

**Distribution and feeding habits of a tropical
Chaoborus population¹**

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With 5 figures and 1 table in the text

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Introduction

The genus *Chaoborus* occupies a rather unique position in plankton communities, as it contains the only large nonpiscine carnivore species using the plankton as a principal food source. The wide distribution of the genus is testimony to its great ecological success. Several early limnologists focused their attentions on *Chaoborus* at some time in their careers (e.g. JUDAY 1921; BERG 1937). More recently, investigators have confirmed the ecological importance of *Chaoborus* in numerous field studies and have begun to specify behavioral patterns and population dynamics of particular species in a variety of waterbodies.

Although most of the studies deal with temperate-zone populations, it is becoming increasingly clear that *Chaoborus* is also an important element of tropical plankton communities (WORTHINGTON & RICARDO 1936; RUTTNER 1952; BURGIS 1971; CRESSA 1971; GREEN 1972). The ecological role of *Chaoborus* in tropical lakes is undoubtedly similar in many respects to corresponding temperate populations, but the latitudinal differences, principally the reduced seasonality of the tropics, can be expected to alter the ecological strategies of the populations in a number of ways that might provide a new perspective on the ecology of temperate populations.

This paper deals with the vertical distribution, horizontal distribution, and feeding habits of the *Chaoborus* population in Lake Lanao, Philippines. Lake Lanao is a large and rather deep lake (Fig. 1, 2) located in the southern Philippines (8° N, 124° E). The physical features of the lake are given by FREY (1969) and the seasonal cycle by LEWIS (1973). The *Chaoborus* population was first reported by FREY, who noted an extensive vertical migration in Lake Lanao. *Chaoborus* was not reported in the first limnological samples of the lake (WOLTERECK 1941), but this is not surprising since the Wallacea expedition samples of Lanao were quite limited. It seems likely that *Chaoborus* is a well-established element of the Lake Lanao plankton.

Methods

The data reported in this paper were taken during 1970—71 as part of a weekly measurement regimen for physico-chemical variables, phytoplankton, primary production, and zooplankton on Lake Lanao. The zooplankton data, from which the following information on *Chaoborus* is drawn, include (1) a weekly vertical series taken at an index station (station 1), (2) a weekly series of 3 vertical tows taken at the same time as the vertical series at the index station and at another station 1 km distant, (3) monthly transect studies including triplicate tows at 10 different locations on the lake, and (4) irregularly timed special sampling programs to test particular hypotheses con-

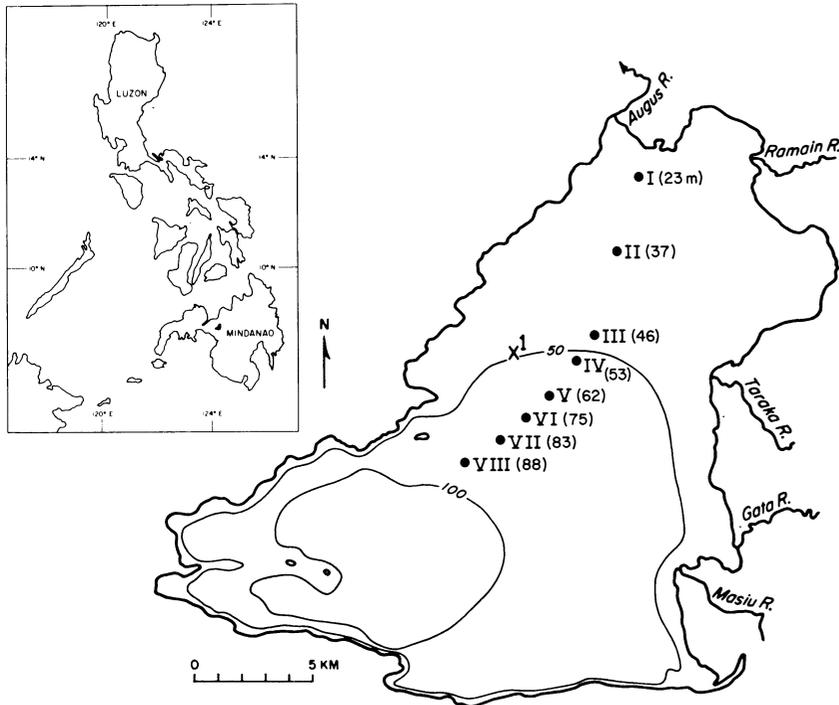


Fig. 1. A map of Lake Lanao showing 50- and 100-m contours (as determined by FREY 1969) and the sampling stations.

cerning the distribution of zooplankton. The following is not a comprehensive analysis but merely draws on the data sufficiently to elucidate some aspects of the distribution and feeding habits of the *Chaoborus* population.

