BENTHIC AND LIMNETIC DISTRIBUTION OF THREE *CHAOBORUS* SPECIES IN A SOUTHERN MICHIGAN LAKE (DIPTERA, CHAOBORIDAE)

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ABSTRACT

The benthic and limnetic distributions, and size-frequency, of the overwintered larval populations of three *Chaoborus* species, *C. punctipennis* (Say), *C. albatus* Johnson, and *C. flavicans* (Meigen) in Frains Lake, Michigan, were investigated on three dates in May and June 1965. The three species made up 91, 3, and 6% of the *Chaoborus* fauna. Little overlap in total length was found between species. *C. flavicans* tended to be concentrated in deeper benthic zones during the day than *C. punctipennis*. *C. albatus*, but not the other two species, underwent an adlittoral benthic migration. All three species migrated into the limnetic zone at night, but none reached the surface. Most limnetic *C. punctipennis* larvae were found higher in the water column than *C. flavicans* larvae.

The larvae of *C. albatus* were stunted, showed late growth, and may have been unable to avoid competition with larvae of the closely related *C. punctipennis*. Differences in distribution and morphology between *C. flavicans* and *C. punctipennis*, although slight, help to explain the apparent lack of competitive exclusion in this genus.

INTRODUCTION

The major features of the ecology of *Chaoborus* larvae and pupae are well known. In most lakes, including the one discussed below, *Chaoborus* is benthic during the day and planktonic at night (e.g., Juday 1921; Eggleton 1932; Berg 1937). In some—chiefly meromictic—lakes, *Chaoborus* larvae are continuously planktonic, migrating from the deep water to or near the surface at night (Hunt 1958; Northcote 1964). The four larval instars differ in their migratory behavior, as was shown in detail recently by Teraguchi and Northcote (1966). Many lakes contain more than one *Chaoborus* species, and Stahl (1966*a*) examined the association of *C. punctipennis* and *C. flavicans* in Myers Lake, Indiana; he was unable to find important differences in the spatial or temporal occupation of that habitat. This study includes information on the benthic and limnetic distribution of the larvae and pupae of three *Chaoborus* species, *C.* (*Sayomyia*) *punctipennis* (Say), *C.* (*S.*) *albatus* Johnson, and *C.* (*Chaoborus*) *flavicans* (Meigen), in Frains Lake, Michigan, during May and June 1965.

Dr. G. W. Saunders, Department of Zoology, University of Michigan, made available the field gear and also provided unpublished data on the morphometry of Frains Lake. His advice has been valuable throughout the study. My best thanks go to K. Roth and J. Low, who assisted with the fieldwork.

THE LAKE

Frains Lake is a small seepage lake located in Washtenaw County, 10 km east of Ann Arbor, Michigan. The major features of Frains Lake morphometry are: maximum depth 9.5 m, mean depth 3.43 m, area 8.3 ha. The lake is dimictic and the bottom waters are anaerobic in summer and in winter. Total alkalinity of the water is around 140 mg/liter. The lake was surveyed in 1940 by the Institute for Fisheries Research, Michigan Department of Conservation, from whom a bathymetric chart is available.

Although a complete overturn occurred in spring 1965 (Saunders, personal communication), the lake was already anaerobic below 7 m by 6 May; on 11 June oxygen was absent below 5 m (Fig. 1).

METHODS

Benthic larvae were collected with a 15.2-cm Ekman dredge, screened in the field through a 0.5-mm screen, sorted in

