirm the importance of fish predation in the distribution of *C. americanus*. Because I was interested in the ability of *C. americanus* to utilize the smaller prey species, the critical stage was the large 4th instar. With the exception of 2 larvae in the Hummingbird experiment, all the larvae that survived at the high prey density reached the 4th instar. The 4th instars began appearing on day 32. That they lasted another 20–28 days on the prey in these lakes shows they were able to survive to the older stages of the 4th

instar. By surviving this long, there is a very good probability that *C. americanus* can live in the lakes with fish (when isolated from the fish). The relatively high survivorship of *C. americanus* at both prey densities demonstrates that there was no rare prey whose threshold density was between the 2 densities used. If such a phenomenon existed, I would have expected little or no survivorship at the lower prey density and good survivorship at the high prey density. The increased growth rates at the higher prey density show that the larvae were able to take advantage of the increased availability of prey.

The elimination of *C. americanus* by fish in North Bog suggests that fish predation is the major factor responsible for the absence of *C. americanus* from lakes with *C. punctipennis* and fish. This is corroborated by the results of a similar experiment in British Columbia by Northcote and Hume (*in press*). They introduced cutthroat trout (*Salmo clarki*) into a small lake and Dolly Varden (*Salvelinus melma*) into another. Neither lake had fish previously. They found that the 2 resident *Chaoborus* species, *C. americanus* and *C. trivittatus*, were preyed upon heavily by the fish. Within 2 years neither *Chaoborus* species was present in plankton samples or fish gut samples. Pope et al. (1973) sampled 26 lakes (with and without fish) on the Matamek River system in Quebec. They found the same 4 *Chaoborus* species that occur in the UNDERC lakes, as well as a 5th unidentified species of the same subgenus as *C. trivittatus*, *Schadanophasma*. *Chaoborus americanus* was present only in lakes without fish and did not co-occur with *C. punctipennis*. A lake containing *C. americanus* and the *Schadanophasma* sp. was stocked in 1970 with Atlantic salmon (*Salmo salar*). Carter and Kwik (1977) reported that since 1973, *Schadanophasma* sp. had been eliminated from the lake, but *C. americanus* was still present. Because this particular lake is 43 m deep, it could be that there is sufficient spatial separation of the fish and *C. americanus* such that predation is minimized, and therefore *C. americanus* is not eliminated. This lake also may be rather atypical because it is a large lake with only 1 species of fish. In most large lakes, one would expect a number of planktivorous species to be present, and the intensity of fish predation to be greater. This shows that, although the exclusion of *C. americanus* by fish appears to be a fairly general phenomenon, the intensity of predation in a lake depends on the interaction of the characteristics of the lake, the *C. americanus* population, and the fish species.

The significance of diel, vertical migratory behavior in zooplankton has long been of interest. McLaren (1963) suggested that perhaps it represented an attempt to maximize growth on an energetic basis. Both Lock and McLaren (1970) and Swift (1976) showed no energetic advantage from fluctuating temperatures (=vertical migration) using laboratory growth experi-

TABLE 6. Predation experiments with 3rd and 4th instar *Chaoborus americanus* and *Chaoborus punctipennis*. All experiments except experiment 8 conducted in 0.95-l containers. Nineteen-litre containers used for experiment 8

Experiment	<i>Chaoborus americanus</i>			<i>Chaoborus punctipennis</i>			Prey density	Replicates
	Instar	\bar{x} length (mm)	Number/container	Instar	\bar{x} length (mm)	Number/container		
3	3rd	7.8	2	3rd	4.3	5	None, Low	6
4	4th	12.3	2	3rd	4.3	5	None, Low	6
5	4th	9.7	2	3rd	4.9	7	None, Low, High	5
6	4th	12.3	2	3rd	4.9	7	None, Low, High	5
7	{ 4th	9.7	2	4th	6.9	7	None, Low, High	5
	{ 4th	12.3	2					
8	4th	12.3	38	4th	6.9	133	Low	1

ments. Zaret and Suffern (1976) presented evidence to support the hypothesis that vertical migration of freshwater zooplankton serves to reduce predation by vertebrate predators. The results of this study also suggest it is advantageous for *Chaoborus* larvae to migrate vertically to minimize predation by fish. The rarity of *C. americanus* in lakes is best explained by the absence of the migratory behavior in this species, and the scarcity of lakes without fish.