The vertical series was always taken with a self-closing, transparent trap of the type described by SCHINDLER (1969). The capacity of the trap is 45.3 l. The samples were always taken at 5-m increments from 0 to 45 m at station 1, where the water is 46 m deep. Vertical tows were taken with a CLARKE-BUMPUS sampler that was recalibrated on each sampling date. Daytime samples were always taken between 09.30 and 11.30, and night samples between 19.00 and 20.00 except as specified.

Census of the samples was always complete for *Chaoborus* — i.e., the samples were not split for counting. All organisms were measured as they were censused. The distance between the midpoints of the segments containing the airbladders was used as the standard measurement. Measurements were made at appropriate magnification to the nearest 0.1 mm, so that the population was split into approximately 50 size categories (0.4—5.3 mm). An allometric relation was established between the standard length and the wet weight of *Chaoborus*. Wet weight was determined first by computing the body volumes from dimensions of organisms of various sizes and then by weighing groups of organisms of a given size after they had been carefully dried on the outside. The two techniques gave agreeing results for the length-weight relation. The relation was rendered linear by log-log transformation, and the resulting regression gave an r value of 0.99. The relation was then converted to dry weight by use of a factor obtained from standard drying of organisms in the laboratory (95 °C, 12 hr). Dry weight proved to be 9.47 % of wet weight. This compares favorably with the average of 8.9 %



Fig. 2. ERTS photograph of Lake Lanao.

obtained by JUDAY (1921) for Lake Mendota *Chaoborus*. The final relation giving dry weight (Y , mg) from standard length (X , mm) is thus

$$\log(Y) = 3.10 \log(X) - 2.71. \quad (1)$$

Feeding habits were determined by dissection of the anterior gut, as described by SWIFT & FEDORENKO (1973). LUGOL's solution, the preservative used in this investigation, did not cause eversion of the gut during preservation.

Taxonomy and general description of the population

Samples of the *Chaoborus* population have been examined by J. B. STAHL, who concludes that there is only one species, and that this species is probably identical with Form 1 of ECKSTEIN (1936). Form 1 was collected by the Sunda Expedition in several Indonesian lakes, although it was not reported from the Philippines. It is unclear at present whether Form 1 requires a new specific name or if it is identical with one of the named species.

The density of the *Chaoborus* population ranged over the study period from 3,800 to 19,000 individuals/m² (29–975 mg/m² dry weight). The population can thus be considered moderately dense by comparison with average temperate zone populations. The seasonal pattern of population composition and density differs greatly from temperate populations, however. There is a slight suppression of development and emergence at the seasonal temperate minimum, but at no time of the year is any size group entirely absent as in temperate lakes.

Some *Chaoborus* populations are primarily planktonic and others primarily benthic. The Lake Lanao population is almost exclusively planktonic but the largest organisms may remain just above or within the sediment during the day under some circumstances.

Vertical distribution and migration

During the daylight hours most of the *Chaoborus* population is found in the deeper water of Lake Lanao. Since the annual average depth of 1% surface light is near 12 m, much of the population spends the day in almost total darkness. This is of course typical behavior for the genus. The details of daytime vertical distribution are, however, of considerable interest.

The data on vertical distribution include sufficiently large numbers of individuals that it is feasible to examine the distribution of various size classes in relation to each other. For this purpose the organisms can be divided into 5 arbitrary size classes extending from 0 to 5 mm (standard length) in increments of 1 mm. A central depth was obtained for each of the 5 size classes on each sampling date by computing the arithmetic mean of depths for all individuals belonging to a given size class. The resulting central depths of the 5 size classes on each sampling date provide a means of comparing differences in vertical distribution with size.

Fig. 3 shows how the daytime central depths of the 5 size classes varied over the year. It is obvious from the figure that the *Chaoborus* population is organized in a definite manner with the smallest organisms nearest to the surface and the larger organisms ranked by size below them. JUDAY (1921) observed that young *Chaoborus*, unlike the older larvae, were more often found in the water column than in the mud of Lake Mendota. A similar trend has been documented by WORTHINGTON & RICARDO (1936) and CRESSA (1971) for tropical African and South American populations. The tendency for smaller organisms to remain nearer the surface during the day has also been documented by numerous others working in the temperate zone, including WOOD (1956), WOODMANSEE & GRANTHAM (1961), TERAGUCHI & NORTHCOTE (1966), MALUEG & HASLER (1967), and FEDORENKO & SWIFT (1972). The great regularity of the size depth distribution observed in Lake Lanao is nevertheless somewhat surprising. In only 7% of the pairwise comparisons of the 5 size classes did a center of depth for larger organisms overlie that for smaller organisms. Even this small deviation must be in part accounted for by sampling error during periods of low abundance for certain size classes.

