

Feeding selectivity of a tropical *Chaoborus* population

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SUMMARY. The *Chaoborus* population of Lake Lanao, Philippines, was sampled weekly over a 65-week period. Specimens representing all four instars, all times of the year, and two points in the daily migration cycle were dissected for determination of gut contents.

Major items in the diet of Lanao *Chaoborus* include *Bosmina*, *Diaphanosoma*, and the copepodid and adult stages of cyclopoid and calanoid copepods. Items that are available but seldom eaten include nauplii and rotifers except *Keratella*. Feeding rate averages 2.5% of body weight per day in instars 3–4.

Predator size affects but does not fully explain prey selection. Electivity values are much higher for *Bosmina* and *Diaphanosoma* than for copepods, even though these food items overlap in size. *Bosmina*, which has the highest electivity value of any prey, is virtually identical in size to the calanoid nauplius, which has one of the lowest electivity values. This and other similar data suggest that prey of the same size differ greatly in palatability or vulnerability.

There is a marked variation in feeding rate and food composition from day to night. The smallest *Chaoborus* feed more during the day than at night, but the opposite is true for *Chaoborus* of moderate to large size. Large *Chaoborus* switch from a daytime emphasis on copepod copepodids and adults to a nighttime emphasis on Cladocera.

Diurnal variation between instars in food composition cannot be explained simply on the basis of the vertical distributions of predators and prey. An interaction of vertical distribution with prey density and predator selectivity does explain the overall *Chaoborus* feeding pattern, however. During the day, larger *Chaoborus* move deep into the water column where food is scarce. Their daytime feeding rate is lower due to low prey density at great depths. Low prey density is partially compensated by relaxation of preference. At night, upward migration of large *Chaoborus* into an area of high prey density permits a resumption of marked selectivity and high feeding rates. Small *Chaoborus* do not descend deep into the water column during the day, as their lower hunting efficiency apparently requires higher food density and use of visual cues to sustain adequate feeding rates. Prey density thus affects both the vertical distribution and feeding selectivity of the *Chaoborus* population.

Introduction

A preliminary study of the feeding habits of *Chaoborus* from Lake Lanao, Philippines,

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suggested that this zooplankton predator exercises considerable feeding selectivity in the Lake Lanao plankton system (Lewis, 1975). A more thorough study was therefore undertaken to document the extent of this selectivity, particularly as it relates to predator size and the daily cycle of vertical migration.

Selective predation is now recognized as an important determinant of community composition and structure in aquatic systems (Hrbacek *et al.*, 1961; Brooks & Dodson, 1965; Hall, Cooper & Werner, 1970). Although fish predation is of particular interest in this regard, the effect of invertebrate predators can under some conditions be markedly different and thus complementary to fish predation (Dodson, 1970). Invertebrate predation may also be important under circumstances that minimize vertebrate predation (Anderson & Raasveldt, 1974).

Since *Chaoborus* is an invertebrate predator of worldwide significance, its feeding habits have been the subject of numerous studies. Generalizations concerning *Chaoborus* predation are elusive, however. In view of the growing body of data relating predation to relative abundance and distribution of zooplankton species, the feeding selectivity of *Chaoborus* assumes increasing importance.

Lake Lanao, like many other tropical and temperate lakes, contains a *Chaoborus* population sufficiently large to affect its prey species among the zooplankton, particularly if it is a selective feeder. The present work evaluates feeding selectivity of the Lanao *Chaoborus* population under natural conditions, and attempts to relate selectivity to vertical distribution of predator and prey, prey size, and prey density.

Methods and Study Site

Lanao is a deep natural lake located on Mindanao (8°N, 124°E, mean depth, 60 m). The physico-chemical features of the lake and its productivity are discussed in detail elsewhere (Frey, 1969; Lewis, 1973, 1974). The *Chaoborus* data reported here are based on samples taken during a comprehensive study of the plankton system and coincide with estimates of the composition and standing crop of all zooplankton species.

The *Chaoborus* population of Lake Lanao consists of a single species which is best called 'Eckstein from 1,' as its taxonomic status is still uncertain (Lewis, 1975). All four instars of the species are present at all times of the year in Lake Lanao. Fish fry, which are present in the limnetic zone at certain times

of the year, are the only other pelagic predators of similar size. Even at their peak, the fish fry are much less abundant in midlake than *Chaoborus*, which appears to be the major predator on herbivorous zooplankton.

The *Chaoborus* population of Lake Lanao was sampled at weekly intervals between September 1970 and October 1971. Although a number of different sampling techniques were used for the purpose of estimating size and spatial distribution of the *Chaoborus* population (Lewis, 1975), the present work is based on weekly vertical metered tows taken from bottom to surface at or near the index station (45 m depth) and on a vertical series of samples taken at the same station (5 m intervals) with a 44-1 transparent Schindler-Patalas trap. From week to week over the last two-thirds of the study period the time of sampling alternated between morning (09.30–11.30 hours) and evening (19.00–20.00 hours) so that changes in feeding habits with time of day could be studied.

Chaoborus samples were preserved immediately in the field with Lugol's solution, which does not cause eversion of the gut as does formalin. Whole organisms or parts of organisms were then recovered from the crops of the *Chaoborus* as described by Swift & Fedorenko (1973). The major fault with this method of study is due to the differences in resistance to maceration of various food items. Although there are some gradations in resistance to maceration between similar prey species and even between different sizes of the same species, the prey are roughly divided into two major groups according to presence or absence of identifiable resistant structures (Table 1). Frequencies of prey lacking resistant structures are easily underestimated and are therefore subject to special interpretation in the analysis of data. Pieces of the other prey items are recognizable even after rather complete maceration and are assumed to be residual until such time as the *Chaoborus* everts its crop to expel skeletal material and debris. This regurgitation occurs spontaneously at intervals of several hours and thus prevents accumulation of resistant parts over long periods (Berg, 1937).