DISTRIBUTION OF *CHAOBORUS PUNCTIPENNIS*

Hypotheses

The dispersal hypothesis, and the resource and habitat utilization hypothesis described for *Chaoborus americanus* also can be applied to the question of the absence of *C. punctipennis* from bog lakes such as Tender Bog. The evidence cited previously for dispersal of *C. punctipennis* (Hilsenhoff 1971) suggests that this species should be able to reach the lakes at UNDERC from which it is absent (Fig. 1). The 2nd hypothesis again is based on size differences between the *Chaoborus* species and the zooplankton prey. The zooplankton in Tender Bog are larger species (Tables 1, 2). *Chaoborus punctipennis* is the smallest of the 4 *Chaoborus* species (Table 2). The 2nd hypothesis is that *C. punctipennis* is absent from Tender Bog because it either cannot efficiently utilize the larger zooplankton species, or withstand the environmental conditions, or both. Again, I did not attempt to separate the effects of these 2 factors.

The last hypothesis involves the direct interaction of *C. americanus* and *C. punctipennis*. *Chaoborus americanus* has its peak of emergence in the middle of May, whereas *C. punctipennis* has its peak near the end of June (von Ende 1975). By the end of June, *C. americanus* is in its 3rd instar (von Ende 1975). Typically, 1st and 2nd instar larvae of *Chaoborus* species reside near the surface waters. Also, recall that 3rd and 4th instar *C. americanus* larvae remain high in the water column in a stained bog lake such as Tender Bog. Therefore, it is possible that *C. punctipennis* larvae hatching in late June in a bog such as Tender Bog

would be subject to sufficiently intense predation by *C. americanus* to be excluded from such a lake.

Methods

To test the dispersal hypothesis, a light trap was set at Tender Bog at night when *C. punctipennis* and *C. flavicans* adults were emerging in nearby Tenderfoot Lake (Fig. 1). The 2nd hypothesis was tested for *C. punctipennis* in the same way that it was for *C. americanus*. I raised *C. punctipennis* *in situ* in Tender Bog. I used the same experimental design, containers, and procedures described above for *C. americanus*. I placed 10, 2nd instar *C. punctipennis* from North Gate Bog in each of 6 containers in Tender Bog on 11 July 1973. There were 3 replicates of each prey density. I suspended the containers at 0.5 m and changed the prey every other day. It was necessary to use 2nd instar *C. punctipennis* because the 1st instars were nearly impossible to see with the naked eye. This will be referred to as experiment 1.

To test the interspecific predation hypothesis, I raised *C. punctipennis* larvae on the plankton in Tender Bog in the presence of 3rd instar *C. americanus*. I placed 3, 3rd instar *C. americanus* and 7, 2nd instar *C. punctipennis* in each container. Three 3rd instar *C. americanus*/litre was the density in Tender Bog at the start of the experiment. The other zooplankton prey species were included to offer *C. americanus* alternate prey, which would mimic more closely the actual situation. I used 2 prey densities (low and high) to determine whether the predation rate was dependent on the abundance of alternate prey. This experiment will be referred to as experiment 2. It was run simultaneously with experiment 1. The rest of the procedures were the same as in experiment 1.