The centers of depth are rather steady over the year, especially for size classes I and II, in view of the vast changes in chemical conditions below the euphotic zone (Fig. 3 B). It is nevertheless reasonable to attempt an explanation of the observed variation in centers of depth on the basis of concurrent physicochemical data. The oxygen concentration on each date at the annual mean center of depth was therefore compared to the center of depth on each date. The comparison was made separately for each size class by means of the SPEARMAN Rank Correlation Coefficient. No significant correlations were obtained, hence there is no evidence that the weekly variations in the center of depth of any size class are due directly to changes in oxygen content of the water column. A similar test failed to relate center of depth and transparency as determined by photocell on the dates of zooplankton samples. Because considerable data are available, it would appear that there exists no simple relation between either transparency or oxygen and the center of depth of any size class on a given date. It is therefore reasonable to suppose that the precise central location of a size class in the water column is determined by a complex of factors. This is entirely consistent with the findings of BERG (1937), LAROW (1970 b), and others whose work suggests that the basic migratory pattern can be affected by a number of secondary factors.

Summarizing the vertical distribution data by computing a center of depth for each of several size classes has the disadvantage of hiding the dispersion of various size classes. The raw data plainly indicate that smaller organisms are much more dispersed around their center of depth during the day than larger organisms. This trend is illustrated in Fig. 3 C, which shows the numbers of organisms at each of the 10

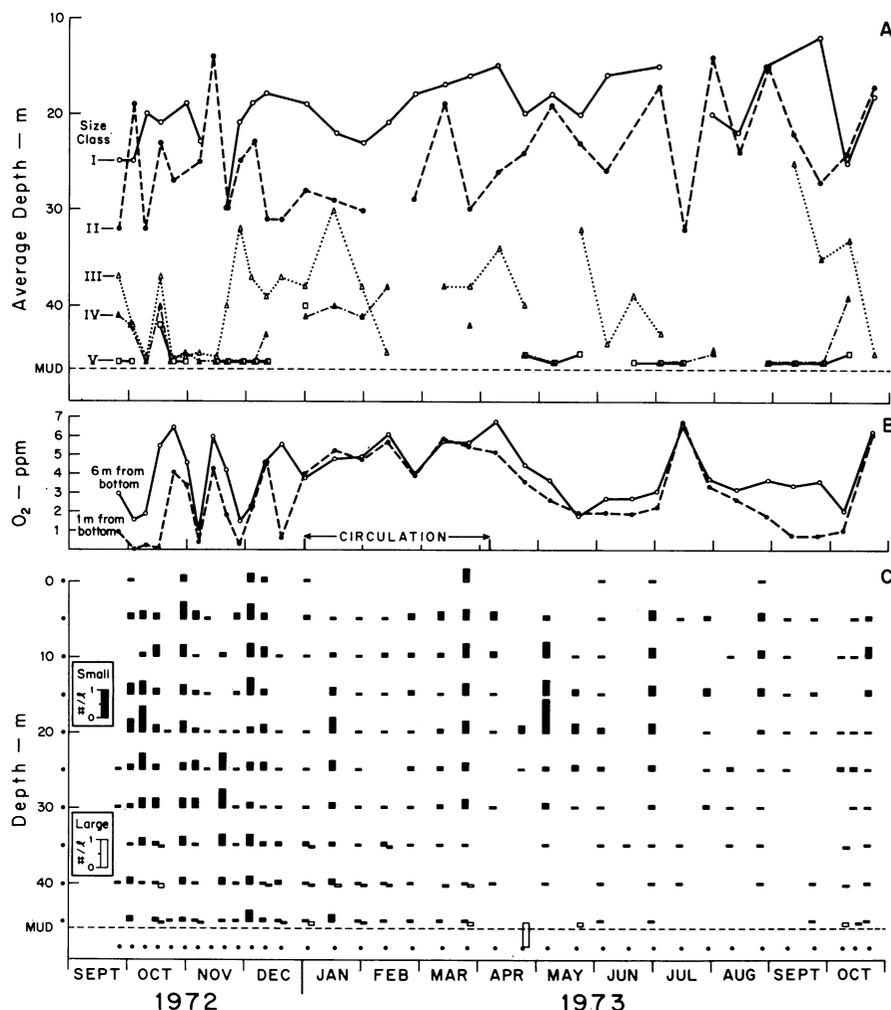


Fig. 3. A. Seasonal variation in the daytime distribution of *Chaoborus* larvae. Five size classes are shown: 0.3–1.0 mm, 1.1–2.0 mm, 2.1–3.0 mm, 3.1–4.0 mm, and 4.1–5.0 mm. Lengths were determined during census as described in text. Breaks in the lines for each size class indicate the absence of any measurable number of organisms for one or more sampling trips. B. Seasonal variation in the oxygen concentration near the bottom of Lake Lanao at station 1. Dashed line indicates oxygen concentration 1 m from sediment; solid line, 5 m from sediment. C. Dispersion of large *Chaoborus* (3.5–5.3 mm) and small *Chaoborus* (0.4–1.5 mm, instar 1) in Lake Lanao over the study period. Height of bars indicates abundance at each of 10 depths in the water column.

sampling depths on each of the daytime sampling dates. For statistical reasons, the size classes are somewhat broader than for the center of depth analysis. For simplicity only two classes of organisms are plotted in the figure. The large *Chaoborus* (3.5–5.3 mm, instar 4 plus larger organisms of instar 3) remain tightly clumped near the bottom at all times of year. The small *Chaoborus* (0.4–1.5 mm, instar 1) are dispersed to a variable degree around a center of depth near the middle of the water column. On

some dates some individuals may even be found at the surface during the day (Fig. 3 C). It is also noteworthy that a few small organisms can be found near the bottom on most dates. Marked clumping of small organisms near the middle of the water column is obvious on some dates but not on others.

