A COMPARISON OF THE SECONDARY PRODUCTION OF *CHAOBORUS AMERICANUS* IN TWO BOGS: EFFECTS OF THE PRESENCE AND ABSENCE OF *CHAOBORUS TRIVITTATUS*

Kim McNaughton

Submitted to Dr. Martin B. Berg

December 1, 1989

ABSTRACT

A study of the production of *Chaoborus americanus* (Diptera: Chaoboridae) in two bog lakes on the UNDERC property in northern Wisconsin demonstrated that the conditions of Forest Service Bog (FSB) were sufficiently more favorable than those in Tender Bog (TB) to result in substantially greater secondary production rates. The factors which presumably favored the larvae in FSB were warmer temperature, greater oxygen concentration, clearer water and greater abundance of zooplankton. *C. americanus* appears to have a one-year life cycle in FSB and a two-year cycle in TB. Comparisons between *C. americanus* in a lake containing a congener, *C. trivittatus*, and a lake lacking this potential competitor showed that both species competed with one another for food sources and also preyed upon one another. Despite these interactions, lake conditions were the predominant factor influencing secondary production rates, overshadowing any effects of the interspecific interaction.

INTRODUCTION

The distribution and growth of several species of *Chaoborus* (Diptera: Chaoboridae) (Figure I) have been studied in a number of lakes at the University of Notre Dame Environmental Research Center (UNDERC) in northern Wisconsin (von Ende 1979, 1981a, 1981b, 1982). The interaction between two congeners, *Chaoborus americanus* and *C. punctipennis*, has been noted as predation of the former on the latter (von Ende 1979). von Ende (1981b) suggested that *C. trivittatus* might similarly affect the development of *C. americanus* in Forest Service Bog (FSB) and Marathon Bog. The present study examined and compared the secondary production rates of *C. americanus* in two different bogs. One bog contained *C. americanus*, and the other possessed two species, *C. americanus* and *C. trivittatus* .

The duration of the larval stage of *Chaoborus* spp. is somewhat variable. "Generation time is governed by body size and such ecological factors as temperature and food supply" (Morgan et al. 1980). A two-year life cycle, determined from growth rates and color variations, has been hypothesized for *C. trivittatus* in Eunice Lake, British Columbia (Fedorenko and Swift 1972). In Lac Gallienne, Quebec, Carter (1977) also suggested a hemivoltine pattern for *C. americanus.* The larval period has not been determined for either *Chaoborus* species on the UNDERC property.

C. trivittatus proved to be the larger species in every lake. *Chaoborus* spp. are selective predators with individual species preferences (Daphnia spp. are often chosen), as well as preferences based on relative size and abundance of potential prey (Elser, et al. 1987, Pastorok 1981). In addition to being carnivorous, *C. americanus* is also thought to be cannibalistic (von Ende 1979). For this reason, *C. americanus* could plausibly prey on *C. trivittatus.* If *C. trivittatus* were cannibalistic as well, it might prey on *C. americanus* in FSB rather than, or in addition to, competing for resources. In a previous study of four lakes at UNDERC, von Ende (1979) compared larval body sizes of *C. americanus* and *C. trivittatus*. In each of these four lakes, *C. trivittatus* proved to be the larger species. Due to the size difference between the two species, *C. trivittatus* would probably feed on *C. americanus* more frequently than vice versa.

Vertical migration of larvae can influence the type of interaction between the two species. Migratory behavior will determine the amount of time the congeners spend in contact with each other, whether they share a habitat or remain completely separated . *Chaoborus* spp. generally migrate in lakes containing fish (Carter 1977, Hare 1986, Roth 1968, von Ende 1979). Many ecologists believe that the migration is an anti-predation mechanism. "Certain *Chaoborus* species which do not migrate have been shown to be largely restricted to fishless lakes or ponds" (Hare 1986). In lakes without fish, *Chaoborus* may (Fedorenko and Swift 1972, Hare 1986, Swift and Fedorenko 1973) or may not migrate (Hare 1986, von Ende 1979). If such migration does occur, it may be attributable to light intensity, oxygen concentration, or energetics due to temperature differences (Hare 1986). Swift (1976) explained that in fishless lakes, migrating larvae may be present, having immigrated from lakes in which the insects experienced predatory or energetic pressures.

Migratory patterns within lakes vary by geographic location, by lake, between species and also within species. Von Ende (1979) found that *C. americanus* does not undergo extensive vertical migration in Tender Bog (TB) (Figure II) or FSB (Figure III). In TB, *C. americanus* generally lives in the upper three meters, while in FSB it remains at three meters during the day and is distributed evenly throughout the water column at night (von Ende 1979).

This project was designed to study the effects of two potentially competitive congeners by a comparison of secondary production rates of *C. americanus* in TB and FSB. The subsequent findings resulted in a consideration of the differences in habitability of the two bogs.

MATERIALS AND METHODS

Preliminary Sampling

A transect was established across the center of each bog to most accurately represent the population density of *Chaoborus*. Within a 48 hour period, three sites along each transect were sampled at both noon (1200) and midnight (2400) (Figures II and III). At each site, one Schindler trap was collected every meter from the surface to four meters in FSB, and to nine meters in TB. Each complete vertical sampling with the Schindler trap was followed by two vertical tows of a "*Chaoborus* net" (80-um mesh), in water slightly removed from the site of the Schindler sampling, to tow in an undisturbed area. These two net tows were then pooled to determine the mean number of individuals captured per tow. The Schindler trap samples were used to determine the vertical distribution and the time of day that samples yielded more *Chaoborus*.

Because no substantial differences in composition were found between sites (Table I), the two sites which yielded the greatest number of larvae were chosen to represent their respective bogs. Subsequently, site number two was used to sample TB, and site three was used in FSB. The diel vertical distribution determined from the samples taken in FSB on May 31 and in TB on June 1 (Figures IV-VII) indicated that more individuals were collected at 1200 in TB and at 2400 in FSB. From this data, the numbers-weighted average depth was calculated using the method described in *Limnological Methods* (1989). To accurately include the surface sample in the calculation, this method was modified by adding 0.5 to each collection depth when multiplying by the number of larvae found at that depth. The mean depth was then obtained by subtracting 0.5.

During the preliminary sampling, different nets and different towing rates were tested. The *Chaoborus* net (Wildlife Supply Co., Saginaw, MI) was made of 80-um mesh Nitex netting, had an opening 0.3 m in diameter, and lacked a flange. This type of net was selected for its ability to capture the highly mobile fourth instar larvae. Throughout the summer the most effective towing rate was consistently maintained by feel. Data from the Schindler trap and *Chaoborus* net collected in the last preliminary sample (June 14) were used to determine the net efficiency (Limnological Methods 1989). With this net efficiency, the number of *Chaoborus* collected with the net was converted to the number that would have been collected by the Schindler trap.