A total of 748 specimens were dissected. These were not chosen entirely at random but rather in such a way that all times of the year

TABLE 1. A complete list of the zooplankton of Lake Lanao organized as items mutually distinguishable in the gut of *Chaoborus*. An asterisk marks forms that are unidentifiable after only moderate maceration. Average weights and percentage contribution to *Chaoborus* diet are indicated to the right

| Species | Wet weight/ individual μg | Numbers in diet % | Biomass in diet % |
|--|--|-------------------------|-------------------------|
| Copepods | | | |
| <i>Tropodiatomus gigantoviger</i> Brehm | | | |
| Adult and copepodids | 14.5 | 8.1 | 32.2 |
| Nauplius | 1.7 | 0.0 | 0.0 |
| Egg clutches | 3.5 | 1.5 | 1.4 |
| <i>Thermocyclops hyalinus</i> (Rehberg) | | | |
| Adult and copepodids | 3.0 | 36.6 | 30.1 |
| Nauplius | 0.30 | 1.0 | 0.0 |
| Egg clutches | 0.45 | 5.1 | 0.6 |
| Cladocera | | | |
| <i>Diaphanosoma</i> † | 4.0 | 17.2 | 18.9 |
| <i>Moina micrura</i> Kruz | 6.0 | 0.8 | 1.3 |
| <i>Bosmina fatalis</i> Burckhardt | 2.4 | 23.0 | 15.1 |
| Rotifera | | | |
| <i>Conochiloides dossuarius</i> (Hudson)* | 0.15 | 0.0 | 0.0 |
| <i>Hexarthra intermedia</i> (Wiszniewski)* | 0.23 | 0.0 | 0.0 |
| <i>Polyarthra vulgaris</i> Carlin* | 0.28 | 0.0 | 0.0 |
| <i>Keratella procurva</i> (Thorpe) | 0.13 | 0.5 | 0.0 |
| <i>K. cochlearis</i> (Gosse) | 0.07 | 6.3 | 0.1 |
| <i>Trichocerca brachyurum</i> (Gosse) | 0.49 | 0.0 | 0.0 |
| <i>Tetramastix opoliensis</i> Zacharias | 0.13 | 0.0 | 0.0 |

* Easily destroyed by maceration.

† Include both *D. modigliani* Richard and *D. sarsi* Richard.

and all instars would be represented by statistically meaningful numbers of specimens. Due to the small number of zooplankton species in the lake, identification of gut contents was most often definite as to species if it was possible at all.

Results

Table 1 lists the limnetic zooplankton species of Lake Lanao (exclusive of Protozoa) and thus provides an overview of potential *Chaoborus* prey. The analysis is divided into six parts: (1) overall composition of food, (2) feeding rate, (3) effects of predator size on food composition, (4) variation in food composition with time of day, (5) relation of food composition to food availability, (6) relation between prey density and predator selectivity.

Overall food composition

Table 1 shows the overall composition of *Chaoborus* gut contents expressed both in

terms of percentage of the numbers of total identifiable items and as percentage of wet biomass of the identifiable items. The biomass percentages were obtained from the mean biomasses of individuals in each food category.

Copepod copepodids could not be distinguished from copepod adults after maceration, so these stages are lumped in Table 1. The two *Diaphanosoma* species were also indistinguishable after maceration and are likewise lumped in Table 1.

Table 1 is based entirely on identifiable food items and therefore does not indicate the percentage of empty guts or of unidentifiable items. Among the 748 specimens, 19% contained empty guts, 38% contained identifiable items from the list in Table 1, and the remaining 44% contained only unidentifiable debris, typically small amounts of material in very advanced stages of digestion.

Table 1 shows that zooplankton of the largest size (calanoid copepodids and adults) and of the smallest size (*Keratella*) serve to

TABLE 2. Comparison of *Chaoborus* instars with respect to food composition. Percentage occurrence in *Chaoborus* guts is indicated for each item. Items with very low percentage occurrences are not shown

| Instar | n | Total length (mm) | Wet weight (μ g) | Empty (%) | <i>Bosmina</i> (%) | <i>Diaphanosoma</i> (%) | Cyclopoid Copep-Adult (%) | Calanoid Copep-Adult (%) | <i>Keratella cochlearis</i> (%) |
|--------|-----|-------------------|-----------------------|-----------|--------------------|-------------------------|---------------------------|--------------------------|---------------------------------|
| 1 | 118 | 0.8-2.9 | 1.2-72 | 53.4** | 0.8** | 2.5* | 10.2** | 0.8 | 1.7 |
| 2 | 250 | 2.9-4.5 | 72-272 | 16.8 | 3.6 | 9.6 | 25.2 | 3.6 | 4.4 |
| 3 | 241 | 4.5-7.4 | 272-1291 | 12.9 | 10.0 | 12.0 | 21.2 | 4.6 | 3.0 |
| 4 | 139 | 7.4-10.1 | 1291-3414 | 2.9 | 8.6 | 7.2 | 13.7 | 7.2 | 0.0 |

* $P < 0.05$, ** $P < 0.01$ (χ^2 -test).

some extent as prey for the *Chaoborus* population, and that the major food items include the Cladocera and advanced copepod stages. In terms of biomass, the cyclopoids, calanoids, and Cladocera contribute almost equally to the *Chaoborus* diet. Calanoids are taken in lower numbers than the other two groups but are larger.

Effects of predator size on prey selection

The *Chaoborus* population is composed of four instars, which can be separated on the basis of standard length (Lewis, 1975). Some effects of predator size on prey selection can be demonstrated by comparison of gut contents in these four instars. Since critical predator size boundaries for the ingestion of various prey may not coincide exactly with instar transitions, the use of instars as size groups is merely an analytical convenience.

Table 2 compares the percentages of empty guts in each of the four instars. In this and other similar cases to follow, the statistical test of the data is for homogeneity among instars, judged on the basis of Chi Square. Tests were of course carried out on the numerical data, not on the percentages reported in the table.

Table 2 shows that the guts of smaller *Chaoborus* are much more frequently empty than those of larger *Chaoborus*. The difference between instars in proportion of empty guts is so great that it suggests a radical difference in the overall food availability for *Chaoborus* of different sizes. Almost all of the published data on *Chaoborus* feeding habits apply to the older instars, so it is impossible to say whether the discrepancy in percentage of empty guts shown in Table 2 is typical of *Chaoborus* populations in general.