The relative dispersion of the small organisms shown in Fig. 3 C was computed for each sampling date as the coefficient of variation in abundance at the 10 sampling depths. Coefficients ranged from 45 to 290 % and averaged 107 %. An attempt was then made to correlate relative dispersion (C.V.) with physicochemical variables. Transparency is not significantly related to dispersion, but dispersion and oxygen concentration at 20 m (near the center of depth) are significantly correlated. The SPEARMAN Rank Correlation Coefficient is 0.67. When oxygen depletion occurs, dispersion of the small organisms is thus significantly less pronounced. It is doubtful that oxygen is the immediate cause for the variation of dispersion, since a few small organisms are found in deep water even during periods of severe oxygen depletion. It is more likely that the correlation is due to a direct relation between dispersion and some other variable, perhaps distribution of food species, which is in turn controlled by oxygen.

Even though the centers of depth and dispersion of various size classes vary from week to week, the rank order of mean depths for various size classes remains highly predictable and is therefore likely to be ecologically significant. It was first hypothesized that the phenomenon might actually reflect the grouping of animals by instar

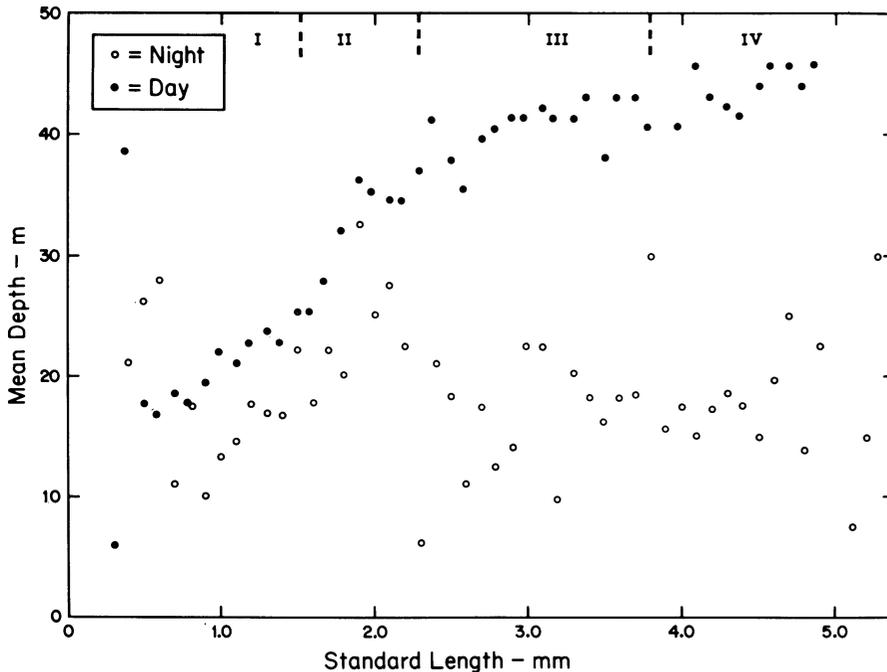


Fig. 4. Centers of depth of *Chaoborus* larvae of various sizes. Organisms were assigned to one of 50 size categories as described in the text, then the annual mean center of depth for each size class was computed. Daytime and night samples were treated separately and are distinguished by solid and hollow data points, respectively. Daytime data include measurements on 2,479 individuals distributed over 47 weekly or biweekly sampling trips. Night data include measurements on 1,361 individuals distributed over 20 biweekly sampling trips. Instar divisions are indicated on the upper abscissa.

rather than by size. The population was consequently split into 50 size groups corresponding to length increments of 0.1 mm and an annual mean center of depth was computed for each of these size groups (Fig. 4). If organisms belonging to a specific instar behave more or less uniformly, one might expect the size groups to be clumped in Fig. 4 according to instar. Fig. 4 instead indicates that mean position in the water column is rather strictly a matter of body size. The association between mean center of depth and body size was tested by SPEARMAN Rank Correlation analysis and proved to be highly significant ($r_s = 0.92$).