Field Work

Site two in TB was 10+ meters deep and was sampled to nine meters to exclude substrate from the samples. Site three in FSB had a depth of 4.5-5m and was sampled to four meters. Five samples were collected from each bog for use in the production calculations. The bogs were sampled once a week from June 17 to July 15. On each collection day, three vertical tows were collected with the *Chaoborus* net from each of the selected sites. Samples from TB were collected at 1200, and FS was sampled at 2400. Midmorning dissolved oxygen concentration and temperature were measured at one-meter intervals and recorded for each bog once during the summer (Table II). On that occasion the pH and Secchi depth were also measured.

Laboratory Work

Chaoborus samples were initially preserved in Lugol's iodine solution to prevent regurgitation of stomach contents. The solution was added to the sample, rather than adding the sample to a jar containing iodine, to prevent overstaining the larvae. When the insects were transferred to vials, they were stored in 80% ethanol, with a few drops of formalin to reduce fungal growth. Each replicate sample from FSB was sorted by species into two vials. Replicates of TB were stored in separate vials. The larvae from each vial containing *C. americanus* were divided into second, third and fourth instars. For each replicate, the number of individuals per instar was counted, and their mean front air bladder length measured.

Instars were determined primarily by size. Due to molting, head capsule size increases incrementally from one instar to the next. Initially, head capsule lengths were measured to become familiar with the range of sizes. Instars were eventually determined at a glance or by comparison with previously classified individuals.

The two species were distinguished in different ways depending on instar. Second instars were classified as *C. americanus* if a compound eye had begun to develop, and as *C. trivittatus* if a compound eye was lacking (Fedorenko and Swift 1972). In third and fourth instars, the most definitive classification was based on the shape of the prelabral appendage (Roth 1967). For individuals with poorly developed prelabral appendages, eye development and head shape (Fedorenko and Swift 1972) were the determining factors.

The diel vertical distribution in each bog was evaluated in two ways by chi-square analysis. The following null hypotheses were tested: 1) The vertical distribution of *Chaoborus* is homogeneous throughout the water column, and 2) The patterns of vertical distribution of larvae are the same at noon as they are at midnight.

Other zooplankton accompanying *Chaoborus* in the samples were identified using keys by Needham (1977). With an idea of the organismic makeup of each bog in mind, crop contents of both *C. americanus* and *C. trivittatus* were examined to determine the insects' diets. Viewing the crop contents of the limited number of fourth instars, and aided by a familiarity with the potential prey available in the chaoborids' habitat, sclerotized parts found in the crops were matched to published figures (Needham 1977, Pennak 1978) and to a pictoral key provided by M. L. Dini (unpublished).

Due to the possibility of a hemivoltine life cycle, attempts were made to distinguish between first- and second-year fourth-instar larvae. Final-instar larvae that were larger and more yellow than the others, characteristic of overwintering (Carter 1977, Fedorenko and Swift 1972), were classified as second-year fourth instars, while smaller, more opaque final instars were considered to be first-year larvae. After all of the samples were sorted and the morphology of the insects had become familiar, both the physical characteristics of the larvae and the numbers of each instar present at each sample date were considered in the determination of the life cycles of *C. americanus* in TB and FSB.

Calculations

Dry weight of the larvae was calculated based on regressions from front air bladder length (Traina, J.A., unpublished MS). Figure I indicates the positions of the air bladders on the larva. Regressions for second and third instar *Chaoborus* in FSB were not available, so regressions from TB were used.

Secondary production was computed using to the size-frequency method (Hynes and Coleman 1968, Waters and Crawford 1973). The back-calculated catch curve method (Waters and Crawford 1973) was used when the number of individuals per m^3 at one instar was less than that of the next instar.

The growth rates of the second and third instars were computed according to the formula $\ln (W_t/W_{t-1})$, where W_t was the biomass at time t, and W_{t-1} was the biomass at time $t-1$.

RESULTS

Lake Conditions

On June 27 at 1010, the Secchi depth at TB was 1.0 m, and the mean pH was 4.13, with a range of 3.89-4.28. The temperature was 19°C at the surface, dropping to 3°C at 4 m and remaining isothermal from four to nine meters (Table II). The surface water contained 4.4 mg/l dissolved oxygen (DO). Within two meters the DO decreased to an anoxic level. On July 9 at 1100, the Secchi depth at FSB was 2.25 m, and the pH at 2 m depth was 4.25. The temperature profile was one of a steady decrease from 23.8°C at the surface to 6.2°C near the sediment. This bog was oxygenated throughout most of its water column.

Zooplankton identified from TB were *Holopedium gibberum*, *Daphnia*, *Diaptomus*, an unidentified cyclopoid and two rotifers, *Keratella* and *Kellicottia*. The zooplankton assemblage in FSB was characterized by high densities of *Holopedium gibberum*, *Daphnia*, the rotifers *Keratella* and *Kellicottia*, and what appeared to be ephippial eggs. Overall, zooplankton were more abundant in FSB.

Distribution

Both bogs exhibited unimodal vertical distributions of *Chaoborus* (not distinguished by species). At TB, the majority of individuals were collected in the upper three meters (Figures IV and V). The modal depth in TB was one meter, with mean depths of 2.77 m and 3.29 m at 1200 and 2400, respectively (Table III). The modal peak in FSB was at two meters, with the remaining larvae shifting from the lower half of the bog at 1200 to the upper half at 2400 (Figures VI and VII). The mean depth was 2.39 m at 1200 and 1.66 m at 2400.

The null hypothesis that vertical distributions were homogeneous was rejected by chi-square analysis ($p<0.001$) (Table IV). The second null hypothesis, that vertical distributions in each bog differed from 1200 to 2400, was also rejected for TB ($p<0.001$) and FSB ($p<0.001$).

Feeding Habits

Due to the limited number of larvae whose crops were large enough to examine, the diet aspect of this research can be considered only preliminary. Larvae were cannibalistic, eating other chaoborids, apparently regardless of species. The insects seemed to prey on the largest individuals they could manage. In TB, *C. americanus* consumed *Chaoborus*, cladocerans (either *Daphnia* or *Diaphanosoma*), *Diaptomus*, *Keratella* and filamentous algae. *C. americanus* in FSB preyed on *Chaoborus* (both spp.), cladocerans, *Diaptomus, Keratella*, *Kellicottia* and diatoms. *C. trivittatus* also consumed *Chaoborus* (those found were too small to identify) and cladocerans. In addition, an individual *C. trivittatus* appeared to be attacking a single *Holopedium gibberum*.