If *C. punctipennis* larvae were able to survive in

TABLE 7. Survivorship of *Chaoborus punctipennis* in Tender Bog, number of 4th instars on day 36 (original cohorts of 10)

Low prey	High prey
9	10
9	9
9	9

TABLE 8. Predation rates of *Chaoborus americanus* on *Chaoborus punctipennis* in experiments 3 and 4 (mean number eaten/container/48 h). *C* is test statistic for Wilcoxon 2-sample test

Experiment	Zooplankton			<i>C</i>
	Absent	Low density	High density	
3	3.5	2.2	26.0	($P > .20$)
4	4.8	4.2	27.5	($.10 < P < .20$)

Tender Bog to 3rd or 4th instar, would they still be vulnerable to predation by later instars of *C. americanus*? To answer this question I conducted a series of short-term predation experiments with 3rd and 4th instars of both species. The details of these experiments are summarized in Table 6. Experiments 3 and 4 had treatment levels of no alternate prey and low density of alternate prey. A third level of the prey treatment was added in experiments 5, 6, and 7 because it was felt older 3rd instar and 4th instar *C. punctipennis* may have been large enough compared to 4th instar *C. americanus* such that the density of alternate prey could affect the predation rate. Experiment 7 was cross-classified for density of alternate prey and size of 4th instar *C. americanus*. The zooplankton densities were determined as in the previous experiments. To determine whether the size of the containers biased the experiments, I ran experiment 8 in 19-l plastic buckets with sealing tops. The buckets had 80 μ m Nitex windows on the sides and in the tops. The density of *Chaoborus* and zooplankton was equivalent to that in the low prey density treatment level in experiment 7. Controls (*C. punctipennis* without *C. americanus*) were run for all treatment combinations in all the experiments. The containers were suspended at 0.5 m in Tender Bog. I ran the experiments for 48 h. The mean lengths of the larvae in Table 6 are based on samples of animals measured live at the beginning of the experiments ($N \geq 30$). I collected *C. punctipennis* from North Gate Bog and *C. americanus* from Tender Bog just prior to each experiment. The animals were not starved. The results of experiments 3 and 4 were analyzed by the Wilcoxon 2-sample test, experiments 5 and 6 by the Kruskal-Wallis test, and experiment 7 by a 2-factor analysis of variance (Sokal and Rohlf 1969).

TABLE 9. Predation rates of *Chaoborus americanus* on *Chaoborus punctipennis* in experiments 5 and 6 (mean number eaten/container/48 h). *H* is test statistic for Kruskal-Wallis test

Experiment	Zooplankton			<i>H</i>
	Absent	Low density	High density	
5	6.0	5.8	5.8	0.185 ($P > .10$)
6	6.4	6.4	5.4	0.880 ($P > .01$)

TABLE 10. Predation rates of *Chaoborus americanus* on *Chaoborus punctipennis* in experiment 7 (mean number eaten/container/48 h)

<i>Chaoborus americanus</i>	Zooplankton		
	Absent	Low density	High density
Small	4.4	3.4	3.6
Large	6.2	6.2	4.8

Results

Adults of *C. punctipennis* were obtained at Tender Bog. On several very warm nights, when the evening temperatures were $\approx 27^\circ\text{C}$, large emergences of *C. flavicans* and *C. punctipennis* occurred on nearby Tenderfoot Lake (7 July 1973, *C. flavicans*; 17 July 1973, *C. punctipennis*). On 9 July 1973, *C. flavicans* adults were caught in the light trap at Tender Bog after sunset. On 4 August 1973 I observed adults of both species on the surface of Tender Bog after sunset.

Ninety percent of the 2nd instar *C. punctipennis* reared alone in experiment 1 survived to the 4th instar (Table 7). There was no significant difference in growth rate or survivorship at the 2 prey densities. In experiment 2 there were no *C. punctipennis* remaining in the containers with *C. americanus* after day 10. The 2nd and early 3rd instar *C. punctipennis* were subject to intense predation by the 3rd instar *C. americanus*. Results of experiments 3 through 6 show that older 3rd instar *C. punctipennis* were also subject to heavy predation by 3rd and 4th instar *C. americanus* (Tables 8, 9). In none of these experiments was there a significant difference in the predation rates due to differences in alternate prey densities. The results of experiment 7 (Table 10) show there also was significant predation on 4th instar *C. punctipennis* by 4th instar *C. americanus*. Analysis of variance reveals that neither the zooplankton treatment ($.25 < P < .50$) nor the interaction ($.50 < P < .75$) were significant. There was a significant difference in predation rates due to the size of the *C. americanus* larvae ($.01 < P < .025$). The larger 4th instars had a greater predation rate.