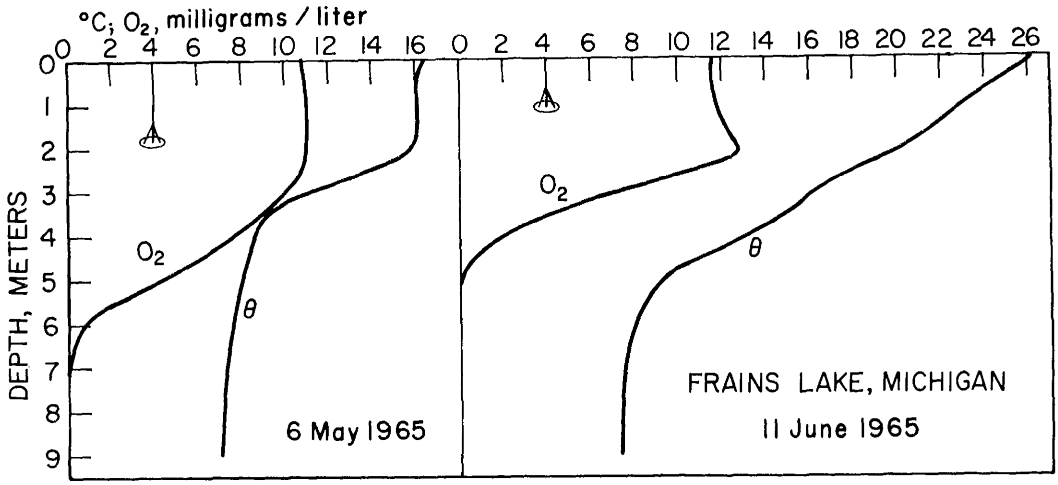

FIG. 1. Vertical distribution of temperature and dissolved oxygen and the Secchi disc limit of visibility in Frains Lake on 6 May and 11 June 1965.

the laboratory, and preserved in Kahle's fluid. Each benthos sampling series consisted of triplicate samples from each of the following depths: 5, 7, and 9 m; and a single sample from 3 m. A 10-liter Juday plankton trap operated from a small crane was used to collect planktonic larvae. The trap was equipped with a No. 10 bolting cloth net and bucket. Plankton samples were taken from a buoy site near the lake's maximum depression. In each sampling series, triplicate trap hauls were made at each meter of depth from the surface to 8 m. It was assumed that nocturnal avoidance of the trap by *Chaoborus* is governed more by the turbulence the trap creates as it descends than by the sight of the trap, so closure was delayed for a few seconds after the selected depth was reached. Plankton samples were preserved with formalin. The samples were sorted and examined in the laboratory, and each larva and pupa was identified, counted, and its total length measured to the nearest 0.5 mm. Measurements were made of preserved larvae, using a dissection microscope equipped with an ocular micrometer. Over 7,000 larvae were examined.

The data were gathered on three dates in late spring 1965. The benthos was sampled at midday on 6–7 May, and plankton samples were obtained every 4 hr during the day and every 2 hr at night, from noon until noon. In addition, a midnight benthos sample (three dredges) was taken at 9 m. The time required to secure each complete plankton series of 27 trap hauls was about 45 min. Benthos was sampled again on 4 June. On 11–12 June, benthos was sampled, and the plankton was sampled hourly from 1800 to 2200 hours, and every 2 hr thereafter until 0600. Midnight benthos samples were again taken at 9 m. Each plankton series on that date took only about 25 min, since a second bucket was used on the trap.

RESULTS

All *C. flavicans* and *C. albatus* larvae collected in May were in the fourth (final) larval stadium. *C. punctipennis* larvae were both third and fourth instars, indicating that some of them had overwintered in the third stadium. A few first and second instar larvae were found in the plankton on 11–12 June; these were not counted. The results therefore apply only to the overwintered populations. Larval instars were determined by a study of larval head length, and the degree of development of the compound eyes and appendages of the head.

Benthic distribution

Population sizes were estimated by taking the product of larval density in each

TABLE 1. *Total* Chaoborus *populations in Frains Lake, in millions, and per cent species composition on three dates in 1965. Estimates based on midday dredge samples*

Date	*C. punctipennis* III	*C. punctipennis* IV	*C. flavicans* IV	*C. albatus* IV
6 May	9.2 (3.4%)	239.3 (88.0%)	16.5 (6.1%)	6.7 (2.5%)
4 Jun	3.0 (1.5%)	175.7* (89.9%)	7.6 (3.9%)	9.1 (4.6%)
11 Jun	0.0 (0.0%)	145.4* (91.8%)	8.1 (5.1%)	4.8 (3.1%)

* Including recruitment from molted third instar larvae.

