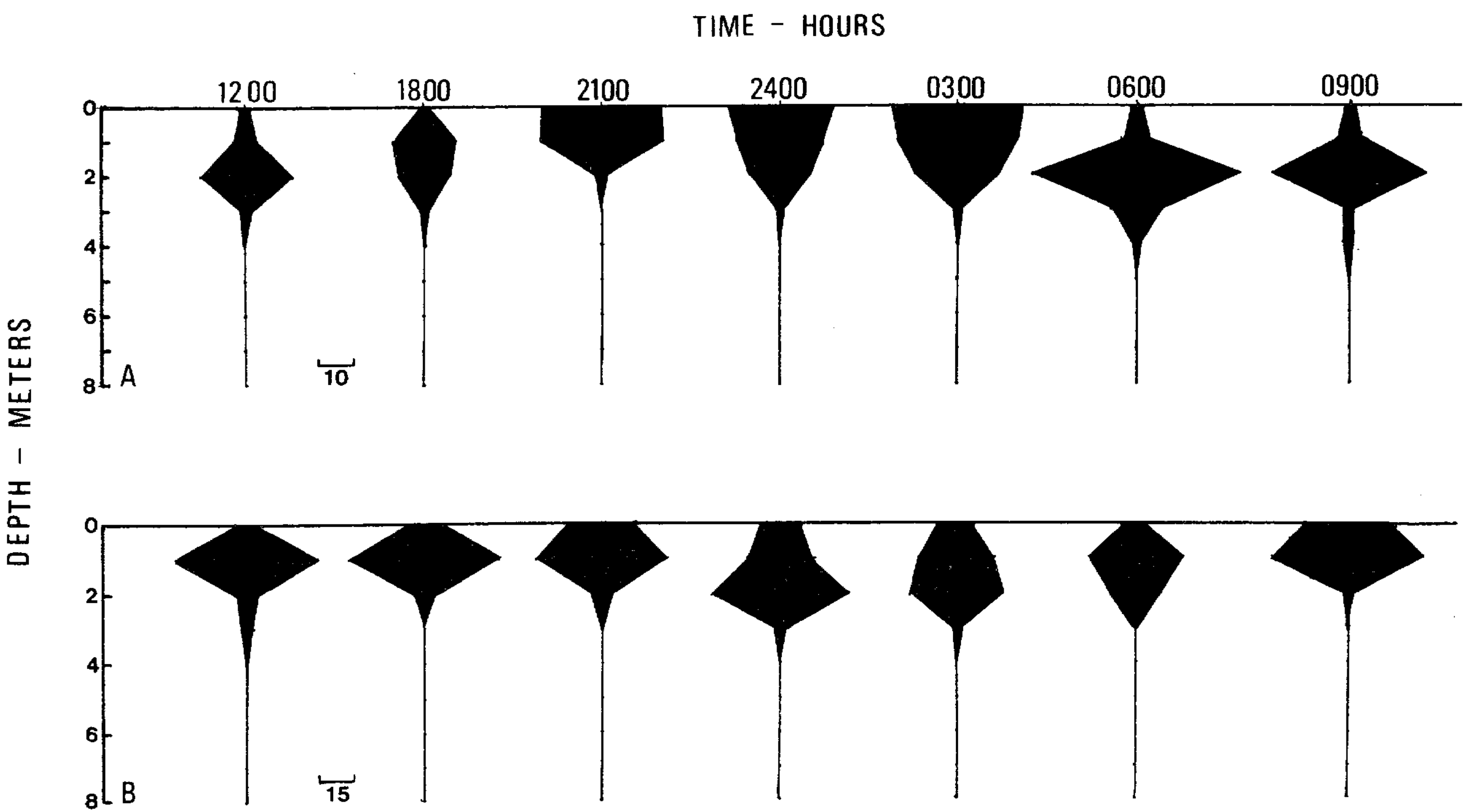
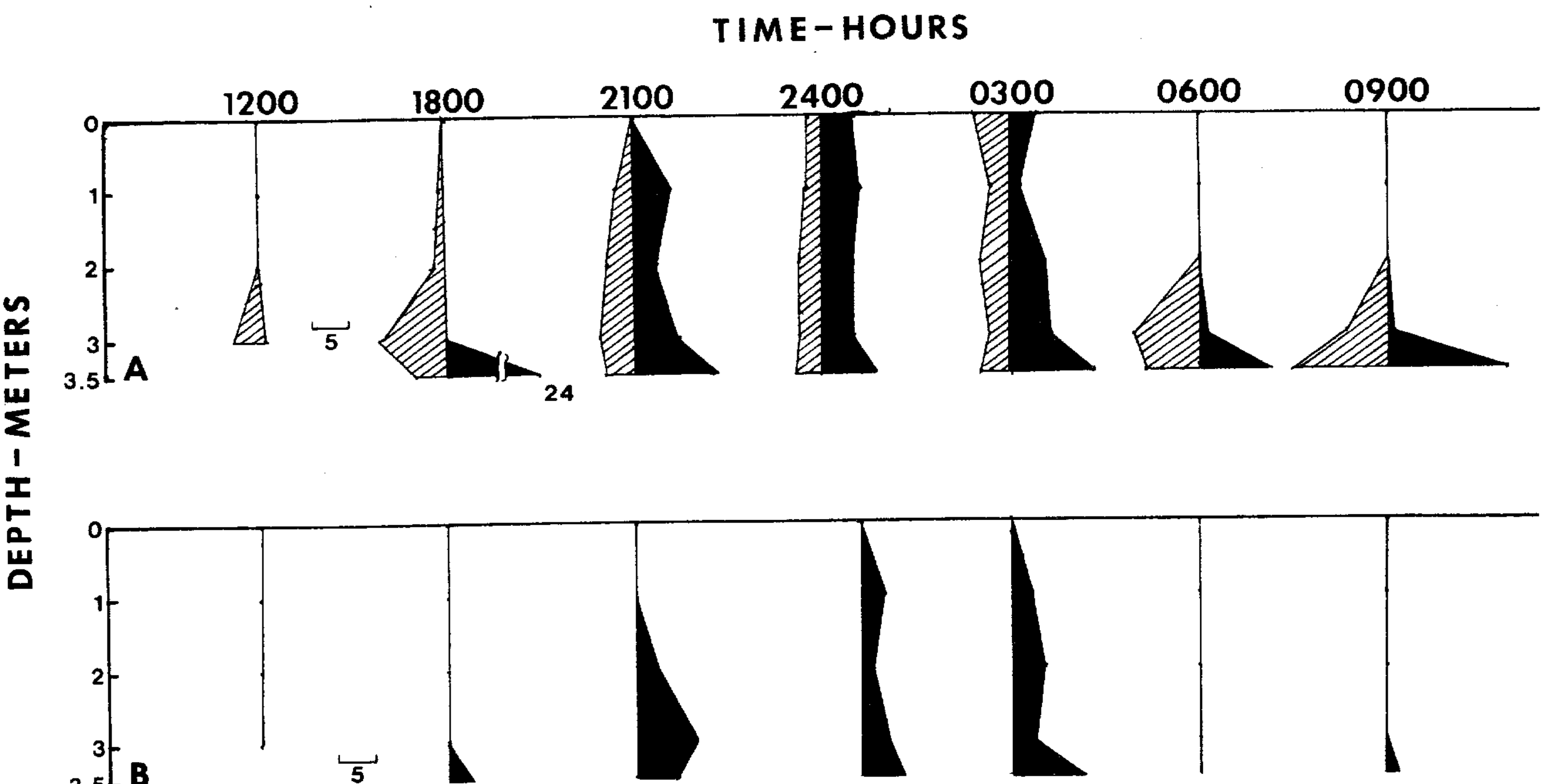
Figure 17. Diel vertical migration of fourth (A) and third (B) instar larvae of <u>Chaoborus americanus</u> in Tender Bog Lake on 4-5 August 1973.