Some additional first instar specimens were selected for special dissection to check the possibility that small food items were merely being overlooked. The crops from these specimens were dissected and irrigated in a small drop of water, which was completely scanned at a magnification of $\times 350$ for algae or protozoans that might have been missed under the dissecting microscope. Nine of eleven specimens were completely empty, and one contained a calanoid nauplius that would have been noticed under the dissecting microscope.

The eleventh contained four individuals of *Tetraedron minimum* (Al. Braun) Hansgirg and one individual of an unidentified unicellular green alga.

The special dissections confirm the original impression that large numbers of first instar *Chaoborus* are indeed empty at any given time. The specimen containing *Tetraedron* was apparently feeding selectively on this alga, however, and this adds a new dimension to the observed feeding of the first instar. At the time when the specimen containing *Tetraedron* was taken, the abundance of *Tetraedron* was 167 individuals/cm³ lake water. Selection of this phytoplankton species is not easily explicable, as *Tetraedron minimum* is very small (at most 25 μm length in Lanao, usually nearer 12 μm), and other larger species were available. The *Chaoborus* containing the four *Tetraedron* was 900 μm in length.

In a study of Barombi Mbo, West Cameroon, Green, Corbet & Betney (1973) also found several *Chaoborus* containing algae but no herbivore remnants. In Barombi Mbo the zooplankton prey density is very low and the percentage of empty *Chaoborus* guts is very high except in the middle of the night. Apparently the *Chaoborus* in Barombi Mbo and in Lanao take algae when extremely hungry to prevent starvation.

Table 2 also compares the percentage occurrence of particular food items in the four instars. For the three numerically most common items (*Bosmina*, *Diaphanosoma* and cyclopoid copepodids and adults) the difference between instars is statistically significant. For the other two items (calanoid copepodids and adults, *Keratella*) the difference between instars is marginally detectable statistically ($0.05 < P < 0.10$), but this is probably due to the small numbers of items in these categories, which reduces the power of statistical discrimination.

Table 2 shows that the size of the predator is partly related to the size of the most common foods. The largest *Chaoborus* do not use the small *Keratella*, and the smallest *Chaoborus* do not use the large prey items to a significant extent. Not all items of appropriate size are important in the diet, however. This applies particularly to nauplii, which are not shown on Table 2 because of their very low percentage occurrence in the gut.

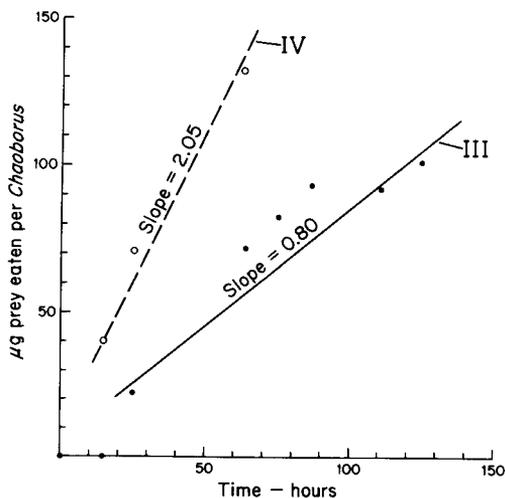


FIG. 1. Rate of prey consumption by *Chaoborus* of instars III and IV under experimental conditions.

Feeding rate

An ideal determination of feeding rates for *Chaoborus* would involve factorial experiments in which the size of predator, identity and size of prey, and environmental conditions were varied. Detailed work of this type was not possible, but an approximation was nevertheless made of feeding rates by means of simple experiments.

Chaoborus of uniform size (8.4 mm total length, instar 4) were confined in dishes with a known number of adult calanoids and placed in a room with 12/12 photoperiod and very dim light during the light portion of the cycle. The decline in number of calanoids was

then noted over a period of several days. Controls showed no mortality of either *Chaoborus* or calanoids under the experimental holding conditions. Three such experiments were conducted, as well as an identical set of experiments for organisms of total length 6.8 mm (instar 3).

The results of the feeding experiments are summarized in Fig. 1. The slopes of the lines give the feeding rates for *Chaoborus* of the two size classes. The rate for the larger *Chaoborus* is of course greater on a per animal basis than for the smaller *Chaoborus*. Expressed as a percentage of body weight, however, rates of prey intake were quite similar in the two size groups: 2.1%/day of the body weight for the smaller organisms and 2.8%/day for the larger ones.

Table 3 summarizes data from the literature on feeding rates for various *Chaoborus* species. For all of the studies except the one by Kajak & Ranke-Rybicka (1970), the food intake as a percentage of body weight was calculated indirectly from other data given by the authors. In many cases the weights of predators and prey were approximated from standard length-weight relationships. The values in the Table are therefore only estimates.

The studies listed in Table 3 were conducted under a wide range of conditions, including different temperatures, prey densities, and prey compositions. Some of these factors are known to affect rate of predation for particular *Chaoborus* species (Fedorenko

TABLE 3. Feeding rates of *Chaoborus* expressed as a percentage of body weight. Most percentages were computed from data reported in the literature (see text)

| Reference | Species, instar | Food | Daily intake (%) |
|-----------------------------|---------------------------------------|--|------------------|
| Anderson & Raasveldt, 1974 | <i>C. americanus</i> (Johannsen) - IV | <i>Diaptomus</i> , <i>Cyclops</i> , <i>Daphnia</i> | 1.7 |
| Dodson, 1970 | <i>C. flavicans</i> (Meigen) - IV | <i>Daphnia</i> | 0.8 |
| | <i>C. nyblaei</i> Zetterstedt - IV | <i>Daphnia</i> | 0.6 |
| | * <i>C. nyblaei</i> - II | <i>Diaptomus</i> | 13.2 |
| Fedorenko, 1975b | * <i>C. nyblaei</i> - III | <i>Diaptomus</i> | 6.7 |
| | * <i>C. nyblaei</i> - IV | <i>Diaptomus</i> | 8.4 |
| | <i>C. flavicans</i> - IV | Copepods, Cladocera | 12.5 |
| Kajak & Ranke-Rybicka, 1970 | <i>C. flavicans</i> - IV | Copepods, Cladocera | 3.6 |
| | <i>C. punctipennis</i> (Say) - IV | Copepods, Cladocera | 4.8 |
| Roth, 1971 | <i>C. sp.</i> IV | <i>Diaptomus</i> , <i>Daphnia</i> | 6.3 |
| Sprules, 1972 | <i>C. punctipennis</i> - III, IV | <i>Cyclops</i> , Cladocera | 0.8 |
| | <i>C. nyblaei</i> - III, IV | <i>Cyclops</i> , Cladocera | 0.1 |
| Allan, 1973 | Eckstein 1 - III | <i>Tropodiptomus</i> | 2.8 |
| | Eckstein 1 - IV | <i>Tropodiptomus</i> | 2.1 |

* Listed by Fedorenko as *C. trivittatus*.