Life Cycle

Because only three or four first instars were collected during the summer, they were not included in this project. Second, third and fourth instars comprised the study of the life cycle and production of *Chaoborus americanus*. In the beginning of the four-week sampling period, densities in TB, accounting for net efficiency, were 1511/m^3 second instars, 6/m^3 third instars , and 106/m^3 fourth instars (Table VI). In FSB, the distribution was 1191 second instars/m^3, 2236 third instars/m^3, and 91 fourth instars/m^3. As the season progressed, the general trend in TB was toward fewer seconds and more thirds. The fourth instars increased in number until July 9, when their numbers began to decrease. In FSB, the number of second instars decreased drastically, third instar numbers decreased more slowly, and the fourth instars generally became more abundant. Fourth instars in TB early in the study had thick bodies with a cloudy coloring which absorbed the iodine more efficiently than the clear second instars. The earlier fourth instars in FSB also appeared to have overwintered, and "new" fourth instars were not noted until July 9, when a small proportion of fourth instars looked clearer, with a smaller body width.

Calculations

Table VII contains the equations for the biomass calculations, as well as the mean biomass ± the standard error for each instar in each bog. These numbers yielded production values of 996.8 mg/m^3/yr for FSB and 81.5 mg/m^3/yr for TB (Table VIII).

The rate of growth from second to third instar was greater in TB. The growth rate for the change from third to fourth instar was greater in FSB.

DISCUSSION

Lake Conditions

The physical conditions of the lakes differed markedly. TB was more acidic than FSB. TB was highly stained, while FSB was relatively clear. Stained bogs are noted for low planktonic primary production (von Ende 1981a). Low densities of phytoplankton cannot sustain a large zooplankton community, which may explain why the zooplankton in FSB were more abundant than that in TB.

FSB is only half as deep as TB, and exhibits temperatures and dissolved oxygen concentrations favorable for growth throughout most of its water column. Thus the samples taken from TB, while composed of a 0.64-m^3 volume, represent only 0.14 m^3 of favorable water, and the production will inherently be lower per cubic meter of water than in FSB.

Distribution

The results of the chi-square tests for a homogeneous distribution in the bogs support the visual evidence (Fig. IV-VII) that the larvae were unevenly distributed. The significant values for chi-square in comparing the distributions in the two lakes at 1200 and 2400 indicate that the overall distribution does change from noon to midnight. A close look at Figures IV-VII, however, shows that extensive vertical migration does not occur in either bog. As von Ende (1979) stated, *C. americanus* in TB does not migrate and is concentrated in the upper three meters. A peak in numbers appears at one meter and though density diminishes rapidly, larvae do persist, despite decreasing temperatures and dissolved oxygen levels, all the way to the bottom.

Considering the percent of individuals at any given depth that are fourth instars (Table V), there is no evidence for instar-specific migration in TB. In FSB, however, the concentration of fourth instars is greater toward the surface. Further studies should be done to determine whether instar-specific migration takes place in FSB.

Larval density in FSB peaked at two meters, the middle of the water column. At noon more of the remaining insects were found closer to the bottom, while at midnight densities were greater toward the surface. The results of this midnight study differed from von Ende's (1979) conclusion that *Chaoborus* are evenly distributed at night. Although a species-specific distribution was not formulated, *C. americanus* must have been involved in this change in distribution, since the numbers of *C. trivittatus* were not sufficiently large to cause the difference. The discrepancy between the larval distribution found in this study and that found by von Ende (1979) can most likely be attributed to changes in abiotic factors in the bogs over the past ten years. Before conclusions are drawn about the nature of this change in distribution, the pattern should be further investigated.

Feeding Habits

Since *Chaoborus* in TB and FSB preyed on essentially everything that was available to them, and the two lakes contained mainly the same food sources, the different larval populations shared a common diet. FSB was qualitatively noted as supporting more zooplankton, probably due to the warmer water temperatures, and greater concentration of dissolved oxygen to a greater depth. The most commonly identified meal was *Chaoborus*. Due to the extent of the study of these individuals, chaoborid parts were probably the most easily identified. More importantly, though, these larvae were large, therefore a choice energy source, and they were relatively abundant. Both *C. americanus* and *C. trivittatus* were cannibalistic and would eat members of either species.

Life Cycle

C. americanus appeared to have a two-year life cycle in TB. Early in the summer, samples contained predominantly second and fourth instars, each in proportion with its relative abundance throughout the sampling period. Due to a lack of third instars, the fourth instars present appeared to have overwintered. In addition, these insects displayed the characteristics of second-year larvae: darker coloration and larger body size.

At FSB, I believe *C. americanus* spends only one year in the larval stage. Second and third instars were larger than those in TB, but fourth instars were smaller. Fourth instars in TB can probably attribute their larger biomass to the contribution of the overwintered individuals. The growth rate from second to third instar was greater in FSB, but the growth rate from third to fourth instar was greater in TB (Table VIII). The results for growth from second to third instar agree with the findings of Fedorenko and Swift (1972), who found that 1) the duration of each instar of *C. trivittatus*, the overwintering species, in Eunice Lake was twice as long as that of *C. americanus*, the species with the one-year larval period, and 2) *C. americanus* gained weight more quickly than *C. trivittatus.* The faster growth rate of third instars to fourth in Tender Bog is most likely caused by the combination of first-year and second-year fourth instar larvae in the calculation. Were the two cohorts to be separated, and only the first-year larvae considered, the growth rate from third to fourth instar should be greater in FSB, indicating a one-year life cycle for *C. americanus.*

Because the experiment began late in the growing season, the early absence of/third instars was not observed, and the life cycle of the larvae could not be determined based on the presence or absence of fourth instars. However, in this lake the colored, larger larvae were first noticed on July 9. According to Carter (1977), fourth instar *C. americanus* in Lac Galliene with a two-year life cycle grew darker and larger throughout the summer. Also, in the study of the development of fast and slow morphs in lakes on the UNDERC property (von Ende 1981b), it was noted that larvae do not pupate until they have turned yellow and accumulated extra biomass.

Differences in Production

Secondary production in TB was an order of magnitude lower than that in FSB. The results of this study suggest that the conditions of the insects' environment had a greater effect on production of *C. americanus* than did the interaction between *C. americanus* and *C. trivittatus*. Several lines of evidence can be offered to support this suggestion. First, the short study period may have been a factor in the smaller production in TB. Because the larvae develop earlier and more rapidly in FSB, third instars predominated in this lake throughout the sampling period, while the number of second instars dominated in TB. Had the study been extended to cover the entire growing season, differences in production may have decreased. Another reason lower production would be expected in TB is that while a greater depth was measured in this lake than in FSB, the water conducive to production was considerably shallower. Those individuals that spent some time in the colder, anoxic waters below two meters in TB experienced periods of decreased metabolism, and therefore decreased growth, which their counterparts in FSB avoided. Although the fourth instars in TB had a mean biomass greater than that in FSB, their numbers were relatively small, and did not contribute as much to production as did the third instars.

In FSB, *C. americanus* and *C. trivittatus* had similar diets which included both species of *Chaoborus*. The competition for food should result in lower production in FSB than in TB. The predation of *C. trivittatus* on *C. americanus* could simply decrease the production of *C. americanus* in FSB. In a more complex interaction, however, this predation could decrease intraspecific competition between *C. americanus* individuals and thereby increase its production in FSB. In addition, *C. trivittatus* is a highly nutritious food source available to *C. americanus* in FSB, but not in TB. These last two observations may help explain the assertion that production is greater in FSB.

