



Competition and the Relative Abundances of Two Cladocerans

J. David Allan

Ecology, Vol. 54, No. 3 (May, 1973), 484-498.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197305%2954%3A3%3C484%3ACATRAO%3E2.0.CO%3B2-Q>

Ecology is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

COMPETITION AND THE RELATIVE ABUNDANCES OF TWO CLADOCERANS¹

J. DAVID ALLAN

Department of Zoology, University of Maryland, College Park, Md. 20742

Abstract. Two cladocerans, *Daphnia parvula* and *Holopedium gibberum*, were studied to determine (a) whether the species were competing and (b) whether the observed coexistence was predictable from competitive relationships alone. Experimental manipulations of intra- and interspecific competition using ¹⁴C-labelled algae, bacteria, and detritus revealed clear competitive effects only with algae. Some resource partitioning was demonstrated. A model was proposed specifying *Holopedium* to be the poorer competitor for mutually shared resources, but also to be less reliant on those mutual resources, owing to its larger niche.

This model predicts coexistence and a higher relative abundance for *Holopedium*. However, the dynamics of field populations did not correspond to this prediction. *Daphnia* was rare and declining throughout the study whereas *Holopedium* exhibited a pronounced burst of growth. Analysis of birth and death processes revealed that *Holopedium* was relatively free from mortality throughout most of the study, while *Daphnia* suffered death rates of 20% per day or higher. This differential mortality explains the discrepancy between the competition model and observed densities. Finally, field studies indicated that mortality of *Daphnia* owing to predation by *Chaoborus* larvae is more than twice that of *Holopedium*. It is concluded that *Daphnia* and *Holopedium* could coexist in a purely competitive system; however, because of selective predation, their observed abundances correspond little to their competitive status.

INTRODUCTION

Evidence exists that competition occurs in natural populations (Connell 1961, Wilbur 1971) and that competition may determine species distributions (Beauchamp and Ulliyot 1932, Connell 1961, Terborgh 1970). A further subject for inquiry is the role competition plays in determining relative abundances in nature.

My primary focus is the importance of competition between two species of Cladocera: *Daphnia parvula* Fordyce and *Holopedium gibberum* Zaddach. As predation plays a well-documented role in the zooplankton (Brooks and Dodson 1965). I also investigated predator selectivity. In order of complexity, the specific questions are (1) Do the two populations in fact compete? (2) Is their coexistence explainable in terms of different use of resources? That is, can it be experimentally demonstrated that each inhibits its own resource acquisition more than that of its competitor? (3) Can we identify the critical food resource (algae, bacteria, or detritus) in the dynamics of competition-coexistence? (4) What predictions regarding the relative abundances of the two species can be made from the analysis of competitive interactions? That is, what priorities may be assigned to competition and predation?

The study has three approaches. First, I performed field experiments varying the level of intraspecific and interspecific competition for ¹⁴C-labeled food. Second, an analysis of population dynamics compared field abundances to those predicted by the competition model, and provided estimates of the

relative contribution of birth and death processes to changes in population density. Third, I conducted field experiments with perch and *Chaoborus* to determine their contribution to zooplankton mortality. These estimated death rates were compared with observed death rates. In synthesizing this information I am attempting to define the role that competitive interactions play in determining the relative abundances of *Daphnia parvula* and *Holopedium gibberum* under field conditions.

COMPETITION

Hummingbird Lake is a small bog lake in southern Gogebic County in the western portion of Michigan's Upper Peninsula. The approximate size is 200 m by 75 m with a maximum depth of 5.5 m. It is located on a tract of land owned by the University of Notre Dame and has remained relatively undisturbed for at least two decades. During the spring and summer Hummingbird Lake has large populations of zooplankton and phantom midge larvae (*Chaoborus* spp.). The predominant cladocerans were *Bosmina longirostris* and *Daphnia parvula* during the summer of 1969, and *D. parvula* and *Holopedium gibberum* during 1970 (Fig. 1). Copepods (*Cyclops* sp.) and yellow perch (*Perca flavescens*) were present in both years.

For a competing pair of species to achieve stable coexistence, each species must limit its own further increase more than it limits or is limited by the other. Experiments were conducted varying the levels of intraspecific and interspecific competition and measuring the relative uptake of labeled food. Then if the food uptake of each species is reduced more by

¹ Received September 21, 1971; accepted October 27, 1972.