TABLE 4. Percentage occurrence of common prey items in *Chaoborus* with a comparison between day (D) and night (N) samples. The first column indicates the percentage of *Chaoborus* containing at least one item

| Instar | All prey | | <i>Bosmina</i> | | <i>Diaphanosoma</i> | | Cyclopoid Copep-Adult | | Calanoid Copep-Adult | | <i>Keratella</i> | |
|--------|----------|------|----------------|------|---------------------|------|--------------------------|------|-------------------------|---|------------------|---|
| | D | N | D | N | D | N | D | N | D | N | D | N |
| All | 81 | 83 | 2 | 16** | 6 | 17** | 22 | 13** | 4 | 5 | 3 | 1 |
| I | 55 | 23** | 1 | 0 | 3 | 0 | 13 | 3 | 1 | 0 | 2 | 0 |
| II | 82 | 89 | 4 | 0 | 8 | 17 | 27 | 17 | 3 | 4 | 5 | 2 |
| III | 84 | 92 | 1 | 27** | 6 | 25** | 22 | 20 | 4 | 6 | 4 | 3 |
| IV | 97 | 98 | 0 | 22** | 4 | 13 | 19 | 6* | 8 | 6 | 0 | 0 |

* $P < 0.05$, ** $P < 0.01$ (χ^2 -test).

1975b), and this may in part account for the variation between studies.

The mean food intake from Table 3 is 4.6% of body weight per day. The Lanao values are thus in rough agreement with other studies, although there is a considerable range in the results. Table 3 is biased towards older instars. Younger instars almost certainly have a higher percentage food intake, judging from the speed of development.

Variations in food composition with time of day

Evening and morning samples of *Chaoborus* are contrasted in Table 4 with respect to prey composition. Since the daylength is very nearly constant for Lake Lanao, the samples were essentially uniform in their timing with relation to sunrise and sunset. Night samples were taken about 1.5 h after sunset, when the *Chaoborus* had assumed their nocturnal position high in the water column. Day samples were taken about 3 h after sunrise, when the animals had descended to their daytime positions.

Day and night feeding habits are first contrasted without regard to instar in the top line of Table 4. Proportion of empty guts is quite low overall and is not significantly different in day and night samples. This indicates that active feeding occurs both during the day and at night for the population as a whole.

Since the instars differ in feeding habits, they must be separated for complete analysis. Table 4 shows that instars 2–4 do not differ significantly between day and night with respect to percentage of completely empty guts. Although it is not apparent from the

table, the mean number of prey per individual is significantly higher at night than during the day, however ($P < 0.01$). Feeding is therefore more rapid at night in instars 2–4.

The first instar is very different from instars 2–4 insofar as its feeding success is much higher during the day than at night (Table 4). The first instar does not descend so deeply into the water column as the larger instars (Lewis, 1975). In fact the mean daytime centre of depth for the first instar in Lanao is about 20 m, which corresponds to a mean light level of 0.2% of surface irradiance. Other instars are much deeper in the water column during the day where there is virtually no light. The use of vision as an aid in hunting would explain why individuals of instar 1 are most successful during the day. Explanation of the opposite trend in instars 2–4 involves prey density, which is to be considered below.

Table 4 also shows considerable differences between day and night in consumption of specific food items. *Bosmina* and *Diaphanosoma*, which are taken principally by larger *Chaoborus* instars, are significantly larger dietary components at night than during the day. The opposite is true for cyclopoid copepodids and adults. The larger *Chaoborus* instars thus switch from an emphasis on Cladocera at night to an emphasis on cyclopoids during the day. The data on calanoids and *Keratella* show no significant differences between day and night, but this may in part be due to the small percentages of prey items in these categories.

Relation of food composition to food availability

The relative abundance of different food items in the diet of *Chaoborus* is potentially

TABLE 5. Predicted percentage food composition for *Chaoborus* based on (1) relative abundance of prey per unit surface area of lake ('abundance only'), (2) daytime (D) and nighttime (N) vertical distribution of predators and prey ($\bar{P}_{i,j}$). All predictions assume equal vulnerability of items. Rare items are excluded from the Table

| Instar | Basis of prediction | Food item | | | | | |
|--------|---------------------|-----------|-------------|----------|-------------|----------------------|---------------------|
| | | Cyclopoid | | Calanoid | | <i>Conochiloides</i> | <i>Diaphanosoma</i> |
| | | Naup | Copep-Adult | Naup | Copep-Adult | | |
| All | Abundance only | 51 | 22 | 2 | 4 | 10 | 3 |
| 1 | Abundance, Dist (D) | 51 | 22 | 2 | 4 | 10 | 3 |
| | Abundance, Dist (N) | 51 | 22 | 2 | 4 | 10 | 3 |
| 2 | Abundance, Dist (D) | 49 | 25 | 2 | 4 | 8 | 3 |
| | Abundance, Dist (N) | 51 | 23 | 3 | 4 | 10 | 3 |
| 3 | Abundance, Dist (D) | 48 | 26 | 2 | 4 | 7 | 3 |
| | Abundance, Dist (N) | 47 | 26 | 2 | 4 | 11 | 3 |
| 4 | Abundance, Dist (D) | 47 | 26 | 2 | 4 | 7 | 3 |
| | Abundance, Dist (N) | 52 | 22 | 2 | 4 | 10 | 3 |

affected by the relative abundance of these items in the environment. Under the simplest possible conditions, proportions of a given item in the habitat and in the diet of the predator would be equal. The degree of departure from this scheme is a measure of the selectivity of the predator, which may in turn be due to variation in either vulnerability or palatability of prey.