The conclusion to be drawn from the results of this study is that, while *C. americanus* and *C. trivittatus* do interact in both a competitive manner, and also using one another as a food source, the dominant factor in the production discrepancy is the difference in lake conditions. FSB is sufficiently warmer and more oxygen-rich to increase the production of *C. americanus* relative to TB, and possibly even to induce a one-year larval period in contrast with a two-year cycle in TB.

Suggestions for Experiment Improvement

To improve the accuracy of findings in this experiment, and increase confidence in the conclusions, several modifications of the experiment should be considered. First, the study should encompass the period of growth from emergence until nearly all individuals have reached the fourth instar. This change would result in more accurate production estimations, and would facilitate the determination of the larval period of *C. americanus* in FSB. Second, the net efficiency values would be more accurate if the Schindler trap samples taken in conjunction with the net tows had been replicated. Also, if the production in these bogs were to be computed again, regressions for second- and third-instar *C. americanus* should be calculated for FSB, and the first-year fourth instars should comprise a size class separate from the overwintered larvae. If these conditions cannot be satisfied, biomass should be determined using the volumetric method of Hynes and Coleman (1968). In this case, the larvae must be measured within a week of capture, to avoid making measurements after disintegration has begun.

ACKNOWLEDGEMENTS

I would like to thank the Bernard J. Hank family for subsidizing the UNDERC course, under which this project was designed. I am grateful to CAPT. George H. Dewhirst, USN, Commanding Officer, NROTC Unit, University of Notre Dame, who granted a delay in my military training to permit my study at UNDERC. I especially appreciate the enthusiasm and dedication of Dr. Martin B. Berg in helping plan the project and in overseeing its execution. Thank-you to Dr. Michael Dini for his instruction in sampling technique and zooplankton identification, and to Dr. Carl von Ende, for contributing the regression formulas and for sharing his knowledge of the specifics of *Chaoborus* at UNDERC. Finally, thanks to Bob Hallahan for extensive help in collecting the larval samples.

LITERATURE CITED

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.

Elser, M.M., C.N. von Ende, P. Sorrano, and S.R. Carpenter. 1987. *Chaoborus* populations: response to food web manipulation and potential effects on zooplankton communities. Canadian Journal of Zoology **65**:2846-2852.

Fedorenko, A.Y., and M.C. Swift. 1972. Comparative biology of *Chaoborus americanus* and *Chaoborus trivittatus* in Eunice Lake, British Columbia. Limnology and Oceanography **17**:721-730.

Hare, L., and J.C.H. Carter. 1986. The benthos of a natural West African lake, with emphasis on the diel migrations and lunar and seasonal periodicities of the *Chaoborus* population (Diptera,Chaoboridae) Freshwater Biology **16**:759-780.

Hilsenhoff, W.L., and R.P. Narf. 1968. Ecology of Chironomidae, Chaoboridae, and other benthos in fourteen Wisconsin lakes. Annals of the Entomological Society of America **61**:1173-1181.

Hynes, H.B.N., and M.J. Coleman. 1968. A simple method of assessing the annual production of stream benthos. Limnology and Oceanography **13**:569-573.

Limnological methods of the cascading trophic interactions project. 1989. P.A. Sorrano, ed. 81 p.

Morgan, C.C., T. Bachiel, G. Bretschke, A. Duncan, A. Hillbricht-Ilkowska, Z. Kajak, J.F. Kitchell, P. Larsson, C. Levique, A. Nauwerk, F. Scheimer, and J.E. Thorpe. 1980. Secondary Production. In (E.D. LeCren and R.H. Lowe-McConnell, eds.) *The Functioning of Freshwater Ecosystems*. Cambridge University Press, Cambridge, England.

Needham, J.G., and P.R. Needham. 1977. *A Guide to the Study of Freshwater Biology.* Holden-Day, Inc., San Francisco, California, USA.

Pastorok, R.A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology **62**:1311-1324.

Pennak, R.W. 1978. *Freshwater Invertebrates of the United States.* John Wiley and Sons, Inc., New York City, New York, USA.

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.

Roth, J.C. 1968. Benthic and limnetic distribution of three *Chaoborus* species in a southern Michigan lake (Diptera: Chaoboridae). Limnology and Oceanography **13**:242-249.

Swift, M.C. 1976. Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology **57**:900-914.

Swift, M.C., and A.Y. Fedorenko. 1973. A rapid method of analysis of the crop contents of *Chaoborus* larvae. Limnology and Oceanograpy **18**:795-798.

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

von Ende, C.N. 1981a. Apparent exclusion of the cladoceran *Bosmina longirostris* by invertebrate predator *Chaoborus americanus.* The American Midland Naturalist **105**:240-248.

von Ende, C.N. 1981b. Frequencies of developmental morphs of *Chaoborus americanus* in four fishless bog lakes. The American Midland Naturalist **105**:401-404.

von Ende, C.N. 1982. Phenology of four *Chaoborus* species. Environmental Entomology **11**:9-16.

Waters, T.F., and G.W. Crawford. 1973. Annual production of a stream mayfly population: a comparison of methods. Limnology and Oceanography **18**:286-296.

Figure I. Chaoborus Larva

The length of a fourth instar larvae is on the order of 12-13 mm.