depth zone and the area of that zone. The lake contained about 272 × 10^6 larvae on 6 May, of which 91% were *C. punctipennis* (88% instar IV, 3% instar III), 3% *C. albatus*, and 6% *C. flavicans* (Table 1). Because no pupae or pupating larvae were found then, these figures reflect the overwintering species proportion. Two-thirds of the third instar *C. punctipennis* larvae molted between 6 May and 4 June, and the remainder had molted by 11 June. Populations of *C. punctipennis* and *C. flavicans* diminished by 27 and 54%, but the *C. albatus* population did not diminish between 6 May and 4 June. Therefore, losses to the larvae of the first two species probably resulted largely from pupation and not from larval mortality. Other workers (e.g., Borutsky 1939) have also found vernal *Chaoborus* mortality to be slight. However, the possibility remains that these losses resulted from size-specific fish predation, since *C. albatus* is smaller than the other two species. Size-selective feeding by fishes was demonstrated recently by Galbraith (1967). *C. albatus* apparently began pupating during the week following 4 June; during the same period the *C. punctipennis* population continued to decrease, but pupation of *C. flavicans* was apparently halted.

There was no difference in lengths of larvae collected from different depths, so all benthic larvae from each date are considered together. The three species showed little overlap in total length (Fig. 2); Stahl (1966*a*) also found little or no overlap between the lengths of *C. punctipennis* and *C. flavicans* in winter and spring. The mean larval lengths (vertical arrows in Fig. 2) on 6 May were: *C. punctipennis* III, 6.29 mm; *C. albatus* IV, 7.77 mm; *C. punctipennis* IV, 9.15 mm; and *C. flavicans* IV, 11.57 mm. Hutchinson (1959) speculated that a size difference of about 130% is necessary to permit two species to cooccur in different niches but at the same level of a food web. The ratios on 6 May were 1.23, 1.23, and 1.26, respectively. That the mean length of fourth instar *C. albatus* larvae was midway between the means of third and fourth instar *C. punctipennis* probably indicates poor growth of *C. albatus*, and not character displacement (Brown and Wilson 1956), for two reasons. First, head lengths of the last instar *C. albatus* and *C. punctipennis* from Frains Lake overlapped broadly; and second, a few *C. albatus* larvae as long as 10.0 mm were found (Fig. 2). Larvae of *C. albatus* are 10–20% longer in Munro Lake, where that species dominates the *Chaoborus* fauna (Roth 1967).

The *Chaoborus* larvae from Frains Lake increased in length during the study period, but not all three species grew at the same time (Fig. 2). Borutsky (1939) found that about one-ninth of the *Chaoborus* biomass in Lake Beloye was added in spring before pupation. Last instar *C. punctipennis* larvae gained 0.51 mm in mean length and those of *C. flavicans* gained 0.42 mm between 6 May and 4 June; *C. albatus* did not change then (–0.09 mm). During the following week, however, the latter gained 0.39 mm, while the other two species decreased in mean length (*C. punctipennis* –0.15 mm, *C. flavicans* –0.21 mm). The diminution in mean length of *C. punctipennis* reflects recruitment from molted third instar larvae, as well as pupation of fourth instars. The *C. flavicans* decrease probably indicates that the early spring hatch of adults does not involve the entire overwintering stock, as was suggested by the larval population estimates for this species. *C. punctipennis*