TIME - HOURS
1200
1800
2100
2400
0300
0600
0900
DEPTH - METERS
0
2
4
6
8
A
10
B
15

Figure 18. Diel vertical migration of third (hatched) and fourth (solid) instar larvae of *Chaoborus americanus* (A) and fourth (solid) instar larvae of *Chaoborus trivittatus* (B) in Forest Service Bog Lake on 1-2 August 1973.



TIME-HOURS
1200
1800
2100
2400
0300
0600
0900
DEPTH-METERS
0
1
2
3
3.5
A
5
24
B

whether a C. americanus larva is responding to light or temperature in determining its daytime distribution.

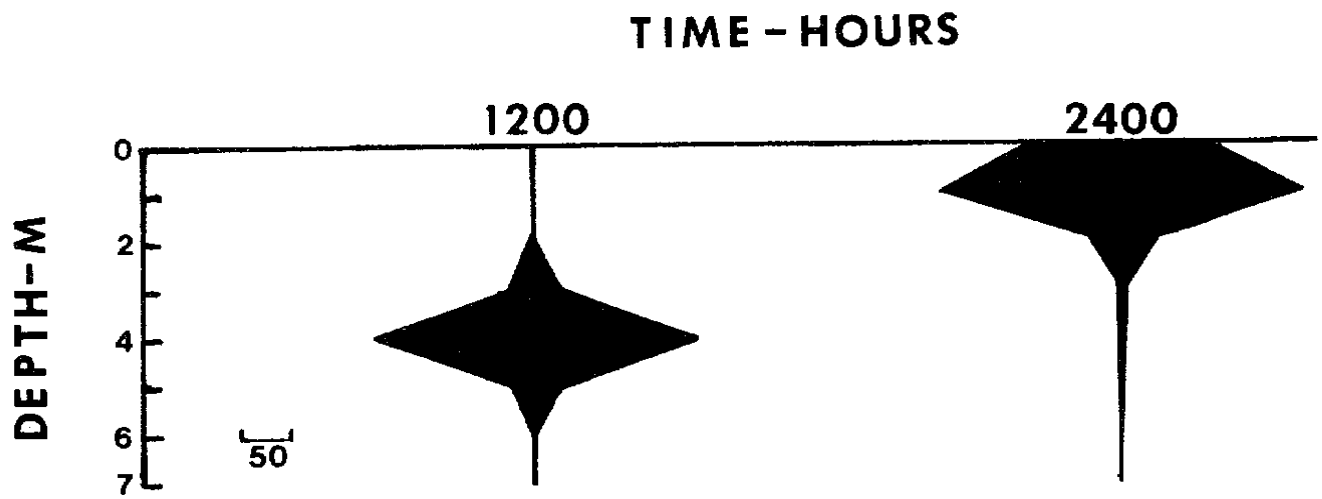
The bottom half of Figure 18 is the pattern of distribution of fourth instar C. trivittatus in Forest Service Bog. The pattern follows that of C. americanus in the same bog, except that either C. trivittatus goes into the sediments during the day, or is at the sediment-water interface because very few larvae can be caught during the day. Fedorenko and Swift (1972) also reported the migration of fourth instar C. trivittatus from beneath the thermocline, where they are during the daylight hours, to the epilimnion and surface waters at night.

The vertical migration of C. punctipennis larvae has been observed by many investigators (Juday 1921, LaRow 1968, Roth 1968, Stahl 1966, Wood 1956). According to all reports the third and fourth instars are benthic during the day, and migrate to the epilimnion or surface waters at night.

As part of a study of North Gate Bog, Imes and Hooper (1969) showed that the fourth instars of C. punctipennis migrated from the bottom of the lake, where they remained during the day, to the surface waters at night. This work was done in late May and early June. Using the plankton trap, I found that the extent of vertical migration by the fourth instars may depend on the age of the larvae within the instar. Figure 19 shows the distribution of the fourth instars at 1200 and 2400 hours on 3 September 1973. It can be seen that there is migration, but that the larvae are not right at the bottom of the lake during the day. The larvae which Imes and Hooper sampled were older, and it may be that the extent of vertical migration increases with age of the fourth instar.

The extent of vertical migration of fourth instar C. punctipennis also seems to decrease in the colder months of the year. Malueg (1966)

Figure 19. Vertical distribution of fourth instar larvae of *Chaoborus punctipennis* in North Gate Bog Lake at 1200 and 2400 hours on 3 September 1973.



TIME - HOURS
1200
2400
DEPTH-M
0
2
4
6
7
50

reported that C. punctipennis did not migrate under the ice of Tub Lake, a small lake in northwestern Wisconsin. The results shown in Table 6 lend credence to this conclusion. The number of fourth instars in a 1.5 m vertical tow at night decreases in October and November, but increases again in early and middle June.

Because all three Chaoborus species in Humminbgird Bog were less abundant than in the other bogs, it was not possible to use the trap for sampling. However, from vertical tows with the large plankton net described earlier, the same general patterns of migration for C. punctipennis, C. flavicans, C. trivittatus were found. That is the larvae are near the bottom during the day and in the epilimnion during the night. Allan (1973) found the same behavior in his study of Hummingbird Bog.

In summary, the third and fourth instars of all of the species found in the lakes with fish undergo diurnal, vertical migration. With C. punctipennis the extent of vertical movement appears to increase with the age of the fourth instars. Chaoborus americanus is not found in lakes with fish. Its vertical migration is much less, and appears to be affected by characteristics of the lake in which the larvae live. In a stained bog, the majority of the mature larvae are at 2 m during the day, whereas in a clear bog the majority of the mature larvae are at 3 m and 4 m.

TABLE 6

MEAN NUMBER OF *C. PUNCTIPENNIS* LARVAE OF TWO 1.5 M VERTICAL TOWS AT 0100 HOURS IN NORTH GATE BOG

	Date				
Instar	9/10/72	10/15/72	11/11/72	6/2/73	6/16/73
4th	646.5	186.5	27.5	246.5	479.5
3rd	63.5	1.5	—	—	—
2nd	17.5	—	—	—	—

CHAPTER IV

EXPERIMENTS

Absence of *Chaoborus americanus* from Lakes with *Chaoborus punctipennis* and *Chaoborus flavicans*

Hypotheses

In this section the lack of co-occurrence of *C. americanus* with *C. punctipennis* and *C. flavicans* is examined. Several hypotheses to explain this phenomena will be presented, and the experiments required to test these hypotheses outlined. Finally, the results of these experiments will be described.

There are a number of factors that could be operating such that *C. americanus* could not co-occur with the other two species. First it could simply be a problem of dispersal. There could be certain lakes that *C. americanus* adults can not get to, and therefore the larvae are not found in those lakes. A second hypothesis to explain the *C. americanus* distribution could be that although *C. americanus* adults are able to get to the lakes from which they are absent, the larvae are unable to survive under the environmental conditions found in those lakes. This would be considered physiological intolerance.

A third factor or process could be competition between *Chaoborus* species, and would be an indirect effect of fish predation. Studies were described in Chapter I that demonstrated that planktivorous fish can dominate a zooplankton community to the extent that generally only the smaller zooplankton species can survive in the presence of the fish. With the exception of *Daphnia pulex* in North Gate and *Holopedium gibberum* in Hummingbird, the zooplankton species in the bog lakes with fish are small. Although *Daphnia pulex* occurs in North Gate and is a large species, the population is short-lived each season. It appears in early spring, and by mid-June has nearly disappeared (Jeff Koenings, personal communication). Thus, the small zooplankton species predominate most of the summer.