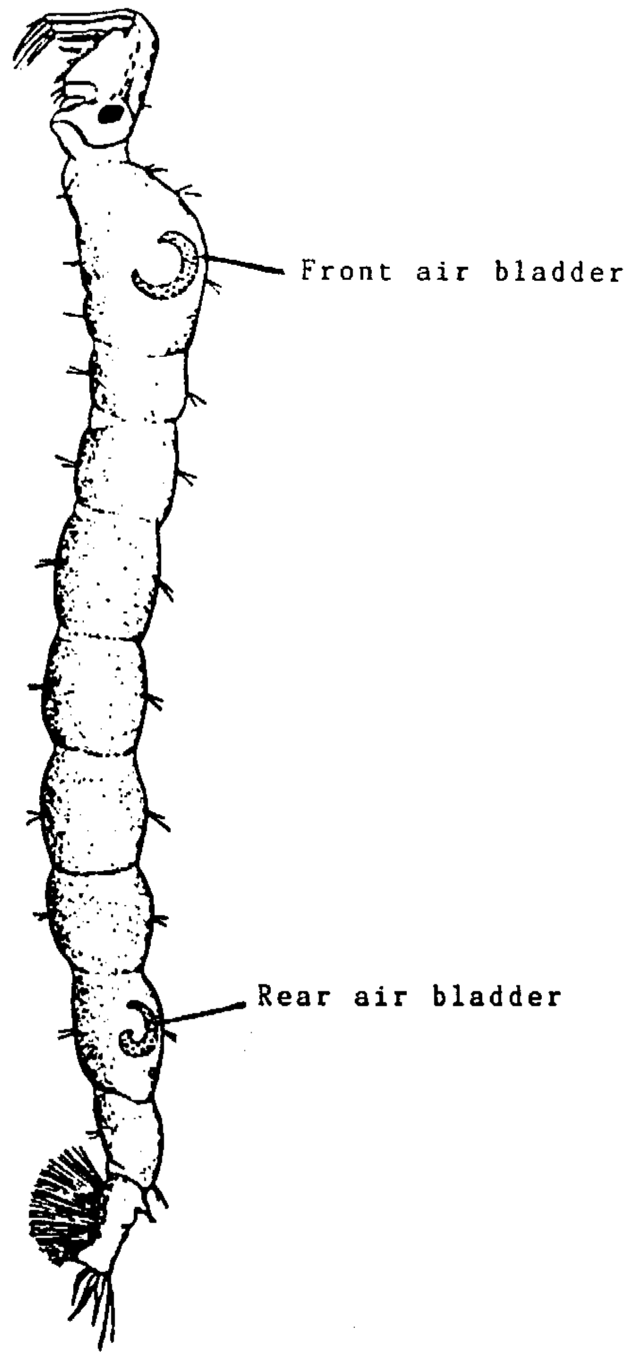
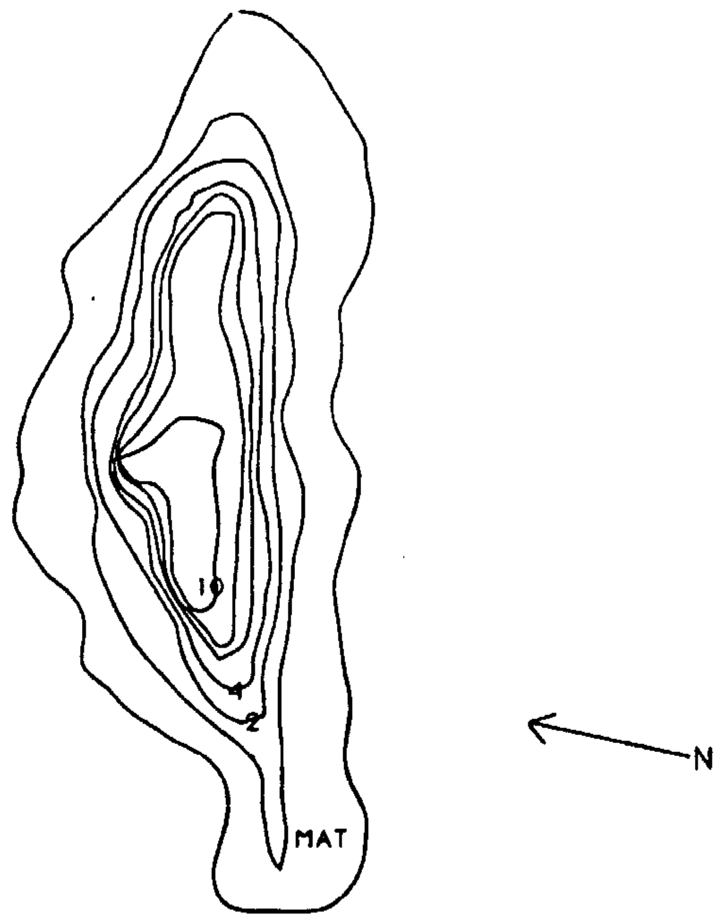
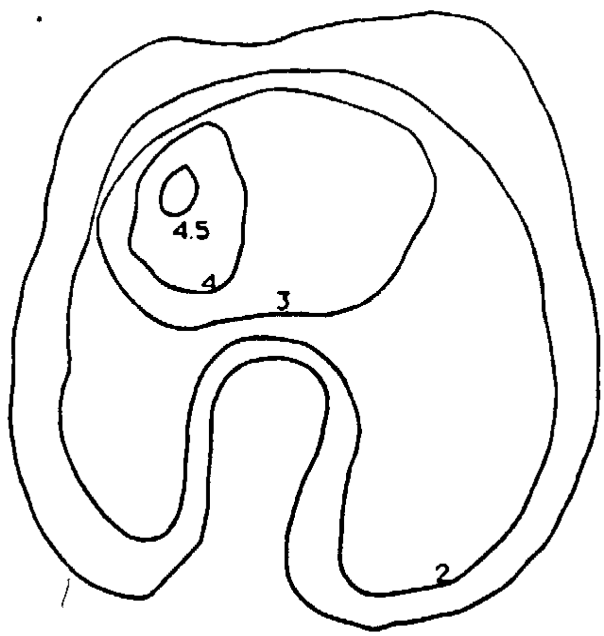


Figure II.



Tender Bog
University of Notre Dame--UNDERC

Figure III.



Forest Service Bog
University of Notre Dame--UNDERC
Depth contour interval=1 meter