In comparing the predation rates in experiments 3–7 (Table 11), we see that this same pattern holds for the predation of the 3rd and the large 4th instar *C.*

TABLE 11. Predation rates calculated as means of treatment levels for each experiment, 3 through 7 (mean number eaten/individual/48 h). Numbers in () refer to experiment

<i>Chaoborus americanus</i> (Instar/ \bar{x} length [mm])	<i>Chaoborus punctipennis</i>		
	3rd instar		4th instar
	4.3 mm	4.9 mm	6.9 mm
3rd/7.8	1.7 (3)
4th/9.7	...	2.9 (5)	1.9 (7)
4th/12.3	2.2 (4)	3.0 (6)	2.9 (7)

americanus on the 4.3-mm *C. punctipennis*. Also, for the smaller 4th instar *C. americanus*, the predation rate on the 4th instar *C. punctipennis* was lower than on the 3rd instars (4.9 mm). However, in comparing experiments 5, 6, and 7, we see the 2 sizes of 4th instar *C. americanus* preyed at the same rate on the 4.9 mm *C. punctipennis*; and the rates for the large 4th instar *C. americanus* on the larger 3rd instar and the 4th instar *C. punctipennis* were essentially the same. The lower predation rate in experiment 4 (as compared to experiment 6) probably was the result of a lower density of *C. punctipennis*. Two larger 4th instar *C. americanus* were capable of eliminating at least 6 *C. punctipennis* from a small container, but only 5 were available per container in experiment 4. Hence, the lower predation rate. In any case, there appears to be a threshold effect. If the size difference between *C. americanus* and *C. punctipennis* is great enough, then the predation rates are about the same. The large 4th instar *C. americanus* (12.3 mm) preys at the same rate on the 4.9 mm and 6.9 mm *C. punctipennis*. The small 4th instar *C. americanus* preys at the same rate as the larger 4th instar on the 4.9 mm *C. punctipennis*, but its predation rate decreases on the 6.9 mm *C. punctipennis*.

Because there was no mortality due to cannibalism by *C. punctipennis* in the controls of experiments 3–7, those results are not presented. Finally, there also was a high predation rate in the 19-l container (experiment 8). After 48 h, 81% of the *C. punctipennis* larvae had been preyed upon. The mean predation rate/individual *C. americanus* was 2.9, compared to 3.1 for the equivalent density in the small containers (experiment 7).

Discussion

Combining my results with those of Hilsenhoff (1971), we see that *C. punctipennis* has good dispersal ability. It should be capable of getting to the lakes at UNDERC in which it is not found. The fact that I found it in North Bog after *Umbra limi* had been introduced further substantiates this fact.

In the rearing experiments there was very good survivorship of *C. punctipennis* in Tender Bog. Again, I am using survivorship into the 4th instar as indication of a good probability of that species being able to complete its life cycle in a lake. On the basis of the experimental design, I would conclude the larvae were able to utilize the larger *Daphnia* and *Diaptomus* species in Tender Bog. However, this may not have been the case. There also was a high density of rotifers (primarily *Keratella*) in Tender Bog during the experiment. These smaller prey undoubtedly were utilized and may have been important to the survival of *C. punctipennis*. Thus, I can state that *C. punctipennis* can survive in Tender Bog, even though the species is not found there. In contrast to the *C. americanus* rearing experiments, there was no difference in growth

rates of *C. punctipennis* at the 2 prey densities. This probably was due to the high density of rotifers, even at the low-prey-density treatment level, that provided for a maximum growth rate under those conditions. Obviously, there was not a rare prey whose threshold density was between the experimental levels. Finally, the experimental conditions may have provided for an accelerated growth rate because the 3rd and 4th instar *C. punctipennis* larvae were prohibited from migrating to the hypolimnion during the day. Consequently, they were exposed to the prey continuously.