Table 5 provides a basis for judging the feeding selectivity of *Chaoborus*. The Table shows the predicted abundance of important prey items in the diet assuming uniform vulnerability and palatability of prey items. The first line of data across the table gives the percentage of individuals under a unit area of lake surface assignable to each kind of food item. The percentages are based on annual average numerical standing stocks for each food type ($n = 63$ for each item). With the assumption that predators and food items are identically distributed beneath the surface, the first line of the table is thus the predicted food composition for *Chaoborus*.

Since the vertical distributions of prey and predator are not uniform and vary in a daily pattern, a more refined prediction can be based on the average numbers of various prey items in the immediate vicinity of a predator. The expected food composition based on vertical distribution of both predator and prey was computed as follows:

$$P_{i,j} = \sum_k C_{j,k} F_{i,k}$$

where $\bar{P}_{i,j}$ is the predicted proportion of item type i in the diet of *Chaoborus* of instar j , $C_{j,k}$ is the ratio of instar j *Chaoborus* at depth k to the total number of instar j *Chaoborus* at all depths, and $F_{i,k}$ is the ratio of food item type i at depth k to the number of total food items at depth k . The summation is over ten sampling depths at 5-m intervals. Separate values of $P_{i,k}$ were computed for all sixty-three sampling dates. Mean annual values, $\bar{P}_{i,j}$, were then obtained separately for the day and night sampling times. Table 5 gives $\bar{P}_{i,j}$ for both day and night.

Table 5 unexpectedly shows that the mean predicted food composition is almost identical across *Chaoborus* instars and from day to night. This contrasts with the conclusions of Fedorenko (1975a), who argues that spatial availability of prey is critical in determining the diet of *Chaoborus* in Eunice Lake, British Columbia. In temperate lakes, spatial separation of zooplankton species is often marked (e.g. Makarewicz & Likens, 1975). In Lake Lanao, and in tropical lakes generally, there is more turbulence in the upper water column and much less change in temperature with depth than in temperate lakes. This may lead to more overlap in the spatial distributions of zooplankton species, and to more uniform coincidence of predator and prey distributions.

In Lake Lanao the relative daily change in predicted predation is greatest for the rotifer

Conochiloides, as the daily movement of this species is less than that of *Chaoborus* instars 2–4 and of most other food items. On the whole, however, the Table shows that the conditional probabilities of coincidence with various kinds of prey are quite constant. For example, given that a prey item is captured, and that no selectivity of any kind occurs, the probability that this item will be cyclopoid nauplius is within 3% of 49% over all instars and through the daily migration cycle. The total density of prey in the vicinity of the predators does change but this is a different matter which does not affect predicted percentage composition of the diet under the assumption of negligible selectivity. The larger instars, which move deep into the water column in the daytime, are exposed to lower prey densities during daylight hours (Fig. 2), but not to a different prey composition (Table 5).

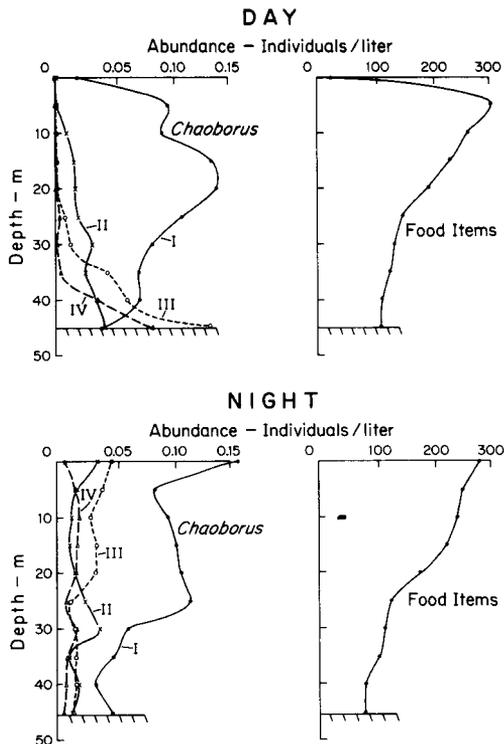


FIG. 2. Mean annual depth distributions of predators (*Chaoborus*, instars I–IV) and prey (all other zooplankton). Above, distributions at 09.30–11.30 hours. Below, distributions at 19.00–20.00 hours. Data averaged from sixty-three weekly samples.

Vertical migration of a predator species creates an ideal situation for development of an avoidance migration on the part of some (but not all) prey species. If such an avoidance pattern exists in any species, it should be evident in data such as those of Table 5. For species practicing predator avoidance through migration, the predicted values based solely on abundance (top line of Table 5) should differ from the values based on both abundance and vertical distribution (\bar{P}_{ij} , succeeding lines of Table 5). There is no marked difference of this type in Table 5, nor among the rarer food items that are listed in Table 1 but not in Table 5. Factors favouring nocturnal upward migration in the herbivores of Lake Lanao seem to be universally stronger than the opposing disadvantages of predation. The more rarely observed 'reversed' migration of herbivores in some lakes (Hutchinson, 1967) may constitute such an avoidance response to predation, however.

Since there are only trivial differences between predicted proportions of various items in the diet from day to night and between instars, it is feasible to adopt an average predicted food composition that is uniform across instars between day and night. The first line of Table 5 will be used for this purpose.

Table 6 compares the predicted food composition from Table 5, based on negligible selectivity, with observed food composition. The departure of observed from expected is statistically significant for all instars. Food items for which observed and expected percentages are both very low have been omitted from the table.