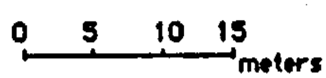


Figure IV. 1200 Chaoborus Distribution
Tender Bog

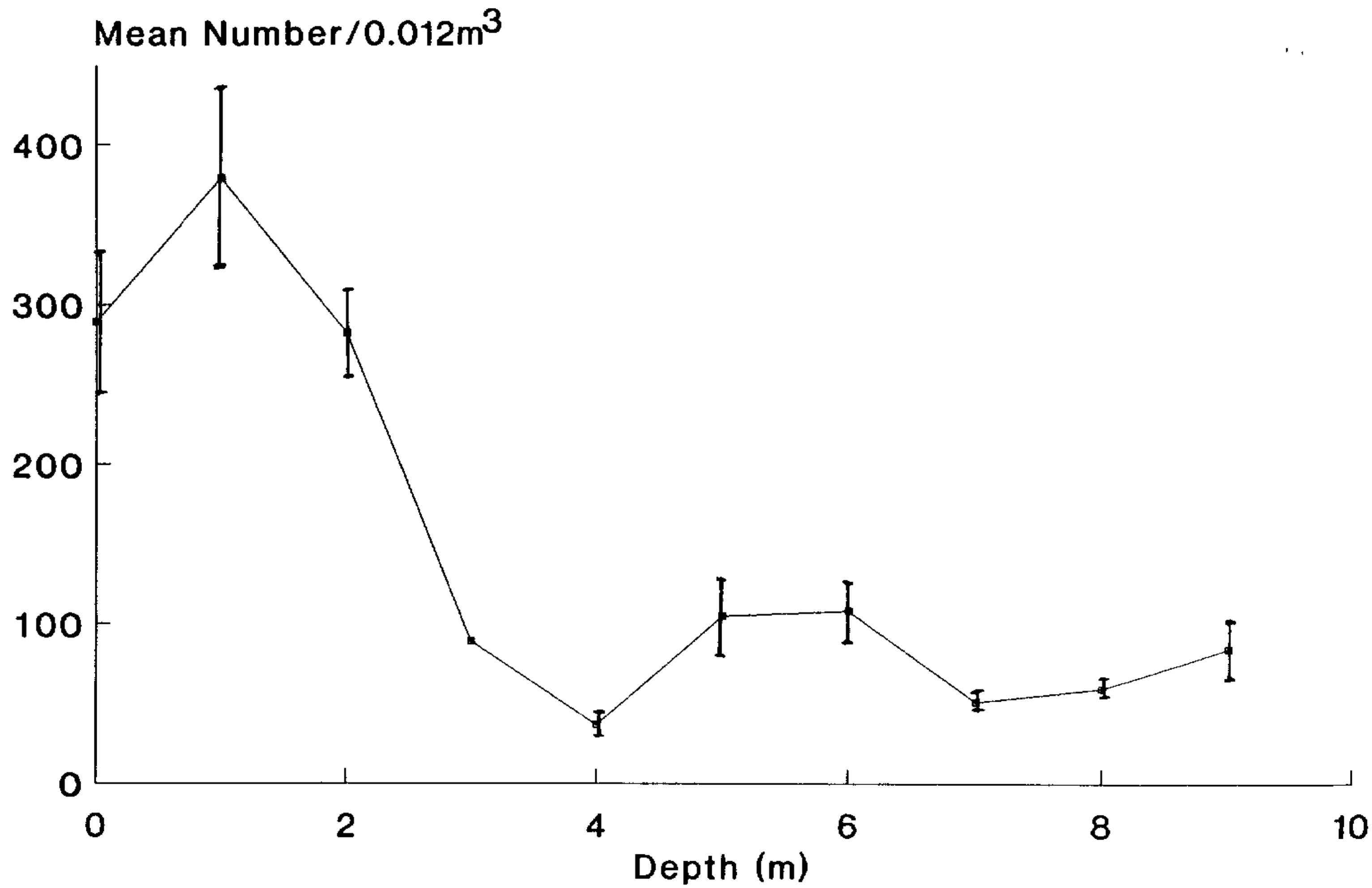


Figure V. 2400 Chaoborus Distribution
Tender Bog

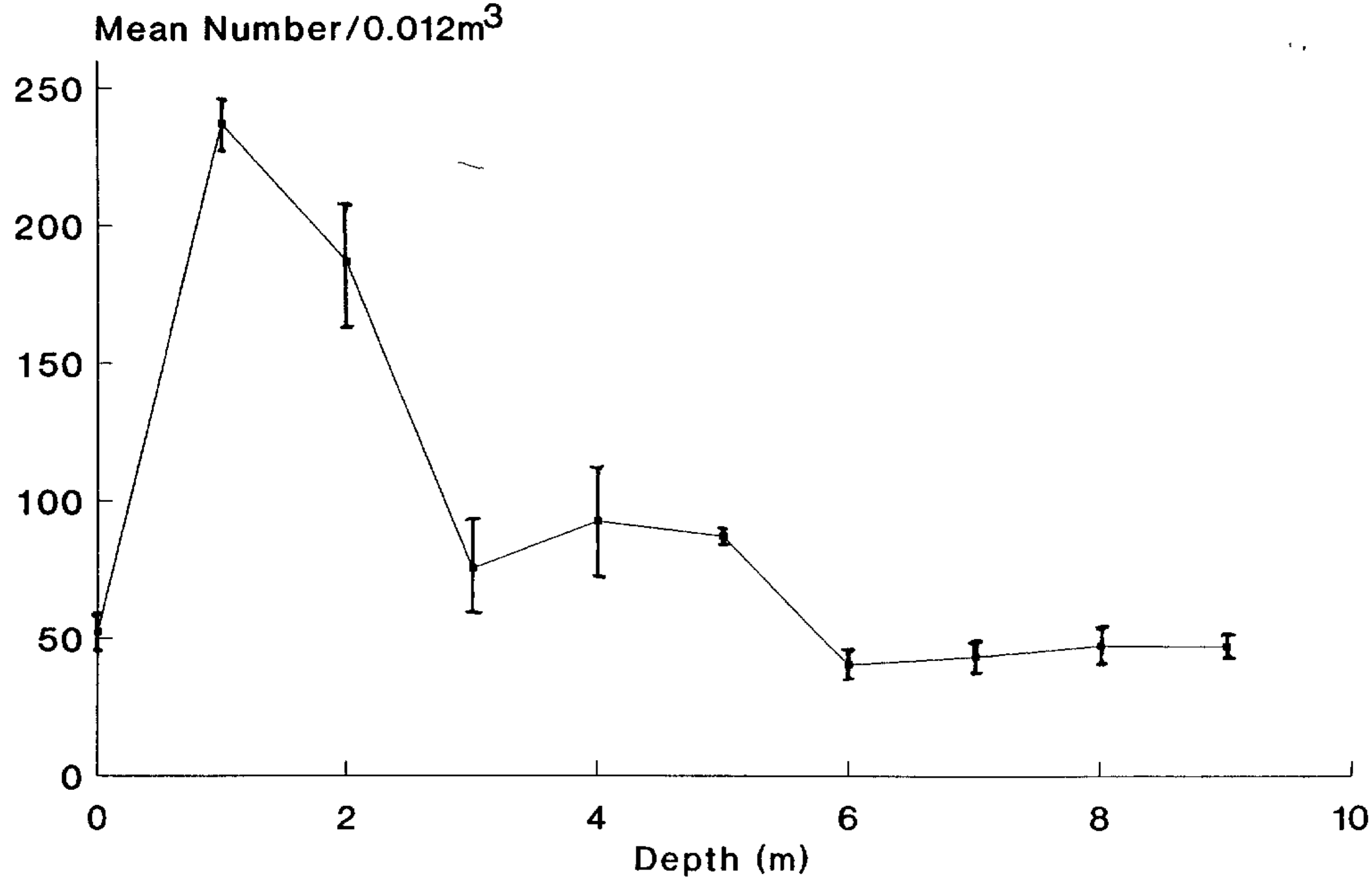


Figure VI. 1200 Chaoborus Distribution