From the results of the predation experiments, I can conclude that interspecific predation is the best explanation for the absence of *C. punctipennis* from Tender Bog. Second- through 4th-instar *C. punctipennis* were vulnerable to significant predation by *C. americanus* 3rd and 4th instar larvae. Because the predation rates were unaffected by the density of alternate prey, I would expect a rather constant rate of predation depending only on the differences in the size of the larvae. The predation rates of 0.8–1.5 *C. punctipennis*/*C. americanus*/day probably are somewhat inflated because the older instars of the 2 species would be expected to have maximum spatial overlap only at night in the actual situation. However, the small size of the experimental containers used did not seem to bias the results, as the predation rate in these containers was only slightly > the rate in the 19-l container.

Interspecific predation between congeners has been reported a number of times in insects (Fox 1975). Frequently it is among species that are cannibalistic. Fox (1975) also suggests that interspecific predation should be common among species with generalized food habits and qualitatively similar resources. *Chaoborus* has all these characteristics. For species that live in an environment with unpredictable food resources, cannibalism may be a strategy that increases the probability of survival of a population. Shallow ponds, which are a typical *C. americanus* habitat (Bradshaw 1973), are an example of such an environment. Bog lakes may be also. In 1976, the *Daphnia pulex* population in Tender Bog disappeared for the season at the end of June. This had not happened in previous years. There also have been summers in which *Holopedium* has been rare in Hummingbird Bog. *Chaoborus* species are similar morphologically and feed on a variety of zooplankton species. Predation by *C. americanus* on *C. punctipennis* is not surprising in view of the size difference between the species, and the tendency in the genus to cannibalize (Saether 1972). The lack of cannibalism by *C. punctipennis* in my predation experiments probably was due to the lack of size differences between the larvae.

Whether the same explanation of interspecific predation holds for the absence of the other 2 species from stained, fishless bog lakes, is not clear. *Chaoborus flavicans* emerges at the end of May in Hum-

mingbird and Tenderfoot lakes (von Ende 1975), but the largest emergence in Tenderfoot Lake was observed in early July. It could be argued that at this time there would be the greatest probability of adult *C. flavicans* reaching Tender Bog. I know that *C. flavicans* adults are capable of reaching Tender Bog. Early instars of this species would be subject to the same predation pressure as *C. punctipennis* larvae. However, because there is less size difference between *C. flavicans* and *C. americanus* larvae, the predation rates on later instars of *C. flavicans* may be lower. Also, it should be determined whether *C. flavicans* can live in Tender Bog when reared alone. *Chaoborus trivittatus* emerges in late August (von Ende 1975). The same explanation should apply for its absence from stained bogs like Tender Bog. The size difference between the larvae of these 2 species would be large. But again, it should be shown that this species can get to such bogs and can survive there.

The absence of *C. flavicans* and *C. punctipennis* from Forest Service Bog (with unstained water) may not be due primarily to interspecific predation. The interaction of *C. americanus* and these 2 species may be less intense because *C. americanus* sits lower in the water column in this bog. To test the same hypotheses described above, experimental containers that allow for vertical movement of *Chaoborus* larvae should be used. An explanation for why *C. trivittatus* is able to coexist with *C. americanus* in these unstained, fishless bog lakes is offered by von Ende (1975, *in press*).