Cyclopoid nauplii are predicted on the assumption of negligible selectivity to be the predominant food item but in fact compose a trivial amount of food for all *Chaoborus* instars. Nauplii may be undesirably small (Table 1). However, it is difficult to attribute the neglect of nauplii entirely to size, as even the smallest nauplii are bigger than *Keratella*, which is commonly present in the gut. Nauplii may be processed in the crop more rapidly than some other items, but this seems insufficient to explain the extreme divergence of the observed and expected use of nauplii. The data thus suggest that nauplii are unpalatable or have an effective escape

TABLE 6. Predicted percentage composition of *Chaoborus* diet, assuming negligible selectivity, compared with the observed percentages. The latter are a composite of day and night samples

| | Cyclopoid | | Calanoid | | Cladocera | | Rotifera | | | |
|-----------|-----------|--------------|----------|--------------|---------------------|----------------|----------------------|----------------------|--------------------|------------------|
| | Naup | Copep-Adults | Naup | Copep-Adults | <i>Diaphanosoma</i> | <i>Bosmina</i> | <i>Conochiloides</i> | <i>K. cochlearis</i> | <i>Tetramastix</i> | <i>Hexarthra</i> |
| Predicted | | | | | | | | | | |
| All | 51 | 22 | 2 | 4 | 3 | 1 | 10 | 1 | 2 | 2 |
| Observed | | | | | | | | | | |
| Instar 1 | 9 | 55 | 0 | 5 | 14 | 5 | 0 | 9 | 0 | 0 |
| Instar 2 | 1 | 52 | 0 | 8 | 20 | 8 | 0 | 10 | 0 | 0 |
| Instar 3 | 1 | 31 | 3 | 7 | 18 | 34 | 0 | 7 | 0 | 0 |
| Instar 4 | 0 | 28 | 4 | 16 | 16 | 35 | 0 | 0 | 0 | 0 |

mechanism. The latter seems most likely but will require experimental proof.

Calanoid nauplii are taken in numbers closer to the predicted than are cyclopoid nauplii. They may be more attractive because they are larger, or may have less effective escape mechanisms. More definite conclusions are difficult due to the low relative numbers of calanoid nauplii.

Cyclopoid copepodids and adults are taken in excess of the expected frequencies, especially by the younger *Chaoborus* instars. For the calanoid adults and copepodids, the discrepancy between predicted and observed is higher among more advanced *Chaoborus* stages, presumably because the smallest *Chaoborus* cannot eat the largest calanoids.

Some additional deductions about the relative vulnerability of ovigerous female copepods can be based on the number of copepod eggs in *Chaoborus* crops. Cyclopoid eggs were present in twenty of the 748 *Chaoborus* guts. Eggs are easily identified because they are very resistant to maceration. In fact no cases were observed in which the membrane of eggs had been broken, although eggs were frequently separated from each other inside the crop. Eggs are probably rejected along with undigestible chitinous parts during the periodic regurgitation and may even hatch normally after their release from the crop.

Of the twenty *Chaoborus* containing cyclopoid eggs, fifteen also contained remnants of the cyclopoid copepodid-adult category, while five did not. This is an indication that *Chaoborus* sometimes obtains an egg sac while the female cyclopoid escapes capture. If each of the fifteen instances in which both

eggs and remains of the copepodid adult category were found in *Chaoborus* represents the capture of a single cyclopoid female, then fifteen of the 145 copepodids and adults found in all the *Chaoborus* crops would have been ovigerous female cyclopoids. The mean ratio of ovigerous females to total individuals in the copepodid-adult class over the year is 0.09, which is very near the apparent proportion of ovigerous females in the food (0.10). Ovigerous females are thus not particularly vulnerable to capture.

The data on calanoid eggs are considerably different. Six of the 748 *Chaoborus* contained calanoid eggs, but the remains of adult calanoids were not found in any of these six animals. The ovigerous females must always have escaped and left the predator with the egg clutch. This may be due to the very large size of the female calanoids. Roth (1971) observed that female copepods were ingested by *Chaoborus* from Frains Lake, Michigan, in such a way that the egg sacs were stripped away from the body and thus were excluded from the diet. The Lanao *Chaoborus* obviously behave differently in this regard.

Selective feeding of *Chaoborus* on both *Diaphanosoma* and *Bosmina* is much more marked than on cyclopoid copepodids and adults (Table 6). Contribution of *Diaphanosoma* to *Chaoborus* diet is as much as six times higher than expected, and the contribution of *Bosmina* is as much as thirty-five times higher than expected, depending on *Chaoborus* instar. *Bosmina* is especially selected by the larger *Chaoborus* but this is less true of *Diaphanosoma*.

Among rotifers, *Conochiloides* is expected

to constitute 10% of food owing to its high abundance, but was never detected in the diet. *Tetramastix* and *Hexarthra*, which were expected in lower numbers, were also completely absent from the diet. Data on *Conochiloides* and *Hexarthra* are subject to special interpretation because these forms easily become unrecognizable in the crop. Nevertheless, complete absence of these items, especially of *Conochiloides*, is difficult to explain without recourse to selectivity, as some freshly-ingested specimens should otherwise have been observed. Moreover, *Tetramastix* has distinctive skeletal parts and should have been observed. Although zooplankton eggs are resistant to maceration, no rotifer eggs attributable to *Hexarthra*, *Tetramastix*, or *Conochiloides* were found. This also suggests that these species were not eaten in significant numbers.

There is a marked feeding bias toward *Kertella cochlearis* among smaller *Chaoborus* which raises the incidence of this item in the food as much as ten times above the predicted level (Table 6). This seems to rule out small size as an explanation for the failure of *Chaoborus* to eat nauplii and other rotifers, as *Keratella* is extremely small (Table 1).

Technical bias attributable to differences in rates of food processing could cause some distortion of the percentages in Table 6. The case for selective predation, especially on Cladocera, is nevertheless inevitable due to the very large divergences between observed and expected food composition.

Relations between prey density and predator selectivity

A daily shift in *Chaoborus* food composition was demonstrated in the comparison of day and night feeding habits. This shift would be most easily explained by marked changes in the available food resulting from the daily vertical migrations. Since it is already clear that this is not a viable explanation (Table 5), shift in food composition must be explained on some other basis. The only other reasonable explanation involves interaction of predator selectivity with prey density.