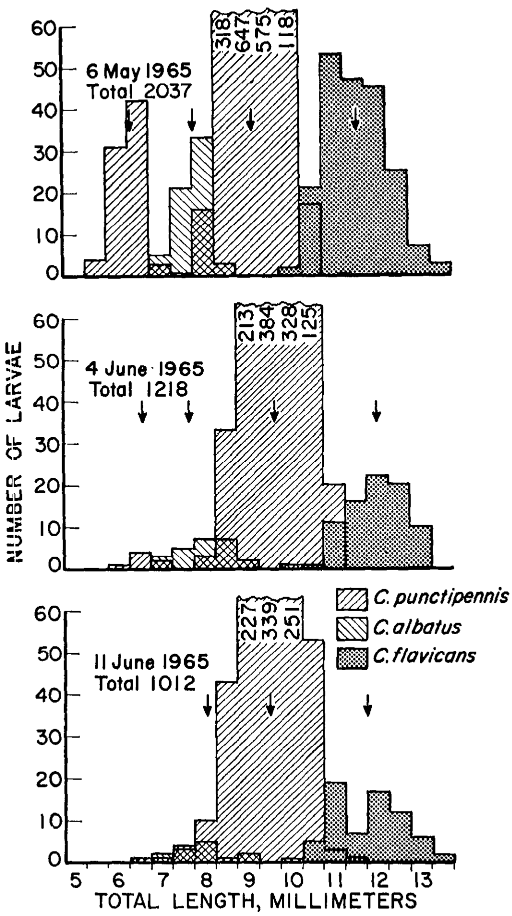

FIG. 2. Length-frequency histograms of Frains Lake *Chaoborus* larvae, based on midday benthic samples collected on three dates in 1965. Vertical arrows represent mean lengths for each species and instar.

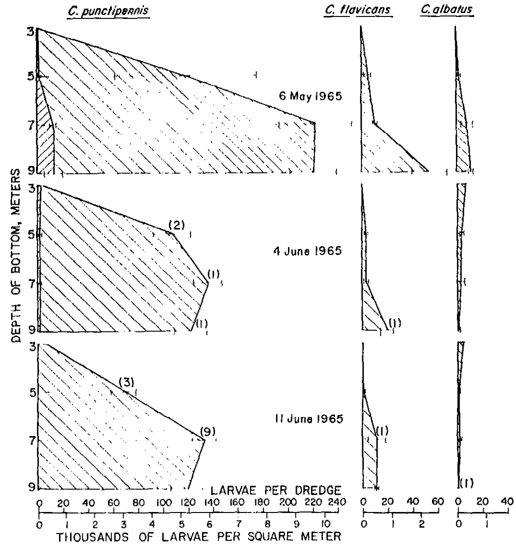

FIG. 3. Bathymetric distribution of midday benthic *Chaoborus* larvae and pupae in Frains Lake on three dates in 1965. Hatches rising to the left: instar IV larvae. Hatches rising to the right: instar III larvae. Horizontal bars show the standard deviations between triplicate dredge samples. Numbers in parentheses represent the total number of pupae in three dredges.

larvae as small as 9.0 mm, and *C. flavicans* larvae as small as 10.5 mm were found to be pupating.

Larval densities were highest in the deepest benthic zone in May (Fig. 3), but since this zone is relatively small, it did not always contain the largest segment of the populations. About 85% of the *C. punctipennis* population was located in the 4–6- and 6–8-m zones on all three dates sampled (Table 2). *C. flavicans* tended to be concentrated deeper, 62–93% of its population occurring in the 6–8- and 8–9.5-m zones on the three dates. Almost half of the *C. flavicans* population was found in the deepest zone on 6 May. The *C. albatus* population was concentrated in the deep-water zones in May, but in June 60% of the larvae of this species were found in the shallowest (2–4 m) zone. This adlittoral shift may be the shoreward benthic migration observed by Borutsky (1939) and Wood (1956). Borutsky supposed that such migrations are temperature-related, pupation being favored in the shallower (and therefore warmer) zone. Since the spring growth of *C. albatus* in Frains Lake occurred after the apparent shift, the movement may also have been related to larval food. The movement of *C. albatus* larvae could have been an artifact of sampling variability, since numbers of *C. albatus* collected were small, and since only single samples were taken at the critical 3-m depth. However, the agreement between the data collected on the two dates in June argues for the reality of the migration. Apparently neither *C. punctipennis* nor *C. flavicans* underwent an adlittoral migration, although the density of the latter increased at 7 m between 4 and 11 June

TABLE 2. *Percentages of the total populations of each of three* Chaoborus *species found in four Frains Lake benthic zones on three dates in May and June 1965*

Depth of zone (m)	Area of zone (ha)	*C. punctipennis*			*C. flavicans*			*C. albatus*		
		6 May	4 Jun	11 Jun	6 May	4 Jun	11 Jun	6 May	4 Jun	11 Jun
2–4	1.73	0.2	2.9	3.1	0.0	0.0	0.0	0.0	57.7	61.2
4–6	1.80	37.6	47.7	37.3	22.0	37.4	6.4	15.3	28.6	15.9
6–8	1.18	48.3	39.3	47.7	30.9	24.6	75.0	60.2	13.1	20.8
8–9.5	0.34	13.8	10.1	11.9	47.1	38.0	18.6	24.5	0.5	2.0

(Fig. 3), so that 75% of its population was found in the 6–8-m zone on the later date.