Feeding selectivity also has been demonstrated with *Chaoborus*. Dodson (1970) showed that fourth instar *C. flavicans* preferred *Daphnia pulex* 1.0 mm in length, when offered *D. pulex* ranging in size from 0.67 mm to 2.0 mm. Sprules (1972) demonstrated that fourth instar *C. americanus* preferred large *Diaptomus shoshone* (2.4 mm) over medium size *Daphnia* (*D. rosea*, 1.5 mm), which were in turn preferred over large *Daphnia* (*D. pulex*, 2.2 mm). These results suggest that the swimming orientation of the prey may be important as well as the size. *Daphnia* swim with the long axis of the body essentially vertical, whereas *Diaptomus* swims with the long axis horizontal, as do *Chaoborus* larvae. Thus, perhaps the diameter of *Diaptomus* is also an important parameter in feeding selectivity by *Chaoborus* larvae. In any case, feeding preference has been demonstrated.

In view of the above information, a third hypothesis for the lack of co-occurrence of *C. americanus* and fish is that because the zooplankton in the fish-lakes is small, *C. americanus* larvae, being relatively large, are unable to survive on the smaller prey available in these lakes. The argument is that *C. americanus* is being out-competed by *C. punctipennis* in North Gate, and in the case of Hummingbird, also by *C. flavicans* and *C. trivittatus*. Because *Holopedium gibberum*, a large zooplankter, is present in Hummingbird, perhaps a form of diffuse competition (MacArthur 1972) is operating in this lake. That is, *C. punctipennis* and *C. flavicans* being smaller do well on the smaller zooplankton prey, and *C. trivittatus*, the largest of the four species, can utilize the large *H. gibberum*; but *C. americanus* fits in between these other species with respect to size. It neither is efficient on the small nor on the large prey, and is outcompeted. It is felt that *H. gibberum*, although it is a large zooplankton species, is able to survive with fish because each individual is surrounded by a gelatinous sheath and is considered to be unpalatable to fish.

Finally, the fourth and most likely hypothesis is that the absence of *C. americanus* from Hummingbird and North Gate bogs is the result of direct fish predation. Fish do prey on *Chaoborus* larvae (Hasler 1945). In Chapter III it was demonstrated that the larvae of the species that coexist with fish commonly (*C. punctipennis*, *C. flavicans* and *C. trivittatus*) undergo the most extensive diurnal, vertical migration. In contrast *C. americanus* larvae migrate very little. Therefore it is reasonable to suggest that *C. americanus* larvae would be more subject to predation by fish because they are always high in the water column.

Experiments to Test Hypotheses

To test the first hypothesis of whether *C. americanus* are able to get to the lakes, a light trap was set up at Hummingbird Bog to attempt to catch *C. americanus* adults in the vicinity of that lake. In evaluating the next two hypotheses, the question was whether *C. americanus* larvae could survive on the prey available and under the physical-chemical conditions in Hummingbird and North Gate bogs. This could best be approached by trying to raise early larval instars of *C. americanus* *in situ* on the prey found in those lakes.

To do this small chambers were constructed from round one quart (0.98 l) polyethylene refrigerator containers, with tight sealing tops. Two rhomboidal "windows" were cut in the sides, and a circular window in the cover.

For screening 80 μm Nitex was glued over the windows with Testor's cement. The dimensions of the containers are shown in Figure 20. The windows and screening were added in an attempt to simulate actual conditions as nearly as possible, by allowing water to circulate through the containers, which in turn enabled the prey to survive.

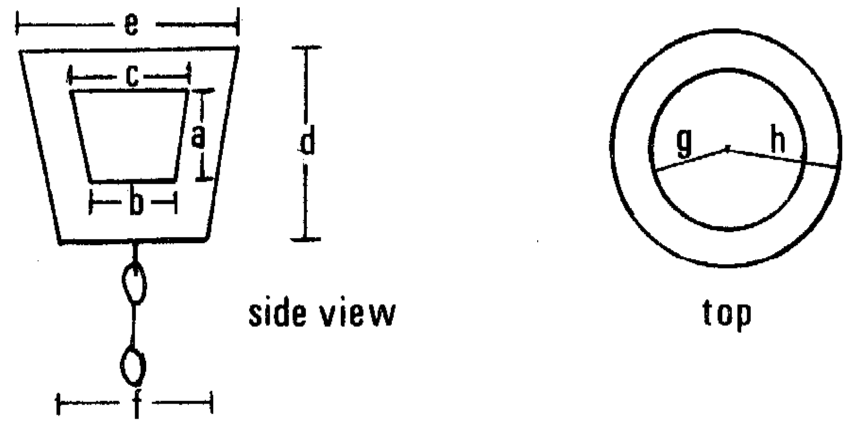
Because the containers would float when filled with water, they were attached from their base to a board by a string and a strip of polyethylene. The strip of polyethylene was glued to the bottom of the container with epoxy glue. By this method it was possible to suspend the containers at any depth desired by adjusting the height of the board appropriately. Also, the containers were free to drift with any currents to the extent their tethers allowed. A sketch of six containers as they appeared suspended is shown in Figure 20.

Ten first instar C. americanus were placed in each container. Because the question of survival of C. americanus was to determine whether they could survive in each lake on the prey available, the size of the prey was of interest. Therefore, in case there was a density effect of a rare species being of optimum size and important for C. americanus larvae survival, such an effect could be detected by raising the larvae at different prey densities. For this reason the experiments were run at Low and High prey conditions. The densities were determined in the following manner in order to duplicate actual prey densities (including day to day variation) as closely as possible.

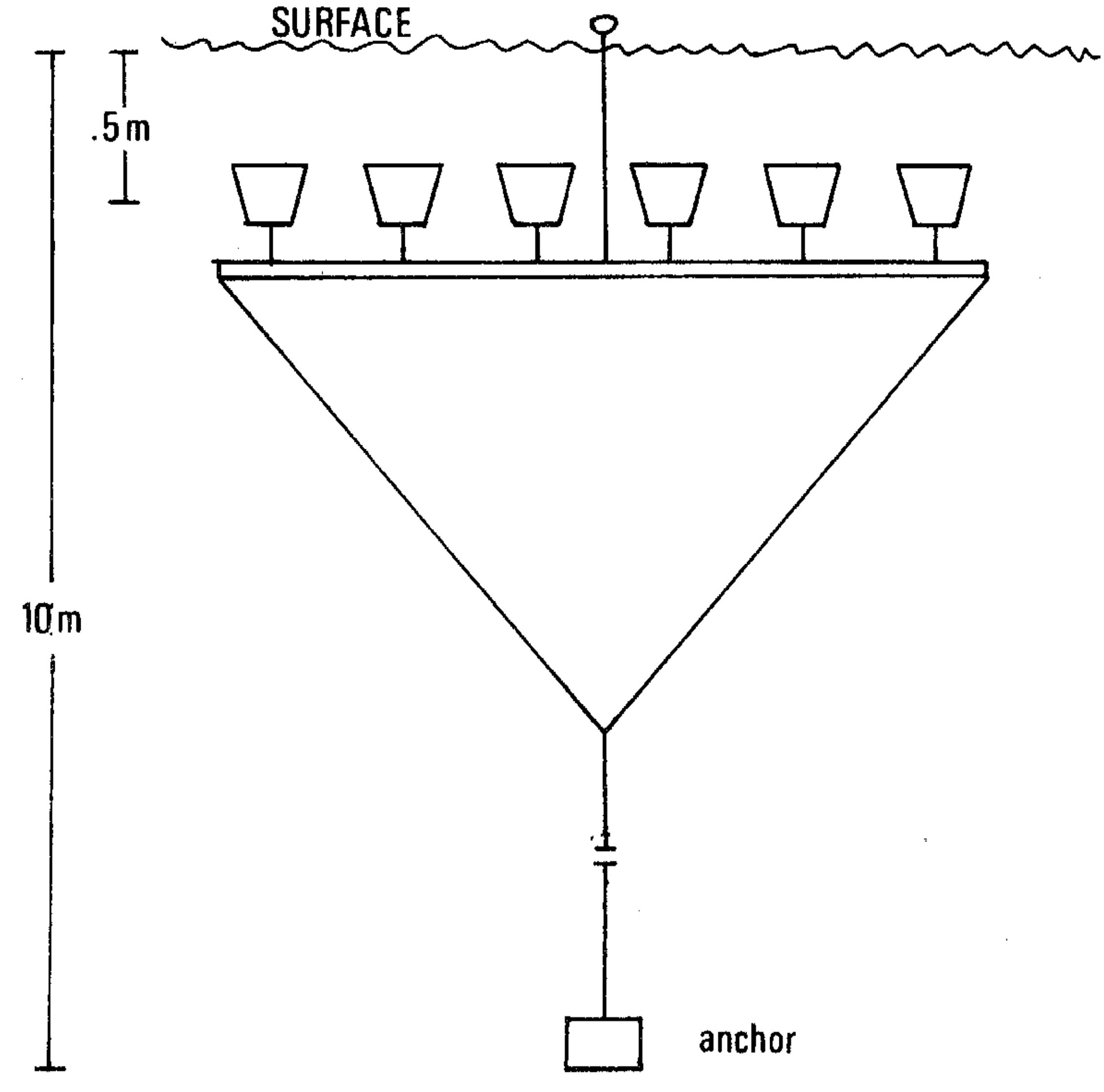
The plankton trap described earlier was used to obtain the plankton sample. The prey allotments for the containers were determined each time the prey were changed (every other day). A plankton sample was taken with the plankton trap which was equipped with an 80 μm Nitex net. The sample