During the day, the large instars of *Chaoborus* are near the lake bottom (Fig. 2). The average food composition is essentially the same here as higher in the water column,

but the food density is much lower. The *Chaoborus* prefer cladocerans to cyclopoids, but, given the low relative abundance of cladocerans (Table 6) in addition to the overall scarcity of prey near the bottom, *Chaoborus* cannot exercise preference without greatly reducing food intake. For this reason large *Chaoborus* tend to feed indiscriminantly during the day. At night, migration carries the larger instars into a zone of high prey density, where food is sufficiently plentiful for them to exercise preference. This explains the dramatic rise in percentage intake of Cladocera at night.

There is little doubt that the older *Chaoborus* migrate down during the day to avoid predation by fishes, and the above explanation seems to account for their concurrent daily change in feeding habits. One remaining difficult point is failure of the younger animals to migrate as much as the older ones (Fig. 2). I suggested previously that this has to do with feeding (Lewis, 1975), yet the foregoing evidence seems to rule out the most obvious possibility that the daytime size distribution of predators partly reflects a daytime size distribution of prey. The explanation given above for a daily cycle in food composition of older instars also offers an explanation for the small amplitude of migration in young *Chaoborus*.

The explanation begins with the assumption that young *Chaoborus* hunt a smaller area and thus require a higher prey density to sustain food intake. This limitation is partly but not fully offset by the ability of small *Chaoborus* to use small food items, which are generally available in higher densities than large food items. High food density does not occur deep in the water column, so small *Chaoborus* must remain high in the water column to sustain food intake. In addition, evidence already given indicates that hunting success is visually augmented in instar 1 during the day, and this can only occur high in the water column. The smaller organisms thus offset lower hunting efficiency by remaining in a zone of higher prey density and by using visual cues. As *Chaoborus* grows larger there is apparently a smooth increase in its hunting efficiency and a consequently higher tolerance for lower prey densities and absence of visual cues. This would explain the

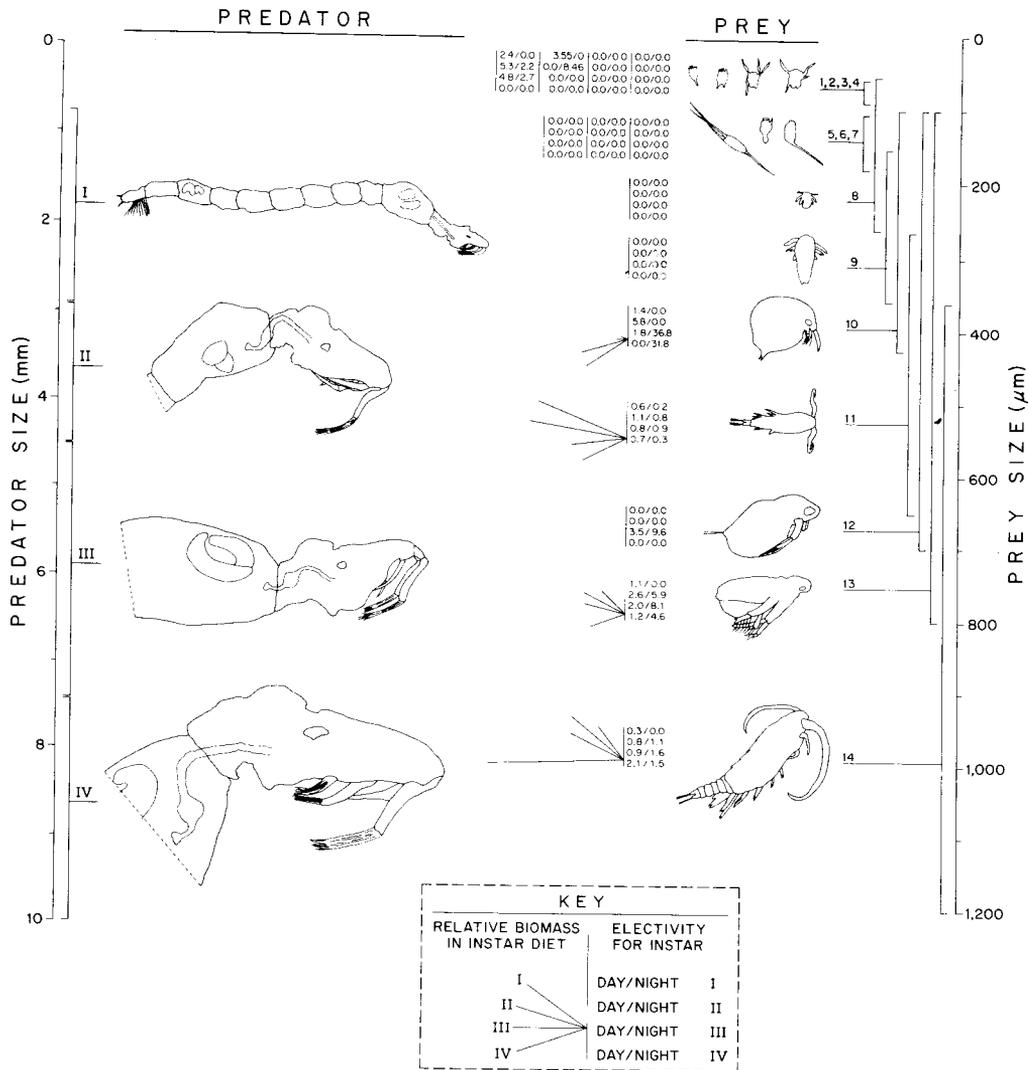


FIG. 3. Drawings of the four *Chaoborus* instars and the zooplankton food categories. All items are drawn to the same scale. Size range for each item is indicated with reference to the axes to the left and right of the drawings. Length of vectors pointing to each instar indicate percentage composition of food as biomass. Numbers indicate electivity computed as described in the text.

smooth increase in mean length of *Chaoborus* with depth in the daytime distribution of the species (Lewis, 1975). Vertebrate predators may reinforce this pattern by applying more pressure to larger organisms, forcing them to migrate to greater depths, but the foregoing analysis suggests that an increase in amplitude of migration with size would be advantageous to *Chaoborus* even if predation were uniform over all sizes.