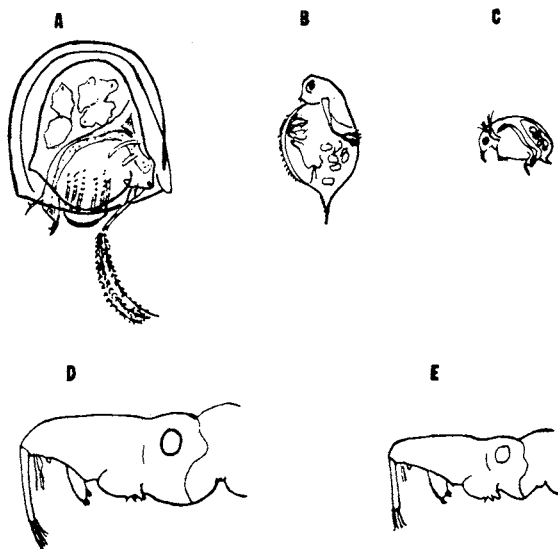


FIG. 1. Zooplankton of Hummingbird Lake drawn to scale. (A) *Holopedium gibberum*: average adult = .8 to 1.0 mm carapace length; (B) *Daphnia parvula*: average adult = .8 to 1.0 mm carapace length; (C) *Bosmina longirostris*: average adult = .35 to .45 mm carapace length; (D) *Chaoborus nyblaei*: average head length of III and IV instar larvae = 1.50 mm; (E) *Chaoborus punctipennis*: average head length of III and IV instar larvae = 0.90 mm. Note the enlarged gelatinous carapace in *Holopedium*, which prompted Hutchinson (1967) to remark it resembles "tapioca in a tow net."

changes in its own density than by changes in its competitor's density, I conclude that they may co-exist on the basis of their competitive relationships alone.

Uptake of ^{14}C -labeled algae, bacteria, or detritus was chosen as an index of competition. A series of replicates of homogenized lake water were labeled and different zooplankton densities were added to each. Only one compartment—algae, bacteria, or detritus—was labeled in a given experiment. Where uptake of labeled food per individual decreases as density increases, this is attributed to competitive resource depletion.

This approach has the limitation that several sources of variability are concealed within the measure. For uptake of labeled food to be precisely related to amount of algae, bacteria, or detritus assimilated, we must know the specific activity of each food type (e.g., each algal species), separate ingestion from assimilation, and choose a sufficiently short time span to minimize the effects of division of the food cells and cycling of the tracer. On the other hand, although these constraints are conceptually resolvable they present immense practical problems and demand sufficient time and labor to render a field competition study impractical. Further, the variability of natural systems will, in my opinion, con-

siderably outweigh many sources of variation inherent in the tracer technique itself. Thus I have chosen to use *relative* uptake of radioactivity, recognizing it to be a crude correlate of food assimilation. The problem of variability is attacked by extensive replication. The value gained is that manipulations may be performed on natural systems, thus carrying the question of competition in zooplankton into field experimentation.

Experimental design

All experiments were carried out in cylindrical 1-litre bottles (9 cm \times 20 cm) of lake water first strained through 220 μ silk bolting cloth to remove zooplankters. Each bottle was inoculated with a 1- μC /ml radiocarbon solution by means of 1-ml-constant pipette. In order to label the food sources, two ^{14}C -labeled compounds were used. Following Sorokin (1968), the algal compartment (plus autotrophic bacteria) was labeled with ^{14}C in a sodium bicarbonate carrier, and the bacteria compartment was labeled by the addition of D-glucose ^{14}C . Each was diluted to a 1- μC /ml solution using .025 N sodium bicarbonate and distilled water respectively.

The detrital compartment was more difficult to label since, as non-living particulate organic matter, detritus cannot incorporate a radioactive element to serve as tracer. Instead, a sample of lake water was allowed to incubate for several days in ^{14}C -bicarbonate, and the sample was autoclaved for 1 hour to break up living particulate matter. This produces a detritus that is considered to be a rough mimic of the natural compartment (Sorokin 1968).

In all cases it is assumed that the tracer did not mix significantly between compartments (from algae to bacteria or detritus, for example) during the course of the experiment. As radiocarbon is incorporated into the carbon chains it is quite stable (Sorokin 1968), and Saunders (1969) determined reasonable values for assimilation using similar techniques in an 8-hour period. The outcome with bacteria indicated that mixing may have been a problem, but it is doubtful that any significant leakage took place in the algae and detritus experiments.

Immediately after labeling, the bottles were sealed and suspended 0.2 m below the surface for approximately 2 hours while the necessary treatments of *Daphnia* and *Holopedium* were prepared. Individuals were collected by tow net and were roughly sorted into species by passing the collection through a series of sieves. The zooplankters were placed in petri dishes and individuals of each species were counted out by means of dissecting microscope and a pipette. In all cases I attempted to include a uniform distribution from small to large size classes.

While the inoculated lake water was incubating I prepared two replicates of the eight species-density

combinations necessary. Low density was set at 50 individuals per 1-litre bottle; high density at 150. Then the experimental systems were briefly removed from suspension, the zooplankton treatments added, and the bottles resuspended. After an 8-hour feeding period each replicate was passed through 220 μ netting and 10 zooplankters representing a uniform size distribution were placed on a membrane filter glued to a 2-inch steel planchet. Direct counting of 10 dried animals for 10 minutes with a Nuclear Chicago gas flow counter provided an estimate of radioactivity.