At night the *Chaoborus* population moves upward in Lake Lanao, as it does in most other lakes. Large individuals in the deep portion of the lake migrate as much as 80 m. Routine night sampling was conducted at station 1 in 46 m of water 1—2 hours after sunset. The composite data for 20 night samples on different dates are shown in Fig. 4. The loss of depth-size ranking at night due to migration is evident from the figure. Since the upward movement may continue into the night, the night sampling data do not represent such a stable depth distribution as the daytime samples, but is clear from the information at hand that the total distance of migration increases with size.

Some revealing experiments have implicated both light and oxygen as principal cues affecting vertical migration of *Chaoborus* (BERG 1937; TERAGUCHI & NORTHCOTE 1966; LAROW 1970 b). Although there are no experimental data in the present case, there is little reason to doubt that the same cues are also important in Lake Lanao. It is worthwhile to note that the water column at station 1 was uniformly oxygenated between 1 January and 1 April (Fig. 3 B), yet the *Chaoborus* population continued to exhibit vertical migration and the daytime depth-size distribution characteristics that prevailed at other times of the year. Mean extent of migration is not significantly greater during stratification than during circulation.

The ecological factors that account for vertical migration in *Chaoborus* have in general been less fully explored than the physico-chemical cues upon which the migration is based. The strict size-depth ranking of the daytime *Chaoborus* population in Lake Lanao together with the persistence of migration during the 3-month period of uniform oxygenation would seem to limit severely the number of viable hypotheses. Generally accepted explanations for migration principally involve predation and feeding, except for McLAREN's (1963) hypothesis, which is based on the metabolic advantages of the daily change in temperature that accompanies migration. McLAREN's hypothesis is weak for the tropics, because temperature gradients are not great. In Lake Lanao during stratification maximum temperature change that an organism could experience in migration from 5 m to 45 m would be 2.0 °C, and the mean value would be much nearer to 1.0 °C (LEWIS 1973). Although HUTCHINSON (1967) argues that the metabolic benefit may still be significant when the temperature difference is small, it is unquestionably much reduced. Moreover, McLAREN's hypothesis is altogether inapplicable during the 3-month period on Lake Lanao when the lake is essentially uniform in temperature. It thus seems more reasonable to assume that the selective force behind the *Chaoborus* migration is principally related to predation and feeding.

The only significant predators on large planktonic *Chaoborus* in Lake Lanao are pelagic fishes, which include several cyprinid species and *Glossogobius*. Assuming that these fishes feed less efficiently in the dark, it is advantageous for *Chaoborus* to remain in deep water during the daytime. This advantage is probably reinforced by deoxygenation of the deep water, which creates a barrier to pelagic fishes. The size-depth distribution during the day requires additional explanation, since it might seem advantageous for the entire population to seek the lake bottom rather than to be distributed according to size through the water column. Without abandoning the predation hypothesis it is possible to explain this size gradation if some counteracting disadvantage to descent can be found which applies unevenly to the size classes. There are three such explanations. (1) First, the smaller organisms may not be able to withstand some physiological stress connected with descent. This can hardly be a chemical factor, such as deoxygenation, since the center of depth for the young animals remains high even

during the circulation period. The only stress that might be involved is thus pressure. One might think that capacity to make pressure adjustments increases with age, which would account for the increased tendency to descend. This explanation is easily falsified by the data, which show that it is not uncommon for individuals of the smallest size classes to be found in deep water even though the center of depth for the smallest size class is higher than for larger organisms. (2) A second possibility is that small *Chaoborus* respond not only to the predation pressure from fishes, but also to predation pressure from larger *Chaoborus*. This may be a secondary benefit conferred upon smaller organisms by the size-depth distribution, but since the dispersion of smaller size classes is rather great and thus overlaps with the larger classes, other factors must be involved. (3) The third possibility is that the daytime food source for small organisms is nearer the surface than for large organisms. It will be shown in the following section on feeding habits that *Chaoborus* does a substantial amount of daytime feeding. The vertical distribution of food species is known and, although the details cannot be presented here, larger food items are generally deeper during the day. Greater centers of depth for large size classes of *Chaoborus* are thus probably explained ultimately by food distribution. Suitable food items are available near the bottom for large organisms, and large organisms probably need to feed less rapidly to remain satiated. In addition, larger *Chaoborus* are likely to be under greater predation pressure at all times, hence they might derive greater benefit from occupying any refuge from predation.

Emergence patterns

During August, at the time of heavy emergences, it was observed on several occasions that large numbers of *Chaoborus* were emerging at the south end of the lake but not elsewhere. Closer observation showed that almost all of the emergence was occurring within an area bounded by the 60-m contour. An examination of oxygen profiles from a number of sampling stations indicated that at this time, oxygen was present in substantial amounts near the bottom except at depths greater than 60 m. This led to the hypothesis that pupating larvae must be restricted in distribution to those portions of the lake having an anoxic zone over the sediment.