Pupae found in the bottom samples (Fig. 3) were not concentrated near shore, as might be expected from Borutsky's observations. However, pupae probably are not sampled from the sediments with the same efficiency as larvae. Workers who have used emergence traps have found that most of the adults emerge nearer to shore than where either larvae or pupae are concentrated in the sediments (Borutsky 1939; Lindquist and Deonier 1942).

Limnetic distribution

No fourth instar larvae were found in the free water during the day (Fig. 4). A few third instar *C. punctipennis* larvae were found near the bottom before sundown, but most of these were also in the sediments then. The nocturnal migration began around sundown on both dates sampled. Total limnetic catches at different times of the night varied considerably, the maximum catch for most larval categories occurring at 0400. Such variations probably do not reflect true changes in planktonic numbers, but rather technical errors and changes in success of the larvae at avoiding the trap. The night's feeding apparently renders the larvae less adept at trap avoidance.

Frains Lake *Chaoborus* did not reach the surface in their vertical migration (Fig. 5). Most larvae were found at 3–4 m during the night, and no larva was found within a meter of the surface. During the night of 6–7 May there was a difference in the vertical strata at which the maximum number of larvae of each species was found. The maximum for instar III *C. punctipennis* usually occurred about a meter above that of the last instar, and the latter were usually about that far above the larvae of *C. flavicans*. Too few *C. albatus* larvae were found to permit conclusions about its distribution. Such differences in vertical distribution were less well marked on 11–12 June, although then larvae of *C. flavicans* entered the water column later than those of *C. punctipennis*. Limnetic pupae of all three species were present on 11–12 June, but no pupa was collected above 3 m (Fig. 5).

No difference could be found in the lengths of planktonic larvae collected from different depths. The length-frequency of planktonic larvae unfortunately could not be compared directly with those from the sediments since different preservatives were used on the two categories. However, comparison of the lengths of benthic larvae collected at night with those found there during daylight showed no difference.

Estimates of *Chaoborus* population den-

TABLE 3. *Per cent efficiency of midday dredge samples to estimate the densities of* Chaoborus *populations collected at midnight from both free water and sediment in Frains Lake during 1965.* ([*day benthos/total night*] × *100*)

Date	*C. punctipennis* III	*C. punctipennis* IV	*C. flavicans* IV	*C. albatus* IV	Pupae
6–7 May	37.1	58.6	127.3	104.2	—
11–12 Jun	—	76.8	69.2	7.7	6.2

TABLE 4. *Per cent participation in nocturnal migration of* Chaoborus *in Frains Lake during 1965.* ([*night plankton/total night*] × *100*)

Date	*C. punctipennis* III	*C. punctipennis* IV	*C. flavicans* IV	*C. albatus* IV	Pupae
6–7 May	34.0	49.5	81.6	11.7	—
11–12 Jun	—	40.1	62.3	53.6	100.0

sity based on midday dredge samples (when no larvae could be collected from the plankton) were smaller than the totals that could be collected at night with both trap and dredge (Table 3). This phenomenon could mean either that 1) the benthic larvae are better able to escape the dredge during daylight; or 2) the night-limnetic part of the larval population is located just above the mud–water interface during the day, and so is not sampled by either trap or dredge. The second alternative seems unlikely, in view of Berg's (1938) observations with the stratification bottom sampler in Esrom Lake, where most of the larvae were in, and not above, the sediments. However, as noted previously, there is considerable variation in the behavior of larvae found in different localities. Fewer *C. punctipennis* larvae, but more of *C. flavicans,* were collected during daylight than at night on 6–7 May, when no larvae were pupating. *C. albatus* was sampled with equal efficiency at either time on that date. On 11–12 June, when some of all three species were pupating, the day–night discrepancy for *C. punctipennis* was smaller than before, but night samples were again more effective than day samples. *C. flavicans* on that date was also better sampled at night—the reverse of the situation in May. Too few *C. albatus* larvae and pupae were collected on 11–12 June to permit conclusions. If the first alternative correctly explains the day–night discrepancy, the reversal shown by *C. flavicans* could be caused by changes in the depth within the mud that the larvae occupy. Both light and turbulence, the most obvious dredge-avoidance factors, would be less important deeper in the ooze. This explanation agrees with Berg's observation that *C. flavicans* larvae were found in the contact layer only while pupae were present.