Discussion

Figure 3 summarizes the feeding habits of the Lanao *Chaoborus* population. The Figure gives day and night electivity values for each prey type. Following the rationale of Dodson (1970), the electivity values (E) in Fig. 3 were obtained by the formula $E = r_i/p_i$, where r_i is the percentage of individuals in the diet of the predator and p_i is the percentage of indi-

viduals available to the predator. Values between 0 and 1 indicate avoidance and values greater than 1 indicate preference.

It is evident from Fig. 3 and the foregoing analysis that size of prey is not the sole determinant of feeding selectivity. Although there are clearly some constraints on maximum and minimum prey size for a given *Chaoborus* instar, the identity of the prey is very important within the range of acceptable prey sizes.

Published information on *Chaoborus* feeding habits has often documented selectivity that is difficult to explain without recourse to factors other than size. In Lake Lanao the general order of selection for food items is very clear: *Bosmina* > *Diaphanosoma* > copepod copepodids-adults > rotifers > nauplii. A close look at the literature reveals some nearly universal regularities that are consistent with this scheme.

The Cladocera are not eaten uniformly by *Chaoborus*. Studies including *Daphnia* usually rank this genus as lowest in order of preference (Main, 1953; Dodson, 1970; Roth, 1971; Sprules, 1972; Swuste *et al.*, 1973; Anderson & Raasveldt, 1974). Only one study gives any evidence of selective preference for *Daphnia* (Allan, 1973). Reports of preference for other genera in the Cladocera are much more common. Several studies indicate that *Bosmina* and *Diaphanosoma* are either preferred or are taken as readily as other available foods (Roth, 1971; Fedorenko, 1975a,b). In contradiction to this trend, Deonier (1943) mentions a preference of *Chaoborus* for copepods over *Bosmina* but without supporting data. Roth (1971) documents an overall preference of *Chaoborus* for *Bosmina* over copepods, as does Fedorenko (1975a,b) for one of her two *Chaoborus* species. One of Allan's (1973) two species preferred *Bosmina* over copepods and *Daphnia*. *Bosmina* thus ranks much higher on a scale of preference than *Daphnia*, and usually higher than copepods. *Diaphanosoma* has not been studied as much, but was a major food item in Fedorenko's studies and appears to have been used as fully as copepod copepodids and adults. R. W. Winner (in preparation) has demonstrated strong preference of *Chaoborus punctipennis* Say for *Diaphanosoma* over *Daphnia* and large calanoids.

Copepod copepodids and adults are almost always among the most important *Chaoborus* foods (Deonier, 1953; Main, 1953; Dodson, 1970; Roth, 1971; Goldspink & Scott, 1971; Sprules, 1972; Swuste *et al.*, 1973; Anderson & Raasveldt, 1974). In many of such situations, other foods are not available in large quantities, so there is little opportunity for selective feeding. One obvious limitation on the use of copepods applies to the advanced stages of the largest copepod species, which can be too large for most *Chaoborus* to ingest.

According to the literature, *Chaoborus* seldom eats copepod nauplii. Roth (1971) and Fedorenko (1975b) document cases in which the incidence of nauplii in the diet of *Chaoborus* is much lower than expected on the basis of naupliar abundance. Extensive feeding of *Chaoborus* on nauplii is reported only by Kajak & Ranke-Rybicka (1970), although a complete breakdown of available food is not given by these authors.

Detailed data are not available on the use of rotifers by *Chaoborus*. Deonier (1943) notes that *Keratella cochlearis* is an important prey item for early *Chaoborus* instars, as it is in Lanao. Green *et al.* (1973) found rotifers in the guts of *Chaoborus* from Barombi Mbo in West Cameroon, where planktonic Cladocera are entirely absent and overall zooplankton density is low. Roth's (1971) data suggest a very low incidence of *Chaoborus* predation on rotifers. Most studies deal with the older *Chaoborus* instars, for which rotifers might be of marginal value as food. This should not be completely prejudicial against observations of predation on rotifers, as rotifers are taken in detectable numbers by all instars except instar 4 in Lake Lanao (Table 2).

To summarize, the literature on *Chaoborus* feeding suggests an order of selectivity that is generally applicable to many different *Chaoborus* species and many different lakes: *Bosmina* > copepod copepodids and adults, *Diaphanosoma* > rotifers > nauplii, *Daphnia*. More intensive investigation of feeding in the first *Chaoborus* instar may show differences between the position of different rotifer genera on this spectrum, and there are some exceptions as noted above, but the data at hand seem sufficiently sound to support this general order. This sequence drawn from the literature is virtually the same as the sequence

constructed from the Lake Lanao data. The sequence obviously cannot be explained solely on the basis of size, although size is without doubt a partial determinant. Further research should explore the mechanism behind the pronounced difference in the ability of *Chaoborus* to exploit Cladocera of different genera, as the factors involved are not obvious.

Some predation studies have emphasized the importance of prey size in governing predator selectivity (Brooks & Dodson, 1965; Brooks, 1968; Dodson, 1970; Hall *et al.*, 1970; Sprules, 1972; Allan, 1973), while other studies have emphasized the importance of visibility and behaviour of prey (Green, 1971; Zaret, 1972; Zaret & Kerfoot, 1975). These factors are compared in a recent review by Zaret (1975). The mechanisms by which these two classes of selectivity operate are different. Selection based on size or some other prey character involves to some degree a predator's choice between alternate food items independent of their relative vulnerability to capture. This mechanism of selectivity is therefore based at least partly on a behavioural trait of the predator. Selectivity arising from differences in the visibility or behaviour of prey, on the other hand, is due to uneven vulnerability of prey, which is not attributable to any preference on the part of the predator. Since these two mechanisms of selectivity are different, they may both operate simultaneously in a given suite of predator-prey interactions. The Lake Lanao *Chaoborus* population is an example of the simultaneous operation of these two sets of factors.

In general, a mixed mechanism of selectivity is highly probable wherever there is a variety of prey types and a great fluctuation in prey density in time or space. Any morphological specialization of the predator that might optimize feeding rate on a particular prey type will almost certainly increase the difference in relative vulnerability of prey types, which would be disadvantageous when overall prey density is low. A behavioural mechanism by which preference is adjusted

vertebrate predators seem to explain fully the vertical distribution and feeding habits of *Chaoborus* in Lake Lanao.

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