The distribution hypothesis was tested by sampling along a special transect running from the shallow north end of the lake to the deeper south end (Fig. 1). The stations were positioned so that the shallowest (I) was located near the 20-m contour and each of seven successive stations beyond this was located at a point 10 m deeper than its predecessor. The 8 stations thus passed from 20 m to 90 m in increments of 10 m.

The distribution hypothesis was tested on 19–20 August during a period of moderate *Chaoborus* emergence. Three stations along the transect (I, III, VIII) were first sampled during the morning (0.8.30–11.30). The boat was firmly anchored at each station and the exact depth of the water column was determined. Three vertical tows were then taken with a metered net through the water column from a point 1.0 m over the sediment to the surface. At the same time, water samples for oxygen were taken exactly 1.0 and 5.0 m above the sediment. The resulting census data for *Chaoborus* and oxygen data are shown in Fig. 5 A.

At dusk on 19 August a vertical series of samples was taken at station III to illustrate the upward movement of the *Chaoborus* population (Fig. 5 B). Subsequent night sampling along the transect commenced at 20.30 and ended at 02.00. As during the day, triplicate metered tows were taken at each station and oxygen samples were taken at 1 and 5 m above the bottom. Results appear in Fig. 5 C.

Data from replicate samples at the same station were quite low in variability after corrections for filtering efficiency of the net. The mean coefficient of variation (S/\bar{x}) for replicates at a single station is 18.0%. Differences between stations in total standing crop are statistically significant as expected, but the overall variation between means for stations is not remarkably great (C.V. = 54.8%).

The most striking aspect of the data is the variation in distribution of the largest size class, and this bears directly on the distribution hypothesis. The daytime samples

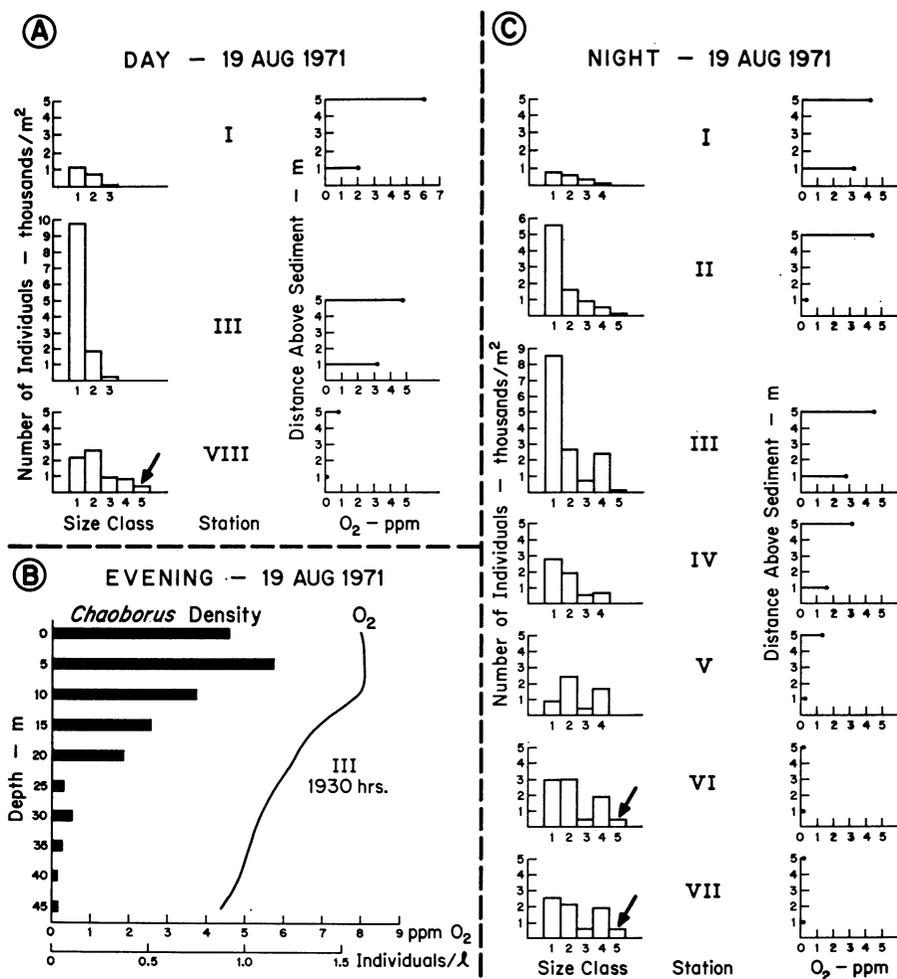


Fig. 5. Horizontal distribution of *Chaoborus* larvae 19 August 1971. A. Size distribution of *Chaoborus* larvae and oxygen 1 m and 5 m above the bottom at stations of shallow, moderate, and great depth. B. Vertical distribution of *Chaoborus* at a station of moderate depth 1.5 hours after sunset on the same date. C. Size distributions and oxygen data at a number of stations sampled between 20.00 and 02.30 on the same night.