Forest Service Bog

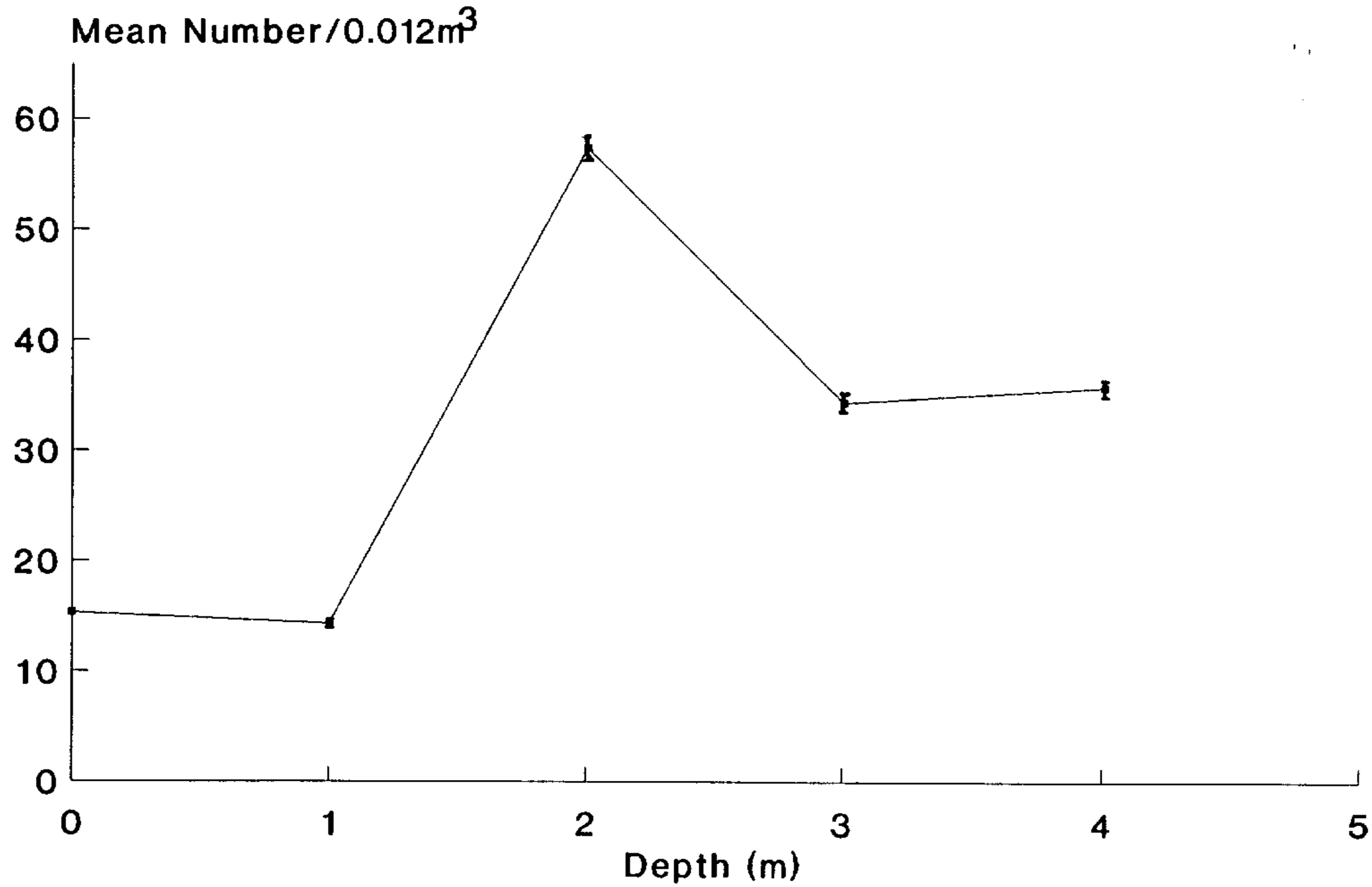


Figure VII. 2400 Chaoborus Distribution
Forest Service Bog

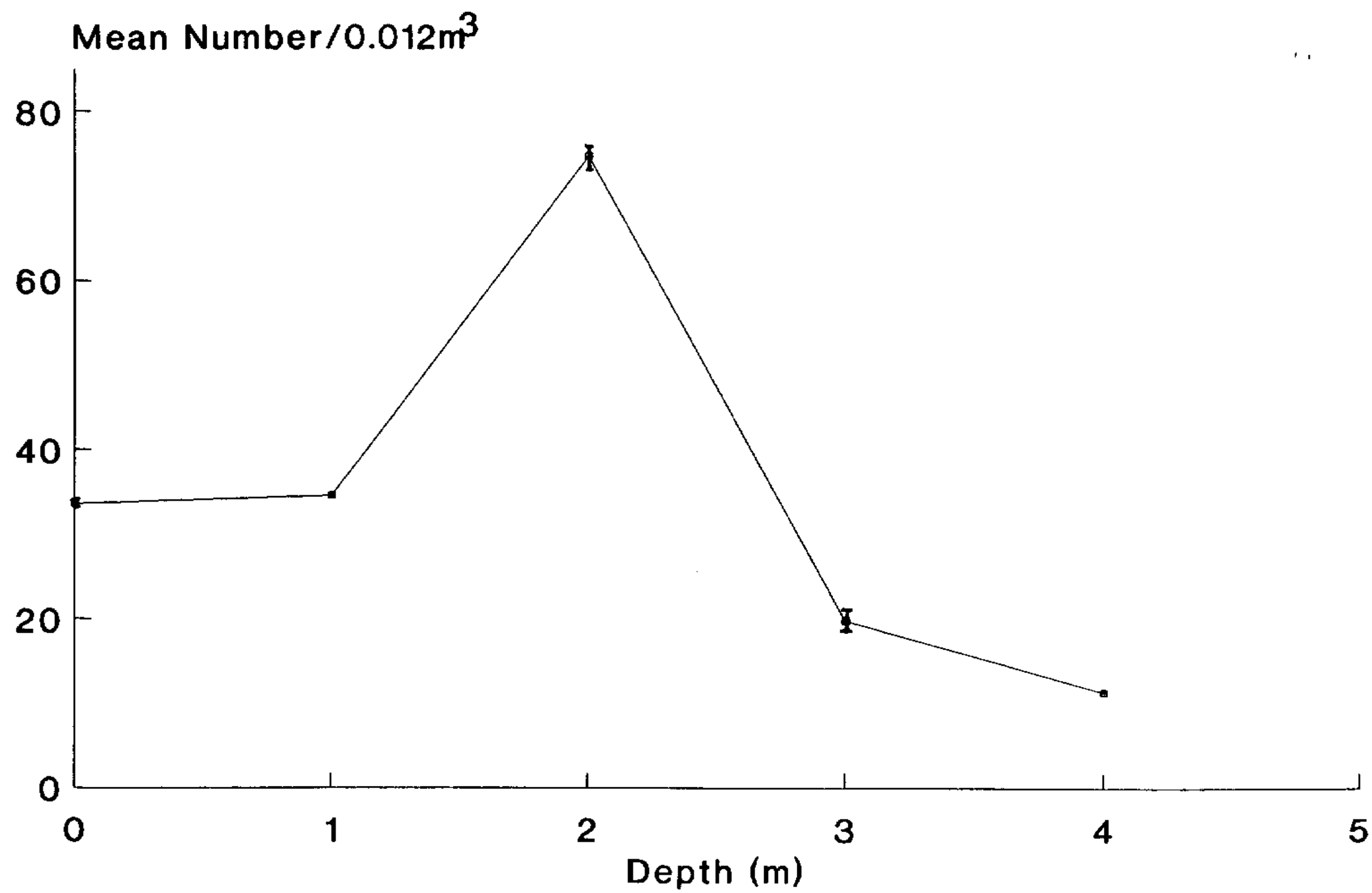


Table I. Preliminary Sampling: Numbers of Larvae Collected with Schindler Trap at One-meter Intervals