Figure 20. (A) Diagram of one quart experimental containers; a = 5.0 cm, b = 6.0 cm, c = 7.5 cm, d = 11.0 cm, e = 12.0 cm, f = 9.0 cm, g = 4.0 cm, h = 6.0 cm. (B) Diagram of containers as suspended in Tender Bog Lake.

A



B



was concentrated to 300 ml. For the Low Prey condition, a 10 ml sample was taken from this 300 ml concentrate. To ensure as random a sample as possible, the concentrate was stirred in a beaker and the 10 ml sample was taken with a glass tube 6 mm in diameter. An automatic pipette was used to draw up the 10 ml sample. This aliquot was essentially equivalent to the actual number of prey per liter found in the lake.

The High Prey density was three times the density of the Low Prey. Thus, a 30 ml sample of the plankton trap concentrate was taken for the High Prey treatment. Because of the large volume of the sample, two 15 ml samples were taken. The High Prey treatment represented three times the actual number of prey per liter in the lake. Three replicates of each of the prey densities were run simultaneously. The containers were suspended at 0.5 m to ensure sufficient dissolved oxygen for prey survival.

The best way to test the final hypothesis of whether it is direct predation by fish that is excluding C. americanus from fish lakes, was to add fish to a lake which had no fish, but had C. americanus larvae. It so happened that in another study a graduate student from the University of Michigan (Edward Brady) was studying mud minnow, Umbra limi, populations. On 26 July 1972, 900 Umbra limi were added to a bog lake about the same size and depth as Tender Bog. In August 1972 and early July 1973 this bog had C. americanus larvae in large numbers and it was the only species of Chaoborus present (E. Brady, personal communication). No fish were present before they were added.

Results

Unfortunately trapping adult C. americanus at Hummingbird Bog was not very successful. Because C. americanus emerges in mid-May, a light trap used at night caught nothing. It was so cold at night (especially around the bogs) that very few insects were flying. Thus, there is no direct evidence that C. americanus adults can get to the fish-lakes. However, the map showing the distribution of Chaoborus species (Figure 1) demonstrates that C. americanus is found in lakes distributed throughout the UNDERC property and strongly suggests that they can reach the lakes which contain fish.

With respect to the second and third hypotheses, Table 7 shows the survivorship of C. americanus to fourth instar in Hummingbird Bog. Survivorship to fourth instar was used as the criterion as to whether C. americanus could survive in a lake. The rationale was that if a larva could survive to fourth instar, which is the hardiest instar, then it is fair to say that it could survive to pupation, and emergence as an adult.

The overall survivorship between the Low and High prey densities in Hummingbird Bog were not significantly different at $\alpha = 0.05$ (Table 8). Thus, there was no optimum prey organism that was rare at the Low Prey density, and had a differential effect on survivorship. The instar distributions, however, at the two prey conditions were significantly different at $P < 0.01$ (Table 9). As one might expect, the larvae grew faster at the higher prey density because more prey were available. These data indicate that C. americanus is not restricted from Hummingbird Bog because of the physical-chemical conditions found in the bog, nor because of their inability to use the array of zooplankton species found there.

Larval survivorship of C. americanus is the same in North Gate Bog as in Hummingbird Bog (Table 10). Again, the total survivorship at the Low and High prey densities were not significantly different at $\alpha = 0.05$

TABLE 7

SURVIVORSHIP OF *C. AMERICANUS* IN HUMMINGBIRD BOG, INSTAR DISTRIBUTION ON DAY 52 (3 REPLICATES PER TREATMENT, ORIGINAL COHORTS OF 10)

Low Prey		High Prey	
3rd Instar	4th Instar	3rd Instar	4th Instar
7	1	0	5
5	3	2	5
6	2	0	6

TABLE 8

STATISTICAL ANALYSIS OF TABLE 7, TOTAL SURVIVORSHIP - GOODNESS OF FIT, G STATISTIC

Low Prey	High Prey	$G_{adj.}$
24	18	0.598 (NS)

NS = Not significant

TABLE 9

STATISTICAL ANALYSIS OF TABLE 7, TOTAL INSTAR DISTRIBUTION - TEST OF INDEPENDENCE, X^2

	3rd Instar	4th Instar	X^2
Low Prey	18	6	
High Prey	2	16	16.832**

** = $P < 0.01$

TABLE 10

SURVIVORSHIP OF *C. AMERICANUS* IN NORTH GATE BOG, INSTAR DISTRIBUTION ON DAY 60 (3 REPLICATES PER TREATMENT, ORIGINAL COHORTS OF 10)

Low Prey		High Prey	
3rd Instar	4th Instar	3rd Instar	4th Instar
7	2	0	7
6	3	0	8
8	1	0	6

TABLE 11

STATISTICAL ANALYSIS OF TABLE 10, TOTAL SURVIVORSHIP - GOODNESS OF FIT, G STATISTIC

Low Prey	High Prey	$G_{adj.}$
27	21	0.560 (NS)

NS = Not significant

TABLE 12

STATISTICAL ANALYSIS OF TABLE 10, TOTAL INSTAR DISTRIBUTION - TEST OF INDEPENDENCE, X^2

	3rd Instar	4th Instar	X^2
Low Prey	21	6	
High Prey	0	21	
			29.037**

** = $P < 0.01$

(Table 11); but the instar distributions at the different prey densities were significantly different at $P < 0.01$ (Table 12). Thus, the same conclusions that were drawn with respect to Hummingbird Bog can be applied to North Gate Bog, also.

As a test of the hypothesis of direct fish predation, the bog to which 900 *Umbra limi* were added was sampled on 9 September 1973. No *C. americanus* larvae were found in any of the samples taken in three 1.5 m vertical tows with the large plankton net described earlier. Considering the volume of water filtered in each sample (159 liters), it is fair to say that direct fish predation had eliminated *C. americanus* larvae from the bog lake. There were a few *Chaoborus* larvae, but they were *C. punctipennis*. Combining the results of these two sets of experiments, there is good evidence for arguing that fish predation is the best explanation for the absence of *C. americanus* larvae from lakes containing *C. punctipennis*, *C. flavicans*, and fish.