CONCLUSIONS

Chaoborus species are distributed in an environment that is patchy on a regional basis. It is a system whose dynamics depend on the rates of migration into and out of a patch, relative to the rates of extinction within a patch. The 2 species in this study, *C. americanus* and *C. punctipennis*, appear to have become well adapted to their respective habitats. *Chaoborus punctipennis* larvae are small and migrate vertically, apparently to minimize fish predation and coexist with fish. Early emergence probably is necessary for *C. americanus* to live in shallow, woodland ponds, but vertical migration is not. We find *C. americanus* in fishless lakes because these habitats are not unlike shallow ponds, most importantly in the absence of fish. It is the adaptations of *C. americanus* to shallow ponds that prevents this species from living in lakes with *C. punctipennis*. In contrast, *C. punctipennis* is excluded from stained, fishless lakes as the result of differences between these 2 species in timing of reproduction and extent of vertical migration. It appears the characteristics of *C. americanus* that enable it to exclude *C. punctipennis* represent more a response to its environment than to congeners. It could be argued that, in this patchy environment, the *Chaoborus* species compete for patches. Interspecific predation

can be considered an extreme form of interspecific interference competition. In the case of *C. americanus*, however, I think interspecific predation represents an extension of the extreme of intraspecific interference competition, i.e., cannibalism. The advantages of cannibalism have been discussed above. I have no estimates of immigration or extinction rates. The experimental predation rates, however, were high. If, as I am suggesting, predation is operating to exclude these 2 species from their alien habitat patches, then the extinction rates probably are nearly equivalent to the immigration rates. For that reason, the UNDERC system is relatively stable in terms of the proportions of lakes occupied by each species. If we assume predation also is significant in the clear, fishless bog lakes, any change in these proportions would require either addition of fish to a lake without fish, or a large loss of fish from a lake with fish.

ACKNOWLEDGMENTS

I thank my advisor, Dr. Quentin Ross, and the rest of my committee, Drs. Robert P. McIntosh, Thomas L. Poulson, George B. Craig, Jr., and Richard W. Greene for their helpful advice throughout this study. Dr. Tom Kane, Dr. Jeff Koenings, and Mr. Ed Brady always provided a forum for informative discussions. Ed Brady was responsible for finding some of the more remote bog lakes. Dr. Robert E. Gordon kindly made the facilities at UNDERC available, and provided work support. Mr. O. J. Stewart was always helpful in providing logistic support. The comments of Drs. Peter Meserve, Jerrold Zar, Robert Pastorok, and an anonymous reviewer were especially helpful in the preparation of this manuscript. While conducting this research I was supported by grants from AEC (to Dr. T. C. Griffing), NASA, and by a Grant-in-Aid-of-Research Award from Sigma Xi. This study is part of a dissertation submitted to the University of Notre Dame in partial fulfillment for the Ph.D. degree.

LITERATURE CITED

- Allan, J. D. 1973. Competition and the relative abundances of two cladocerans. *Ecology* **54**:484-498.
- Bradshaw, W. E. 1973. Homeostasis and polymorphism in vernal development of *Chaoborus americanus*. *Ecology* **54**:1247-1260.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. *Science* **150**:28-35.
- Carter, J. C. H., and J. K. Kwik. 1977. Instar distribution, vertical distribution, and interspecific competition among four species of *Chaoborus*. *Journal of the Fisheries Research Board of Canada* **34**:113-118.
- Connell, J. H. 1973. Population ecology of reef-building corals. Pages 205-245 in O. A. Jones and R. Endean, editors. *Biology and geology of coral reefs*. Volume 2. Biology 1. Academic Press, New York, New York, USA.
- . 1975. Some mechanisms producing structure in natural communities. Pages 460-490 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts, USA.
- Culver, D. C. 1973. Competition in spatially heterogeneous systems: an analysis of simple cave communities. *Ecology* **55**:974-988.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351-389.
- . 1975. Experimental evaluation of ecological domi-