TENDER BOG 1200

Depth(m)	Site 1	Site 2	Site 3
0	207	305	355
1	211	560	367
2	37	195	50
3	88	91	88
4	38	58	14
5	20	142	152
6	41	132	151
7	63	399	51
8	63	47	68
9	80	143	30
TOTAL	848	1712	1326

FOREST SERVICE BOG 2400

Depth(m)	Site 1	Site 2	Site 3
0	30	30	41
1	37	35	32
2	68	67	96
3	7	19	33
4	16	8	10
TOTAL	180	172	240

Table II. Physical Conditions of the Habitats

TENDER BOG June 27, 1989 1010

Depth (m)	Temp (C)	D.O. (mg/l)
0	19	4.40
1	13	0.60
2	6.5	0.25
3	4.0	0.15
4	3.0	0.10
5	3.0	0.10
6	3.0	0.08
7	3.0	0.08
8	3.0	0.05
9	3.0	0.05

FOREST SERVICE BOG July 9, 1989 1100

Depth (m)	Temp. (C)	D.O. (mg/l)
0	23.8	6.30
1	23.5	5.90
2	16.2	2.20
3	10.0	5.40
4	6.2	0.30

Table III. Mean Depth and Modal Depth

Bog	Time	Mean Depth (m)	Modal Depth (m)
Tender	1200	2.77	1.0
Tender	2400	3.29	1.0
Forest Service	1200	2.39	2.0
Forest Service	2400	1.66	2.0

Table IV. Chi-square Analysis

Percent of the vertical sample collected at each depth

Depth (m)	T 1200	T 2400	FS 1200	FS 2400
0	19.5%	5.8%	9.7%	19.3%
1	25.5	26.1	9.1	19.9
2	19.0	20.5	36.5	43.0
3	6.0	8.3	21.9	11.3
4	2.5	10.1	22.8	6.5
5	7.1	9.6		
6	7.3	4.4		
7	3.4	4.8		
8	4.0	5.2		
9	5.7	5.2		
Total %	100.0	100.0	100.0	100.0

H_0: The percent of the total sample found at each depth is the same at 1200 and 2400.

Tender $x^2 = 43.48$ ($P < 0.001$)

Forest Service $x^2 = 69.27$ ($P < 0.001$)

H_0: The vertical distribution in Tender Bog is homogeneous.

1200 $x^2 = 947.9$ ($P < 0.001$)

2400 $x^2 = 301.8$ ($P < 0.001$)

H_0: The vertical distribution in Forest Service Bog is homogeneous.

1200 $x^2 = 64.3$ ($P < 0.001$)

2400 $x^2 = 63.3$ ($P < 0.001$)

Table V. Percent of each Schindler Sample that is Fourth Instar

TENDER BOG

depth (m)	1200	2400
0	0.4%	15.9%
1	10.5	9.1
2	3.1	4.5
3	10.1	8.8
4	12.7	2.9
5	3.5	3.1
6	5.9	9.1
7	3.3	30.7
8	2.2	6.3
9	4.0	4.3

FOREST SERVICE BOG

depth (m)	1200	2400
0	2.2%	6.9%
1	7.0	14.5
2	1.2	3.1
3	1.0	3.4
4	0.9	2.9

Table VI. Mean Numbers Collected per Sample Date

TENDER - Mean Number of *C. americanus* individuals per m^3, adjusted for net efficiency

Instar / Date	2	3	4
6/17	1510.9	6.3	105.5
6/24	1380.8	23.0	144.8
7/1	1453.6	55.8	147.3
7/9	595.3	106.7	91.7
7/15	130.2	315.6	38.6.7
TOTAL	5070.8	507.4	527.9

FOREST SERVICE - Mean Number of individuals per m^3, adjusted for net efficiency

	C. americanus			*C. trivittatus*
Instar / Date	2	3	4	
6/17	1191.1	2235.7	91.1	190.7
6/24	385.7	2183.9	125.0	263.6
7/01	107.1	2120.4	81.1	127.1
7/09	39.3	1793.9	190.4	227.1
7/15	13.2	1332.1	172.5	136.4
TOTAL	1736.4	9666.0	660.1	944.9

Table VIIa. Biomass Calculations by Instar

Tender 2nd	*$y^2 = \{20.39\ (x) + 0.04\}^2$
Tender 3rd	$y^2 = \{25.32\ (x) + 0.51\}^2$
Tender 4th	$y^2 = \{37.89\ (x) + 4.98\}^2$
Forest Service 2nd	used Tender regression
Forest Service 3rd	used Tender regression
Forest Service 4th	$y^2 = \{41.40\ (x) + 6.90\}^2$

Table VIIb. Biomass in Micrograms

Instar	2nd	3rd	4th
TB	13.53 ± 0.94	43.98 ± 6.68	339.61 ± 73.95
FSB	14.08 ± 1.92	56.20 ± 5.41	256.08 ± 35.87

*y in $(\text{micrograms})^{1/2}$

Table VIII. Production Calculated by the Size Frequency Method

TENDER BOG

Inst	# indiv	#/m^3	indiv W*	B	dN/dt	W	W(dN/dt)	*3SC**	Total
2	3245	1020	13.53	13800.6					
					918	28.8	26438.4	79315.2	
3	325	106	43.98	4486.0					
					-4	191.8	-767.2	(-2301.5)$	187311.2
4	338	106	339.61	35998.7					
					106	339.6	35998.7	107996.0	

Production for *C. americanus* in Tender Bog = 187.3 mg/m^3/yr.

FOREST SERVICE BOG

Inst	#indiv	#/m^3	indiv W	B	dN/dt	W	W(dN/dt)	*3SC	Total
2	486	342	14.08	4815.4					
					-1564	35.1	-54896.4	(-164689.2)	
3	2707	1906	56.20	107117.2					
					1776	156.1	277233.6	831700.8	931572.0
4	185	130	256.08	33290.4					
					130	256.1	33290.4	99871.2	

Production for *C. americanus* in Forest Service Bog = 931.6 mg/m^3/yr.

* All biomass measurements in micrograms.
** Multiplied by 3 size classes
$ Negative values in parentheses were not included in the production value, since the number of larvae at one instar was smaller than the number at the next instar (see text)

GROWTH RATES (ln W_t/W_{t-1})

Tender	2nd-3rd instar	1.17	Forest Service	2nd-3rd instar	1.38
	3rd-4th instar	2.04		3rd-4th instar	1.52