Absence of *Chaoborus punctipennis* from Tender Bog

Hypotheses

The two most obvious hypotheses for the absence of *C. punctipennis* from Tender Bog are (1) the inability of *C. punctipennis* adults to reach Tender Bog, or (2) that the larvae are unable to survive under the environmental conditions found in Tender Bog. The remaining hypotheses depend on the characteristics of *C. punctipennis* and *C. americanus* with respect to each other, and with respect to the other zooplankton species found in Tender Bog.

First the timing of recruitment of both species must be considered with respect to the dynamics of the zooplankton populations in Tender and

North Gate bogs. As shown in Chapter III, in Tender Bog C. americanus larvae pupate from fourth instar and emerge as adults about the middle of May, not long after the ice has left the bog. First and second instar C. americanus are present as the zooplankton populations start to increase. In North Gate and Hummingbird bogs, C. punctipennis emerges near the end of June. Also, in general the zooplankton prey are smaller in the bogs in which C. punctipennis and fish are present.

A third hypothesis to explain the absence of C. punctipennis from Tender Bog follows from these facts. The prey zooplankton in Tender are small (juvenile Daphnia pulex, nauplii and copepodids of Diaptomus leptopus) when the zooplankton populations begin to increase and C. americanus is in first and second instars. However, when C. punctipennis emerges at the end of June, the size range of D. pulex and D. leptopus in Tender Bog would have shifted to the larger, older age classes. It could be argued that there would not be sufficient small prey for the early instars of C. punctipennis to survive. Thus, perhaps because of the timing of recruitment and the size of the prey zooplankton in Tender Bog, C. americanus is better able to exploit the resources available and exclude C. punctipennis from Tender Bog.

A fourth hypothesis has to do with the direct predatory interaction of the two Chaoborus species. Previously it was stated that the early instars of all four species of Chaoborus remain in the upper portion of the water column throughout the day. It was also demonstrated that the third and fourth instars of C. americanus in Tender Bog show relatively little diurnal, vertical migration. Table 13 shows the daytime numbers of the last three instars of C. americanus in Tender Bog on 17 July 1973. The majority of the C. americanus are in the third instar. The fourth hypothesis is that since C. punctipennis emerges at the end of June, the larvae that would hatch from the eggs laid by any adult female C. punctipennis that happened to land on Tender Bog, could possibly be subject to predation by third instars of C. americanus. Both would be occupying the same portion of the water column of Tender Bog. The early instars of C. punctipennis could be considered prey for C. americanus, along with the other zooplankton species.

Experiments to Test Hypotheses

To test the hypothesis about the dispersal power of C. punctipennis a light trap was set at Tender Bog at night. For evaluating the next two hypotheses concerning the ability of C. punctipennis larvae to survive in Tender Bog, it was necessary to determine whether C. punctipennis could survive on the prey available and under the environmental conditions found in Tender Bog.

For this reason ten second instar C. punctipennis, from North Gate Bog, were placed in each of six quart containers in Tender Bog. These were the same kind of containers described earlier for the C. americanus rearing experiments. It was necessary to use second instars because the first instars were very small (1 mm), clear, and nearly impossible to see with the naked eye. They could have easily been missed or lost in a container. Three of the containers were treated with High Prey density, and three with Low Prey density. This was in case of rare species being of optimum size, as explained for the previous experiments. Likewise, the prey densities were determined in the same manner as described above for C. americanus, and the prey were replaced every other day. The containers were suspended at 0.5 m in Tender Bog.

To test the last hypothesis of C. punctipennis - C. americanus interaction, it was necessary to determine how C. punctipennis grew on the prey found in Tender Bog, but in the presence of C. americanus larvae. In another set of six containers, 7, second instar C. punctipennis were placed with 3, third instar C. americanus in each container. Three, third instar C. americanus per liter was the density of C. americanus third instars in Tender Bog when the experiment was started (Table 13). Again, there were three containers at Low Prey density, and three at High Prey density. All containers were suspended at 0.5 m in Tender Bog. New zooplankton were added every two days, after removing the old zooplankton and noting the survivorship of the Chaoborus larvae. The larvae were also removed each time, and then returned to the containers after the new zooplankton were added.

In the event that C. punctipennis larvae were able to survive in Tender Bog, or even if they were preyed upon as second instars, what if a larva were able to make it to third or fourth instar, would it still be vulnerable to predation by later instars of C. americanus? To answer this question, a series of predation experiments with third and fourth instars of both species were conducted. For convenience these experiments will be referred to by number (3 to 7). All the experiments were conducted with the one quart containers described above. Because in a bog alternate prey would be available, as well as early instars of C. punctipennis, the treatment levels in Experiments 3 and 4 were 1) no alternate prey and 2) low density of alternate prey. For Experiments 5, 6, and 7, the treatment levels were 1) no alternate prey, 2) low density of alternate prey, and 3) high density of alternate prey. The third level of the prey treatment was added because it was felt that older third instar and fourth instar C. punctipennis may have been large enough

TABLE 13

MEAN NUMBER OF *C. AMERICANUS* LARVAE PER PLANKTON TRAP (TWO SAMPLES OF 30.4 1 EACH), DAYTIME, 7/17/73, TENDER BOG

		Instar		
		2nd	3rd	4th
	surf.	10.0	37.0	2.5
Depth	1m	19.5	103.5	7.0
	2m	2.5	12.5	22.5

compared to fourth instar C. americanus larvae such that the density of alternate prey could affect the predation rate. Experiment 7 was also cross-classified according to small and large fourth instar C. americanus. The zooplankton densities were determined as they had been in previous experiments. High density of alternate prey was three times the low density of prey. Controls (C. punctipennis without C. americanus) were run for all treatment combinations in all the experiments. The descriptions of the experiments are listed below. The sizes are the average body length of the larvae used in the experiments.

#3 - Predation of large (7.8 mm), 3rd instar C. americanus on small (4.3 mm), 3rd instar C. punctipennis; 6 replicates per treatment level; 5 C. punctipennis and 2 C. americanus per container.

#4 - Predation of large (12.3 mm), 4th instar C. americanus on small, 3rd instar C. punctipennis; 6 replicates per treatment level; 5 C. punctipennis and 2 C. americanus per container.

#5 - Predation of large, 4th instar C. americanus on medium (4.9 mm), 3rd instar C. punctipennis; 5 replicates per treatment level; 7 C. punctipennis and 2 C. americanus per container.

#6 - Predation of small (9.7 mm), 4th instar C. americanus on medium, 3rd instar C. punctipennis; 5 replicates per treatment level; 7 C. punctipennis and 2 C. americanus per container.

#7 - Predation of small and large, 4th instar C. americanus on medium (6.9 mm), 4th instar C. punctipennis; 5 replicates per treatment combination; 7 C. punctipennis and 2 C. americanus per container.

Finally, to determine whether the size of the container was biasing the predation experiments, Experiment 8 was run with large, fourth instar

C. americanus and medium, fourth instar C. punctipennis in 19 liter plastic buckets. As with the smaller containers, the buckets had windows with 80 μm Nitex on the sides and in the cover to allow for circulation of water through the containers. The control container had 133 C. punctipennis and a low density of alternate prey, whereas the experimental container had 133 C. punctipennis and 38 C. americanus and a low density of alternate prey. There was only one container for each treatment level. The alternate prey density was the same as described above for the Low Prey condition in Experiments 3 through 7.

For all the predation experiments, the containers were suspended in Tender Bog at 0.5 m. The experiments were run for 48 hours. The C. punctipennis larvae were taken from North Gate Bog and the C. americanus from Tender Bog just prior to each experiment. None of the animals were starved.

The results of Experiments 3 and 4 were analyzed by the Wilcoxon Two-Sample Test, Experiments 5 and 6 by the Kruskal-Wallis Test, and Experiment 7 by Analysis of Variance.