reveal the presence of larger organisms only at station VIII, where there is an anoxic water layer over the sediment. It is of course possible that during the day the larger organisms are present at the shallower stations but remain in the mud. At dusk, however, the entire population migrates to the surface. This migration is verified by the vertical series shown in Fig. 5 B and by routine samples adjacent to the superficial sediments that failed to reveal any large, nonmigrating *Chaoborus*. The data obtained on the night of 19 August can thus be considered to represent the entire *Chaoborus* population unless large nonmigrating *Chaoborus* were continuously hidden in the deep sediments at stations I—V. Even this possibility would not explain selective emergence within the 60-m contour unless pupation can be suppressed by oxygenated water.

The night samples clearly show that the largest organisms in the population are present in significant numbers only at those stations where oxygen is severely depleted

near the bottom. This may be related to JUDAY's (1921) observation that Lake Mendota *Chaoborus* were consistently more abundant in deeper water, although he does not give a complete analysis by size class. ROTH (1968) reports no difference in length-frequency of *Chaoborus* at various depths in Frains Lake, Michigan, but the interpretation is complicated by the shallowness of the lake and the marked benthic tendencies of the population. The concentration of larger *Chaoborus* in the deeper water of Lake Lanao explains the observed emergence of adults within the 60-m contour and is consistent with the hypothesis that oxygen controls the horizontal distribution of large *Chaoborus*. At other times of the year, when oxygen depletion occurred over shallower portions of the lake, substantial numbers of large *Chaoborus* were more widely distributed. Obviously some mechanism is required to explain the distinctive distribution of large organisms. There are four possible explanations: (1) the presence of oxygen near the bottom suppresses pupation and causes the largest organisms to hide continuously in the deep sediments; (2) the largest organisms are stimulated to pupate by unavailability of anoxic conditions, and thus quickly disappear from oxygenated areas; (3) the large organisms actively seek deoxygenated water by downslope movement; and, (4) large organisms are eliminated by predation from oxygenated areas. The third possibility seems at present most likely, but conclusive evidence is still lacking.

Feeding habits

Because *Chaoborus* does not macerate its food immediately, gut contents are a highly useful means of approximating food composition. The examination of gut contents of *Chaoborus* from the Lake Lanao samples led to the recovery of food items in various stages of digestion. In some cases, food items were recovered virtually intact, but more often characteristic structural features served as identification. No attempt was made to identify food items in an advanced stage of digestion. Even so, the technique is biased to favor detection of food items most resistant to maceration. Antennal segments and tarsal claws of Cladocera are resistant and easily identified, as are antennae and leg segments in copepodids and adult copepods. Loricated rotifers (*Keratella*) are more residual than soft-bodied forms (*Conochiloides*, *Hexarthra*). The data must be evaluated with these biases in mind. It seems accurate to say that the detection efficiency for all forms was approximately the same except for soft-bodied rotifers and copepod nauplii, which are difficult to identify after maceration.

From a total of 409 dissections, 27.1% of individuals were completely empty, 37.6% contained a small amount of debris residual from an old meal, and the remaining 35.3% contained recently ingested material. Identification of the food items in the

Tab. 1. Composition of food found in the anterior gut of *Chaoborus*. The results are based on the dissection of 408 animals evenly distributed over the 14-month study period and selected without regard to body size. Composition is expressed as the total number of individuals of all food species. Per cent of mean standing crop, also computed in terms of individuals, is indicated on the last line.

	Cladocera			Cyclopoids		Calanoids			Total copepods	<i>Keratella</i>	Other rotifers	<i>Chaoborus</i>
	<i>Diaphanosoma</i>	<i>Bosminopsis</i>	<i>Moina</i>	Total cladocera	Nauplii	Copep + adults	Nauplii	Copep + adults				
Number eaten	37	56	2	95	2	72	0	11	85	24	0	0
% of food	18.1	27.4	1.0	46.6	1.0	35.2	0	5.4	41.7	11.8	0	0
% of standing crop	3.8	1.3	0.4	5.5	54.1	20.9	2.5	3.3	80.8	0.3	11.6	1.0

guts of organisms that had recently eaten was almost always unambiguous due to the small number of zooplankton species in the lake. The composition of the food is summarized in Tab. 1. The data in the table are an average for the 14-month sampling period and therefore include all sizes of *Chaoborus* from a selection of day and night samples. A detailed analysis will be presented elsewhere.

Copepods, principally cyclopoids, comprise the major portion of the standing crop in Lake Lanao, but their abundance is not fully reflected in the diet of *Chaoborus*. The copepodids and adults appear to be selected in preference to nauplii. Nauplii go unnoticed more frequently in the analysis, but even so one could reasonably expect a much higher incidence of nauplii if food choices were random. There is thus circumstantial evidence for preference of larger copepod stages, or conversely, for greater vulnerability among the larger copepod stages.