Half of the mature *C. punctipennis* larvae, and 80% of the *C. flavicans* larvae participated in the nocturnal limnetic migration in May (Table 4), suggesting that at that time most *C. punctipennis* larvae migrated every other night and that at least some *C. flavicans* larvae became limnetic every night. Fewer of both species migrated in June. Numbers of *C. albatus* larvae collected are insignificant. Pupae were apparently absent from the sediments at night, indicating that pupae migrate every night. Maximum limnetic catches (collected at 0400) and night benthic samples were used in the calculation of per cent participation.

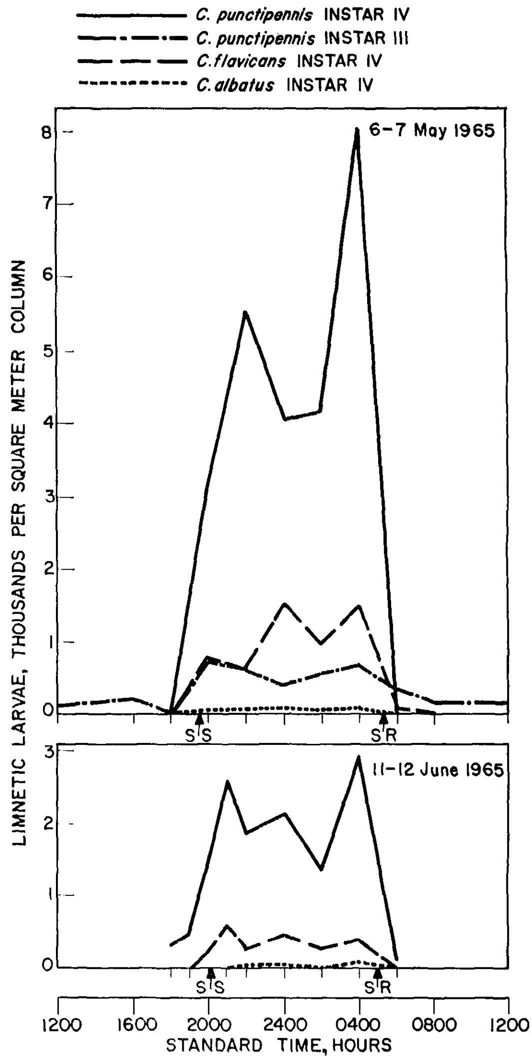

FIG. 4. Numbers of limnetic *Chaoborus* larvae per square meter column (0–8 m) in Frains Lake at various times of the day and night, 6–7 May and 11–12 June 1965. SS = sunset; SR = sunrise.