Results

With respect to the first hypothesis of dispersal, the results from the light trap set at Tender Bog were more successful than those at Hummingbird Bog because it was a warmer period of the summer. On several very warm nights, when the evening temperatures were around 27°C, large emergences of C. flavicans and C. punctipennis occurred on Tenderfoot Lake (7/9/73- C. flavicans, 7/17/73 - C. punctipennis). On 9 July C. flavicans adults were caught in the light trap at Tender Bog. On 4 August adults of both species were observed on the surface of Tender Bog after sunset. During this time large numbers would accumulate at night on the doors and windows of the laboratory located on the edge of Tenderfoot Lake. Thus, it certainly appears that these two species can get to Tender Bog.

Ninety percent of the second instar *C. punctipennis* reared alone in Tender Bog survived to fourth instar (Table 14). There are no significant differences in the growth rates, nor in the survivorship at the Low and High prey densities. If an adult, female *C. punctipennis* were to land at Tender Bog and laid eggs which hatched, the larvae would be able to live on the zooplankton in Tender Bog.

The results from the reciprocal predation experiment, however, suggest the explanation for the absence of *C. punctipennis* from Tender Bog. For those containers in which 3, third instar *C. americanus* were placed along with 7, second instars of *C. punctipennis*, no *C. punctipennis* remained after ten days. It is thus quite clear that early instars of *C. punctipennis* are subject to heavy predation by third instars of *C. americanus* at both low and high alternate prey densities.

Experiments 3 through 8 were run to determine whether predation occurred in the later instars. The results of these experiments are shown in Tables 15 through 21. Because the outcome of Experiments 3 through 6 were essentially the same for the different sizes and instars of the two species, I will discuss these results collectively.

In all cases there was heavy predation by *C. americanus* larvae on the *C. punctipennis* larvae. The results for the controls are not shown, but there was no mortality due to cannibalism by *C. punctipennis*. In Experiments 3 and 4 (Tables 15 and 16), there was no significant difference ($\alpha = 0.05$) in the predation rates as the result alternate prey being available.

In Experiment 7, a 2 X 3 factorial design was used to determine whether the alternate prey density or the size of the fourth instar *C. americanus*

TABLE 14

SURVIVORSHIP OF *C. PUNCTIPENNIS* IN TENDER BOG, INSTAR DISTRIBUTION ON DAY 36 (3 REPLICATES PER TREATMENT, ORIGINAL COHORTS OF 10)

Low Prey		High Prey	
3rd Instar	4th Instar	3rd Instar	4th Instar
0	9	0	10
0	9	0	9
0	9	0	9

TABLE 15

EXPERIMENT NO. 3: PREDATION OF 3RD INSTAR *C. AMERICANUS* ON 3RD INSTAR *C. PUNCTIPENNIS* (MEAN NUMBER EATEN IN 48 HOURS, WILCOXON 2-SAMPLE TEST)

No Zooplk.	Zooplk.	C
3.5	2.2	26 (NS)

NS = Not significant

TABLE 16

EXPERIMENT NO. 4: PREDATION OF 4TH INSTAR *C. AMERICANUS* ON 3RD INSTAR *C. PUNCTIPENNIS* (MEAN NUMBER EATEN IN 48 HOURS, WILCOXON 2-SAMPLE TEST)

No Zooplk.	Zooplk.	C
4.8	4.2	27.5 (NS)

NS = Not significant

TABLE 17

EXPERIMENT NO. 5: PREDATION OF 4TH INSTAR *C. AMERICANUS* ON 3RD INSTAR *C. PUNCTIPENNIS* (MEAN NUMBER EATEN IN 48 HOURS, KRUSKAL - WALLIS TEST)

No Zooplk.	Low Zooplk.	High Zooplk.	H
6.4	6.4	5.4	0.880 (NS)

NS = Not significant

TABLE 18

EXPERIMENT NO. 6: PREDATION OF 4TH INSTAR *C. AMERICANUS* ON 3RD INSTAR *C. PUNCTIPENNIS* (MEAN NUMBER EATEN IN 48 HOURS, KRUSKAL - WALLIS TEST)

No Zooplk.	Low Zooplk.	High Zooplk.	H
6.0	5.8	5.8	0.185 (NS)

NS = Not significant

affected the predation rate on fourth instar C. punctipennis. The predation rates and the analysis of the results are shown in Tables 19 and 20. As shown by the predation rates, even fourth instar C. punctipennis are subject to predation by C. americanus. From an Analysis of Variance we find that again there was no effect due to the density, or presence or absence of alternate prey ($\alpha = 0.05$). There was, however, a significant difference ($P < 0.05$) due to the size of the C. americanus larvae. That is the larger fourth instar C. americanus had a greater predation rate than the smaller fourth instar.

Finally, the results of Experiment 8, in the 19 liter containers, appear in Table 21. These results show that there is a high predation rate even in a large container, where there is a greater chance for the spatial separation of the two species. Thus, the small size of the containers used in the previous experiments did not seem to bias the results by affording greater chance for interaction between the species.

The results of the above experiments indicate that predation by third and fourth instar C. americanus larvae is the most likely explanation for the absence of C. punctipennis larvae from Tender Bog. Also, the results of Experiment 7 suggest that the relative size of the C. americanus and C. punctipennis larvae is important in determining the predation rates of the former on the latter. Although the similar experiments were not conducted for C. flavicans and C. trivittatus in Tender Bog, it is felt that the same explanation can be used for the absence of these two species. Chaoborus flavicans does emerge at the end of May in Hummingbird and Tenderfoot lakes, but the largest emergence in Tenderfoot Lake was observed in early July. It can be argued that at this time there would be the greatest probability of adult C. flavicans reaching Tender Bog. Early instars of

TABLE 19

EXPERIMENT NO. 7: PREDATION OF 4TH INSTAR *C. AMERICANUS* ON 4TH INSTAR *C. PUNCTIPENNIS* (MEAN NUMBER EATEN IN 48 HOURS)

		Zooplankton		
		None	Low	High
C. amer.	Small	4.4	3.4	3.6
	Large	6.2	6.2	4.8

TABLE 20

ANALYSIS OF VARIANCE OF EXPERIMENT NO. 7

Source of variation	df	MS	Test Results
C. americanus	1	27.571	*
Zooplankton	2	3.027	NS
C. amer. X Zooplk.	2	1.531	NS
Error	23	3.592	

NS = Not significant
* = $P < 0.05$

TABLE 21

EXPERIMENT NO. 8: PREDATION OF 4TH INSTAR *C. AMERICANUS* ON 4TH INSTAR *C. PUNCTIPENNIS* (IN 19 LITER CONTAINERS)

	Start		48 Hours	
	punct.	amer.	punct.	amer.
Control	133	0	132	0
Experimental	133	38	24	38

this species would be subject to the same predation pressure as C. punctipennis larvae. Since the emergence of C. trivittatus occurs in late August, there is no problem in applying the same reasoning to this species.

A predation experiment was conducted in late August with fourth instars of C. flavicans and of C. americanus, but no predation occurred by either species. If a C. flavicans larva were able to survive to fourth instar in Tender Bog, it would appear to be safe from predation by C. americanus larva. No fourth instar C. flavicans, however, were ever found in the samples from Tender Bog.

Coexistence of Chaoborus americanus and Chaoborus trivittatus

It has been shown that C. punctipennis, C. flavicans, C. trivittatus are absent from Tender Bog because of predation by C. americanus. If, however, this argument is to be consistent, a late emerging species such as C. trivittatus should not be able to coexist with C. americanus, as it does in Forest Service Bog.