The clearest evidence given by Tab. 1 is for selective predation on *Cladocera*, which are represented in the diet in 10 fold excess of their abundance in the lake. Other authors have indicated preferences of *Chaoborus* for copepods (DEONIER 1943; SPRULES 1972), while DODSON (1972) has documented a case of repressive predation of *Chaoborus* on *Daphnia rosea*. The exact composition of the plankton and the nature of the waterbody itself could be expected to influence the selectivity of feeding in individual cases. Selective predation of *Chaoborus* on Cladocera in Lake Lanao is clearly sufficiently marked to constitute a major factor affecting community composition. The failure of the Cladocera to play a greater role in the Lake Lanao plankton could reasonably be accounted for by such intense feeding pressure. An important distinction that should be recognized in this connection between Lake Lanao and a temperate lake is the reduced opportunity for prey species to develop life history adaptations to seasonal fluctuations in predator density.

Summary

The *Chaoborus* population of Lake Lanao was sampled at weekly intervals for 14 months. Organisms were counted and measured to permit separation of size classes during analysis and computation of biomass. A satisfactory allometric relation was developed to relate the standard length measurement to dry weight of individual organisms.

The Lake Lanao *Chaoborus* population is moderately dense and is distinct from characteristic temperate populations in that all sizes of organisms can be found at any time of the year. The population is principally planktonic during the day and entirely planktonic at night. During the daytime the centers of depth for size classes of smaller organisms consistently overlie the centers of depth for size classes of larger organisms. Weekly variation in the center of depth for specific size classes is relatively small and cannot be explained in terms of dissolved oxygen or transparency. The dispersion of small *Chaoborus* about their center of depth is much greater than for large organisms. Dispersion of small organisms is not related to transparency but is significantly related to dissolved oxygen. The correlation is most likely to be caused by the relation of some third factor, such as food distribution, to dispersion. The size-depth ranking of *Chaoborus* in the water column is the most consistent aspect of vertical distribution and is also best explained by food distribution and predation pressure. Small *Chaoborus* must feed rapidly and require smaller food items that are located higher in the water column. In addition, predation pressure on smaller larvae is likely to be less, so that the benefits they derive from remaining high in the water column would be greater.

Emergence of adult *Chaoborus* was restricted to the deepest portion of the lake on several occasions. Transect studies revealed that the largest organisms were absent from shallow water where the oxygen reached the bottom, and active downslope movement of larger *Chaoborus* is postulated to explain the observations.

Lake Lanao *Chaoborus* feed both during the day and night. The gut contents indicate markedly selective feeding on Cladocera. The advanced copepod stages are more frequently found in the gut than are nauplii. Selectivity in feeding seems to be strong enough to affect community composition at all times of the year.

Acknowledgements

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Discussion

PASTOROK: Are planktivorous fish present in the lake? Size selection on larger *Chaoborus* show to be possible in lab (unpubl. data, PASTOROK & HYATT) could account for vertical migration of bigger animals.

LEWIS: Predation is a necessary component of the explanation that I have formulated, but will not by itself account for order by size in the water column among *Chaoborus*. Food distribution is thus added to predation to complete the explanation. Lake Lanao contains endemic cyprinids and *Glossogobius*. Predation pressure on the *Chaoborus* may well be less severe than in some temperate lakes due to inefficiencies in exploitation of the food source by the limited variety of fishes.

PASTOROK: Have you looked at spatial co-occurrence of copepods and cladocera with *Chaoborus*? Since most lab experiments show preference for copepods over cladocera, your feeding data may just be the result of differential encounter frequency in nature.

LEWIS: I am not able to distinguish vulnerability from palatability in this study. The distributions of copepods and cladocera with relation to the predator is part of another work that is now unfinished. The feeding habits of *Chaoborus* may well vary between lakes.

PARMA: What might be the light stimulus for the population to migrate over the enormous distance while the stimulus of decreasing or increasing light intensity can react only a short time in this tropical area?

LEWIS: It is likely that the rhythm is not actually triggered by light, but is merely corrected to seasonal changes in day length on the basis of light data taken by the organisms at the time of ascent. Also in this particular case, there is very little seasonal change in day length, hence little correction of the endogenous rhythm would be needed.

PARMA: There might be a selective rejection of prey from the gut during sampling and preserving.

LEWIS: Formalin sometimes causes eversion of the pharynx, but in this study I used LUGOL's solution, which apparently does not cause eversion. Regurgitation at the time of capture may occur, although I have no evidence that it does. It seems unlikely that regurgitation would be highly selective, hence I would not expect this to affect the conclusions.

CARLANDER: Might swimming ability explain that the smaller *Chaoborus* are less able to make the migrations?

LEWIS: No. A few smaller *Chaoborus* we found at the greater depths or migrating like the larger *Chaoborus*.