DISCUSSION

The occurrence of the larvae of more than one *Chaoborus* species in the same

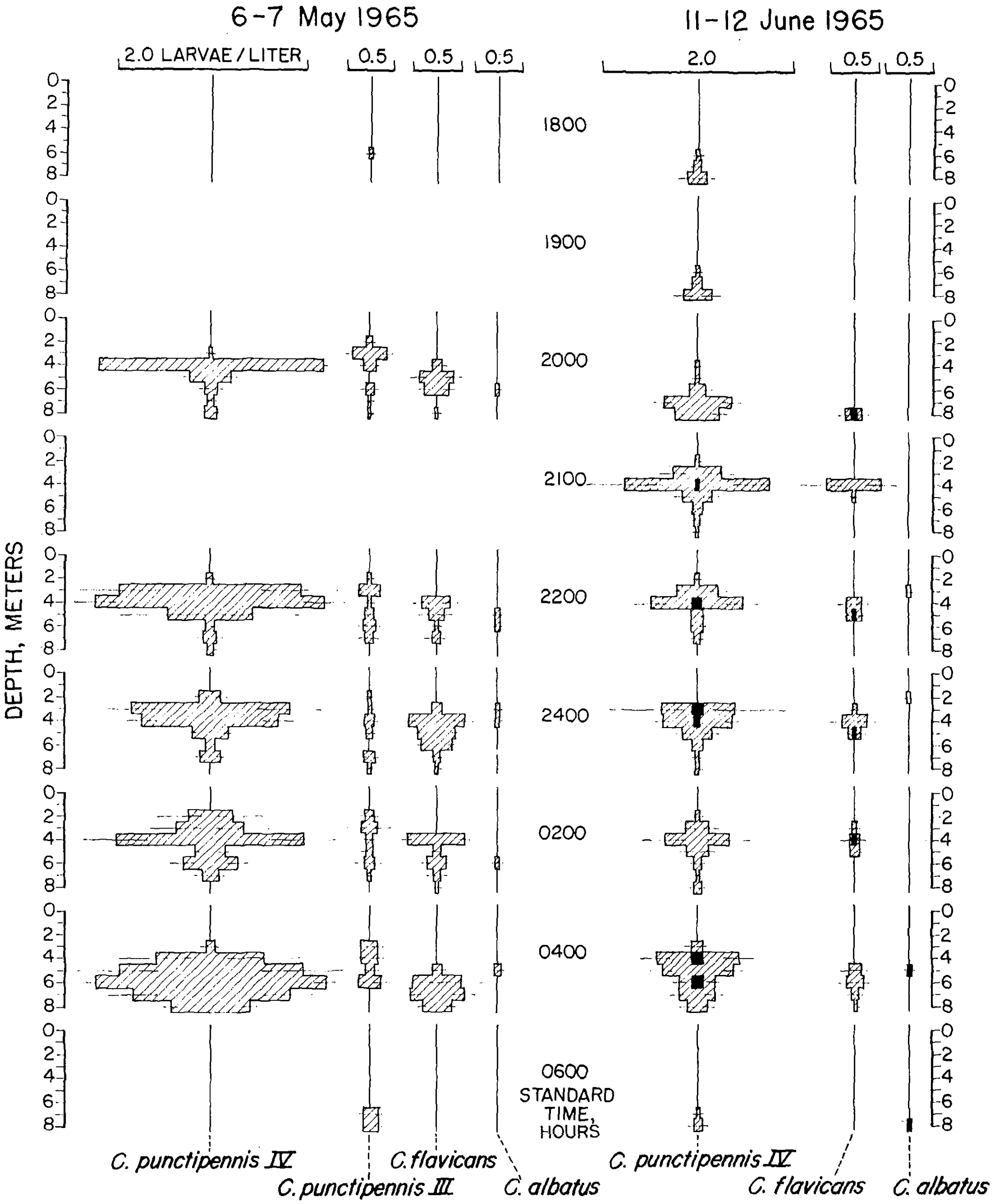

FIG. 5. Bathymetric distribution of limnetic *Chaoborus* larvae and pupae in Frains Lake at various times of the night, 6–7 May and 11–12 June 1965. Horizontal bars show the standard deviations between triplicate trap samples. Hatched areas = larvae; solid areas = pupae.

body of water presents a problem in interspecific competition. Such cooccurrences are frequent enough to suggest that competitive exclusion does not happen (Stahl 1966*b*), although this could be an illusion created by frequent reinoculation from nearby waters (Roth 1967). If, however, the observed species associations are actually long-enduring, one expects the cohabiting species to have somewhat different biologies. Stahl (1966*b*) has developed the point of view that the larvae of the various *Chaoborus* species are ecological equivalents; he is then forced to assume that when such species occur together they are not resource-limited. Because it is theoretically unlikely that any two species have identical requirements (*see* Hardin 1960), it is proper to look more closely at their association in search of properties not in common between them. When differences are found, it is not always easy to decide whether they are important enough to guarantee niche differentiation.