Figure 18 shows the vertical distribution of C. americanus in Forest Service Bog. It can be seen that compared to the C. americanus distribution in Tender Bog (Figure 17), the third and fourth instars are deeper during the day, and at night are evenly distributed throughout the water column. Thus, it can be suggested that predation by mature instars of C. americanus on early instars of C. trivittatus in Forest Service Bog might be less than in Tender Bog because the mature C. americanus larvae are not in the upper two meters during the day in Forest Service, where the early instars (first and second) of C. trivittatus would be. This difference in behavior is probably related to the degree of staining of the water of the respective bogs.

Another difference in the two bogs is the density of C. americanus. The density of C. americanus in Tender Bog is about three times as great as it is in Forest Service. That is, the total number of C. americanus larvae in the combined samples taken at the surface, 1 m, 2 m, 3 m, and 4 m in Tender Bog with the plankton trap, at 2400 hours, on 4 August 1973 was 360 larvae. The total number of C. americanus larvae in the surface, 1 m, 2 m, 3 m, and 3.5 m samples in Forest Service Bog, at 2400 hours, on 2 August 1973 was 106. Therefore, the predation pressure of C. americanus larvae should be less in Forest Service Bog because of the fewer numbers of C. americanus larvae.

Finally, the two bogs differ in one other way. Both were sampled for zooplankton, through the ice, in December 1973, and March 1974. On both dates zooplankton (Diaptomus leptopus) was found alive and doing well in Forest Service Bog. In fact the females of D. leptopus were carrying eggs. In Tender Bog, however, no zooplankton other than C. americanus larvae were found. Sprules (1972) showed the large Diaptomus were a desirable prey for fourth instar C. americanus. Thus, there is an alternate source of prey available in the winter in Forest Service Bog.

Combining the above observations, a plausible explanation for the presence of C. trivittatus in Forest Service Bog is that because (1) the mature larvae of C. americanus do not occupy the upper strata of the bog during the day, (2) C. americanus larvae are in lower density in Forest Service Bog, and (3) an alternate source of prey is available for C. americanus larvae throughout the winter, predation pressure by C. americanus on early instars of C. trivittatus is much less than in Tender Bog. Thus, C. trivittatus is able to coexist with C. americanus under these conditions.

There is an interesting difference in the distribution of instars of *C. americanus* in Tender and Forest Service bogs (Tables 22 and 23). In Tender Bog (Table 22) *C. americanus* presents an expected pattern of progression through the four instars, with each instar increasing in numbers as the molting occurs from the previous instar. This is seen on dates 6/1, 6/10, 6/30, 7/14, 8/18. By 30 July for example, second instars are a small proprotion of the total number of larvae.

In Forest Service Bog there is a different pattern. At the beginning of the summer, the *C. americanus* population is further along in development, as can be seen on 1 June, than is the *C. americanus* population in Tender. Yet, on 28 July and 10 August in Forest Service, there are still a large number of second instars present. In contrast, by 14 July the majority of larvae in Tender are in the third instar.

There are two possible explanations for this difference. First it could be that *C. americanus* has more than one generation per summer in Forest Service Bog. On the other hand, it could be that the population staggers pupation throughout most of the summer. The first explanation implies that Forest Service is a more productive lake than Tender. The second suggests Forest Service is less productive. To answer this question production estimates are required throughout the summer for both bogs. Likewise, estimates of prey preference are required. Although there is one more cladoceran species in Forest Service, all species may not be equally available as prey. For example, the gelatinous sheath of *Holopedium gibberum* may render it hard to catch and handle.

TABLE 22

MEAN NUMBER OF _C. AMERICANUS_ LARVAE OR PUPAE OF TWO 1.5 M VERTICAL TOWS IN TENDER BOG IN 1973 (SAMPLES COLLECTED BETWEEN 2400 AND 0100 HOURS)

Stage	Date 5/17	6/1	6/15	6/30	7/14
Pupae	5.0	—	—	—	—
4th Instar	89.5	18.5	56.5	115.0	127.5
3rd Instar	—	—	5.0	211.5	672.0
2nd Instar	—	5.5	834.5	730.5	191.0
1st Instar	0.5	673.0	48.5	—	—

Stage	Date 7/30	8/11	8/23	9/9
4th Instar	136.5	334.0	238.5	415.0
3rd Instar	429.0	220.0	52.5	1.5
2nd Instar	15.5	7.0	1.0	—
1st Instar	—	—	—	—

TABLE 23

MEAN NUMBER OF *C. AMERICANUS* LARVAE OF TWO 1.5 M VERTICAL TOWS IN FOREST SERVICE BOG IN 1973 (SAMPLES COLLECTED BETWEEN 2400 AND 0100 HOURS)

	Date				
Stage	5/17	6/1	6/15	6/28	7/12
4th Instar	51.0	19.5	29.0	13.0	66.0
3rd Instar	—	—	16.0	13.0	21.5
2nd Instar	—	80.5	53.0	15.5	37.5
1st Instar	47.0	—	—	—	—

	Date				
Stage	7/28	8/10	8/26	9/9	10/4
4th Instar	74.0	37.0	47.5	39.0	43.0
3rd Instar	26.5	38.5	34.5	23.5	—
2nd Instar	36.5	104.0	13.0	1.5	—
1st Instar	—	—	—	—	—

DISCUSSION

The pattern of distribution of *Chaoborus americanus* in relation to the other three *Chaoborus* species appears to be determined by a number of factors. First, the absence of *C. americanus* from lakes with *C. punctipennis* and *C. flavicans* is best explained by direct fish predation. Those species (*C. punctipennis*, *C. flavicans* and *C. trivittatus*) whose mature larvae undergo diurnal, vertical migration can coexist with fish, presumably because they are deep in the water column during the daylight hours when fish feed. *Chaoborus americanus* third and fourth instar larvae, however, are subject to predation because they remain up in the water column continuously. The fact that most lakes have fish accounts for the low frequency of occurrence of lakes with *C. americanus*.

In those lakes in which no fish are found, *C. americanus* is the dominant species. The coexistence of *C. americanus* with any other species depends on the result of the interaction of the characteristics of the species and the characteristics of the lakes. In darkly stained bog lakes, *C. americanus* mature larvae remain high in the water column. The early instars of all species, as well as the later instars of some species, are thus vulnerable to predation by mature *C. americanus* larvae. It is believed that this predation pressure explains the absence of congeners of *C. americanus* from stained bogs such as Tender Bog.

In the clear bogs with no fish, *C. americanus* mature larvae sit lower in the water column during the day. Also, zooplankton prey overwinter in the clear bogs. Under these conditions, *C. trivittatus* is able to coexist with *C. americanus*, and to overwinter as early instars. It is not fully understood why *C. punctipennis* and *C. flavicans* also can not survive in such bogs.

The present evidence suggests that there may not be sufficient small prey (rotifers) available for the early instars or these two smaller species. Preliminary analyses of zooplankton samples from Forest Service Bog have revealed a low density of rotifers. Tender Bog, in which early instars of C. punctipennis larvae grew well, has a high density of rotifers. Therefore perhaps the rotifer fauna (or comparably sized zooplankters) are important for the survival of early instars hatching from eggs laid by a migrant female of C. punctipennis and C. flavicans.

The observed distribution of the four Chaoborus species among the four lakes studied reflects the result of the interaction of consistent properties of the species. This is substantiated by the fact that there are other lakes at UNDERC with the same combinations of Chaoborus species. For example, Ziesnis and Marathon bogs have the same Chaoborus species as Forest Service Bog; Brady's Bog and North Bog are similar to Tender Bog. Other evidence comes from the results of a survey of a series of lakes in Quebec. These results were reported in 1973, while this study was in progress. Pope et al. (1973) in sampling 26 lakes on the Matamek River system found the same four species that occur in the UNDERC lakes. A fifth, as yet unidentified species of the same sub-genus as C. trivittatus, Schadanophasma, was also found. More importantly, Pope et al. report all the combinations of species that are found in the UNDERC lakes, as well as a few other combinations. In general, however, the trends are the same in the Quebec lakes: (1) C. americanus does not occur in the lakes with fish, whereas C. punctipennis, C. flavicans, and C. trivittatus do; (2) C. americanus co-occurs with C. trivittatus or Schadanophasma spp. but not with the other species. Also, C. americanus does not exhibit the vertical migratory behavior of the other species.