- nance in a rocky intertidal algal community. *Ecological Monographs* **45**:135-159.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnology and Oceanography* **15**:131-138.
- Fox, L. R. 1975. Cannibalism in natural populations. *Annual Review of Ecology and Systematics* **6**:87-106.
- Hamilton, A. L. 1971. Zoobenthos of fifteen lakes in the Experimental Lakes Area, northwestern Ontario. *Journal of the Fisheries Research Board of Canada* **28**:257-263.
- Hilsenhoff, W. L. 1971. Repopulation of Hartlaub Lake by *Chaoborus* four years after elimination with Toxaphene. *Annals, Entomological Society of America* **64**:308-309.
- , and R. P. Narf. 1968. Ecology of Chironomidae, Chaoboridae, and other benthos in fourteen Wisconsin lakes. *Annals, Entomological Society of America* **61**:1173-1181.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* **53**:749-753.
- Hutchinson, G. E. 1967. A treatise on limnology. Volume 2. John Wiley and Sons, Incorporated, New York, New York, USA.
- LaRow, E. J. 1968. A persistent diurnal rhythm in *Chaoborus* larvae. I. The nature of the rhythmicity. *Limnology and Oceanography* **13**:250-256.
- . 1969. A persistent diurnal rhythm in *Chaoborus* larvae. II. Ecological significance. *Limnology and Oceanography* **14**:213-218.
- Levins, R., and D. C. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings, National Academy of Sciences, USA*. **68**:1246-1248.
- Lock, A. R., and I. A. McLaren. 1970. The effect of varying and constant temperatures on the size of a marine copepod. *Limnology and Oceanography* **15**:638-640.
- McLaren, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada* **20**:685-727.
- Northcote, T. G., and J. M. B. Hume. *In press*. Initial impacts of experimental fish introductions on macrozooplankton communities of small oligotrophic lakes. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* **45**:285-305.
- Pope, G. F., J. C. H. Carter, and G. Power. 1973. The influence of fish on the distribution of *Chaoborus* species (Diptera) and density of larvae in the Matamek River System, Quebec. *Transactions, American Fisheries Society* **102**:707-715.
- Roth, J. C. 1967. Notes on *Chaoborus* species from the Douglas Lake region, Michigan, with a key to their larvae (Diptera: Chaoboridae). *Papers of the Michigan Academy of Science, Arts and Letters* **52**:63-68.
- . 1968. Benthic and limnetic distribution of three *Chaoborus* species in a southern Michigan lake (Diptera: Chaoboridae). *Limnology and Oceanography* **13**:242-249.
- . 1971. The food of *Chaoborus*, a plankton predator in a southern Michigan lake. Doctoral dissertation. University of Michigan, Ann Arbor, Michigan, USA.
- Saether, O. A. 1972. Family Chaoboridae. *In* *Das Zooplankton der Binnengewässer*. *Binnengewässer* **26**:123-133.
- Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. *Journal of the Fisheries Research Board of Canada* **26**:1948-1955.
- Slatkin, M. 1974. Competition and regional coexistence. *Ecology* **55**:128-135.
- Sokal, R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman and Company, San Francisco, California, USA.
- Sprules, W. F. 1972. Effects of size-selective predation on high altitude zooplankton communities. *Ecology* **53**:375-387.
- Stahl, J. B. 1959. The developmental history of the chironomid and *Chaoborus* faunas of Myers Lake. *Investigations of Indiana Lakes and Streams* **5**:47-102.
- . 1966. The ecology of *Chaoborus* in Myers Lake, Indiana. *Limnology and Oceanography* **11**:177-183.
- Swift, M. C. 1976. Energetics of vertical migration in *Chaoborus trivittatus* larvae. *Ecology* **57**:900-915.
- Vandermeer, J. H. 1973. On the regional stabilization of locally unstable predator-prey relationships. *Journal of Theoretical Biology* **41**:161-170.
- von Ende, C. N. 1975. Organization of bog lake zooplankton communities: factors affecting the distribution of four *Chaoborus* species (Diptera: Chaoboridae). Doctoral dissertation. University of Notre Dame, Notre Dame, Indiana, USA.
- . *In press*. Regional coexistence of four *Chaoborus* species. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*.
- Wood, K. G. 1956. Ecology of *Chaoborus* (Diptera: Culicidae) in an Ontario Lake. *Ecology* **37**:639-643.
- Zaret, T. M., and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography* **21**:804-813.