C. albatus is morphologically very similar to its consubgener, *C. punctipennis,* and it may be that despite the tendency of *C. albatus* to exploit the shallow parts of the lake in spring it is unable to avoid competition with *C. punctipennis.* The stunted size of *C. albatus* in Frains Lake, as well as its relative rarity and late growth all suggest that this species is an unstable member of the lake's *Chaoborus* fauna. *C. albatus* is apparently more successful in unstratified lakes of small to moderate size, where it frequently dominates *C. punctipennis* or is the only *Chaoborus* species (e.g., Roth 1967; Stahl 1966*b*; Woodmansee and Grantham 1961).

C. flavicans in Frains Lake appears more successful than *C. albatus* at avoiding competition with *C. punctipennis. C. flavicans* tended to be concentrated in deeper benthic zones, occupied a deeper stratum during nocturnal migration, and migrated more frequently than *C. punctipennis.* Furthermore, the two species belong to different subgenera, and their feeding organs differ both in size and form (experiments are clearly needed to determine the significance of this last fact).

Chaoborus species ecology requires studies of greater refinement. However, the interspecific differences shown here, while slight, suggest that the problem of cooccurrence in this genus can be explained without postulating identical niches in benign environments.

REFERENCES

BERG, K. 1937. Contributions to the biology of *Corethra* Meigen (*Chaoborus* Lichtenstein). Kgl. Danske Videnskab. Selskab, Biol. Medd., **13**(11): 1–101.

———. 1938. Studies on the bottom animals of Esrom Lake. Kgl. Danske Videnskab. Selskab, **9**(11): 1–255.

BORUTSKY, E. V. 1939. Dynamics of the total benthic biomass in the profundal of Lake Beloye. [Transl. from Russian.] Works Limnol. Sta. Kossino, **22**: 196–218.

BROWN, W. L., JR., AND E. O. WILSON. 1956. Character displacement. Syst. Zool., **5**: 49–64.

EGGLETON, F. E. 1932. Limnetic distribution and migration of *Corethra* larvae in two Michigan lakes. Papers Mich. Acad. Sci., **15**: 361–388.

GALBRAITH, M. G., JR. 1967. Size selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fisheries Soc., **96**: 1–10.

HARDIN, G. 1960. The competitive exclusion principle. Science, **131**: 1291–1297.

HUNT, B. P. 1958. Limnetic distribution of *Chaoborus* larvae in a deep Florida lake (Diptera). Florida Entomologist, **41**: 111–116.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Naturalist, **93**: 145–159.

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

LINDQUIST, A. W., AND C. C. DEONIER. 1942. Emergence habits of the Clear Lake gnat. J. Kansas Entomol. Soc., **15**: 109–120.

NORTHCOTE, T. G. 1964. Use of a high-frequency echo sounder to record distribution and migration of *Chaoborus* larvae. Limnol. Oceanog., **9**: 87–91.

ROTH, J. C. 1967. Notes on *Chaoborus* species from the Douglas Lake region, Michigan, with a key to their larvae (Diptera: Chaoboridae). Papers Mich. Acad. Sci., **52**: 63–68.

STAHL, J. B. 1966*a*. The ecology of *Chaoborus* in Myers Lake, Indiana. Limnol. Oceanog., **11**: 177–183.

———. 1966*b*. Coexistence in *Chaoborus* and its ecological significance. Invest. Indiana Lakes Streams, **7**: 99–113.

TERAGUCHI, M., AND T. G. NORTHCOTE. 1966. Vertical distribution and migration of *Chaoborus flavicans* larvae in Corbett Lake, British Columbia. Limnol. Oceanog., **11**: 164–176.

WOOD, K. G. 1956. Ecology of *Chaoborus* (Diptera: Culicidae) in an Ontario lake. Ecology, **37**: 639–643.

WOODMANSEE, R. A., AND B. J. GRANTHAM. 1961. Diel vertical migrations of two zooplankters (*Mesocyclops* and *Chaoborus*) in a Mississippi lake. Ecology, **42**: 619–628.