It has been shown that predation is operating in this system, but how does predation fit into the overall dynamics of the different combinations of Chaoborus species? By considering the distribution of the Chaoborus species from a midge's point of view, it is easily realized that the lakes represent an environment in which the habitat consists of discrete patches (lakes) varying in size and distance from one another. Because adult Chaoborus are able to get from lake to lake, migration between patches of habitat occurs in this system (UNDERC lakes). Predation has been demonstrated to be important in the distribution of the species of Chaoborus. It can be classified as a source of extinction.

It is helpful to consider the UNDERC lakes as being divided into three different kinds of habitat, each with distinct combinations of Chaoborus species. They are: (1) fish lakes, (2) stained, fishless bog lakes, and (3) clear, fishless bog lakes. Each of these habitats has a defining characteristic. The observed combinations of Chaoborus species are the result of the interaction of the Chaoborus species with the defining characteristic of the habitat (fish and C. americanus), or with the other Chaoborus under the conditions peculiar to that habitat. Thus, the Chaoborus species distribution can be viewed as a system in which species are able to migrate between patches, but the rates of extinction vary for different species in different kinds of habitat patches.

Consider three general relationships that could exist between the extinction rate (e) of a species in a given habitat patch, and the migration rate (m) to that habitat patch. Extinction as used here refers to the death of individual larvae of a single species, not the change in number of species as used by MacArthur and Wilson (1967). The units in the migration rate are also the number of larvae that hatch per unit time from eggs laid by an adult female that migrates to a given lake. First the extinction rate could be equal to the migration rate ($e=m$). Second the extinction rate could be less than the migration rate ($e<m$). Finally the extinction rate could be much less than the migration rate ($e\ll m$). These three conditions coincide well with the variation in the intensity of the particular extinction mechanisms operating to determine the *Chaoborus* species combinations found at UNDERC and reported in the literature.

First the situation in which $e=m$ is represented in the cases of the exclusion of *C. americanus* from fish-lakes by fish, and the exclusion of congenerics from Tender Bog by *C. americanus*. In both cases, for the observed combinations of *Chaoborus* species to persist, e must equal m for the excluded species. That is, none of the propagules survive. It should be pointed out that it is the difference between the two rates that is important. The extinction rate does not have to be large to result in exclusion if m is also small. Although there is no data to verify the mechanisms operating, the absence of *C. flavicans* and *C. trivittatus* from North Gate Bog, and *C. punctipennis* and *C. flavicans* from Forest Service Bog, can be accounted for by having $e=m$. A few early instars of *C. flavicans* were found in North Gate Bog, but never fourth instars. It is suspected that the small prey size in North Gate Bog may be important in the absence of *C. flavicans* and *C. trivittatus* from this lake. The absence of *C. punctipennis* and *C. flavicans* from Forest Service Bog was discussed earlier.

In the second case, $e<m$, there is a potential source of extinction, but it is not of sufficient magnitude to exclude the species from a given lake. Admittedly, I have no estimates of the migration rates, but there is evidence from this study that the extinction rates of those species that

coexist with the fish are much lower in the lakes with fish than they are for C. americanus. That is, the ability to migrate vertically in the water column diurnally, enables C. punctipennis, C. flavicans, and C. trivittatus to survive with fish, even though they may suffer some predation (Hasler 1945). Also, because C. punctipennis and C. flavicans occur most frequently in the UNDERC lakes, m might be greater for these species. It is reasonable to consider it proportional to the number of habitats occupied (Slatkin 1974). An explanation was also presented in Chapter III for the coexistence of C. americanus and C. trivittatus in Forest Service Bog. The essence of the argument was that for several reasons, the extinction rate of C. trivittatus due to predation by C. americanus is lower in Forest Service Bog, than in Tender Bog. That is, the extinction rate is low enough that the species can coexist.

A consequence of having $e < m$ is that the relative proportions of potentially coexisting species in any given lake are less predictable. Variation in the extinction rate will determine how many propagules survive, but the pressure will never be sufficient to drive a species to extinction. Therefore the variation in the proportions of coexisting species in different patches will be a function of the variation in the intensity of the extinction rate, or in some cases the migration rate, between patches. For example, the predation pressure of fish on C. flavicans, C. punctipennis, and C. trivittatus is not likely to be as constant as it is on C. americanus, because in most cases it would require the fish to dive into anoxic regions to feed. Whether fish do this is probably dependent on the abundance of alternate prey. If alternate prey were low, then predation on the Chaoborus species normally found in fish-lakes could be expected, but it would not be expected to be of high intensity throughout the year. Predation pressure on _C. americanus_, however, would always be expected to be high. Personal observations agree with this general prediction. In the UNDERC lakes with _C. punctipennis_ and _C. flavicans_, variation in the proportions of the two species varies between lakes and sometime between years.

Alternate prey also appear to be important to the coexistence of _C. americanus_ and _C. trivittatus_. Therefore fluctuations in zooplankton densities may affect the extinction rate of _C. trivittatus_ when the two species coexist.

Migration rates between lakes could also be affected by predation pressure in, and the productivity of a given lake. Both of these factors influence the total population size which would in turn affect the number of migrants. Thus this also could lead to unpredictability of coexisting species proportions.

The third relationship that could exist between _e_ and _m_ is that $e \ll m$. This would be the case in which the migration rate of a species from other lakes would be high enough to swamp the extinction rate in a particular lake, and thus allow for the persistence of that species in that lake by constant reinvasion. There appears to be an example of this in the literature. In Hamilton (1971), one lake has four species of _Chaoborus_, _C. americanus_, _C. brunskilli_, _C. flavicans_, and _C. punctipennis_. Although it is not known whether this lake has fish, it is a small lake which is located near some very large lakes. It would be expected that the large lakes have fish and consequently _C. punctipennis_ and _C. flavicans_. A possible explanation for the composition of this small lake could be that it is a lake without fish, which would be expected to have _C. americanus_ and _C. brunskilli_ (closely related to C. *trivittatus*). The presence of C. *punctipennis* and C. *flavicans* could be due to high migration rates, from the nearby large lakes, which are large enough to override high extinction rates.

Evidence that reinvasion of lakes can be very rapid is the fact that C. *punctipennis* was present in the bog to which fish were added one year after the manipulation. They had not been there before.

Thus, in general the distribution of *Chaoborus* species among the lakes at UNDERC is well described by considering UNDERC as a region having discrete patches of three slightly different habitats. The *Chaoborus* species are able to migrate between patches, but their ability to survive in any one habitat depends on the difference between the extinction rate and the migration rate in that habitat. The purpose of this study was to determine the processes responsible for the high extinction rate of certain species in particular habitats.

Migration and extinction are important ecological system besides aquatic systems. Admittedly, these rates are usually difficult to measure. As habitats become less discretely bounded and tend to intergrade with one another, the complexity of these systems increases and it becomes more difficult to estimate the importance of these processes. In spite of these problems, in many cases it may be better to consider the dynamics of a system in terms of the differences in these rates.

In conclusion, it is important to point out that when attempting to explain patterns of coexistence and exclusion of species, the species of interest must be considered in the context of the dynamics of the community or ecosystem of which they are a part. Levins et al. (1973) summarized this succinctly, "An understanding of the coexistence pattern requires the integration of analyses of regional extinction-migration dynamics, local community structure, the autecology (sic) of species' niches, and the behavior of species in contact." I think this study has demonstrated this to be true.

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