Statistics

Two designs were employed in the 1970 experiments with *Holopedium* and *Daphnia*. The first ("Design I") is a three-way analysis of variance. The species main effect compares the mean responses of *Daphnia* and *Holopedium*. The density main effect compares the mean response of both species at low intraspecific density and high intraspecific density. The mixing main effect compares the mean response of the two species alone to the mean response together (intraspecific vs. interspecific competition). Interaction terms are designated as species-by-density, species-by-mixing and density-by-mixing. The treatments are 50 D, 150 D, 50 H, 150 H, 50 D + 50 H, 150 D + 150 H. The second ("Design II") is also a three-way analysis of variance, with the same species main effect. Other main effects compare the mean response of both species under low and high *Daphnia* density and the mean response of both species under low and high *Holopedium* density. Interaction terms are designated as species-by-density of *Holopedium*, species-by-density of *Daphnia* and density of *Holopedium*-by-density of *Daphnia*. The treatments are 50 D + 50 H, 50 D + 150 H, 150 D + 50 H, 150 D + 150 H. Note that the designs partially overlap.

Pilot experiments during 1969 indicated that considerable replication would be necessary to overcome variance in the system, and that replicates may have shown similar behavior due to some similarity with which they were handled. Therefore, each experiment was conducted with two replicates per cell and an attempt was made to randomize the effects of handling and physical positioning. Furthermore, each experiment was repeated three times over successive days to provide additional replication. The difference between days was treated as a block effect. The main effect of blocks was partitioned out, but all interaction terms involving blocks became part of the pooled error term. The three main effects are fixed; only blocks are considered random. Under both designs the main effects of density and mixing have alternative hypotheses predicting a decrease in the uptake of labeled food under increasing competition. Accordingly, the null hypothesis was tested against a one-tailed alternative. For all interaction terms the null hypothesis was tested against a two-tailed alternative.

Results

Algae.—Under Design I all main effects are significant and there are strong differences among blocks (Table 1). The density effect ($P < .01$) represents decreased uptake of labeled food under high intraspecific competition. The mixing effect ($P < .05$) represents decreased uptake owing to interspecific competition. As knowledge of the specific activity of the food is necessary to evaluate any differences in food uptake between the two species, and as the focus here is change in uptake with change in density, no further attention will be paid to the between-species main effect. Finally, none of the interaction terms are significant.

Under Design II (Table 2) highly significant effects appeared, due to differences among blocks,

TABLE 1. Analysis of variance under Design I: Competition between *Daphnia* and *Holopedium*

Source	¹⁴ C-labeled algae (high density) ^a			¹⁴ C-labeled algae (low density) ^b			¹⁴ C-labeled bacteria (high density) ^c			¹⁴ C-labeled detritus (high density) ^d		
	DF	MS	F	DF	MS	F	DF	MS	F	DF	MS	F
Blocks	2	464.	8.0***	1	3699.	58.5***	1	2700.	12.5***	2	57.7	17.1***
Species	1	608.	10.4**	1	50.0	.8	1	9517.	44.1***	1	68.0	20.2***
Density	1	399.	6.9**	1	143.	2.3	1	181.	.8	1	3.2	.9
Mixing	1	162.	2.8*	1	9.7	.2	1	367.	1.7	1	4.7	1.4
Species-by-density	1	70.4	1.2	1	.6	.01	1	544.	2.5	1	.3	.08
Species-by-mixing	1	4.4	.07	1	106.	1.7	1	211.	1.0	1	.3	.09
Density-by-mixing	1	88.1	1.5	1	233.	3.7+	1	96.6	.4	1	4.1	1.2
Species-by-density-by-mixing	1	21.0	.4	1	20.1	.3	1	67.4	.3	1	.4	.1
Error ^e	38	58.3		39	63.2		22	216.		37	3.4	

*** = .001

** = .01

* = .05

+ = .10

^aDensities were 50 per litre versus 150 per litre. Experiment conducted July 5, 7, and 9, 1970.

^bDensities were 15 per litre versus 45 per litre. Experiment conducted July 21 and 22, 1970.

^cDensities were 50 per litre versus 150 per litre. Experiment conducted July 23, 24, and 26, 1970. Missing data prevented use of Block 3.

^dDensities were 50 per litre versus 150 per litre. Experiment conducted August 2, 3, and 4, 1970.

^eAll interaction terms involving blocks are pooled into the error term.

TABLE 2. Analysis of variance under Design II: Competition between *Daphnia* and *Holopedium*

Source	¹⁴ C-labeled algae (high density) ^a			¹⁴ C-labeled algae (low density) ^b			¹⁴ C-labeled bacteria (high density) ^c			¹⁴ C-labeled detritus (high density) ^d		
	DF	MS	F	DF	MS	F	DF	MS	F	DF	MS	F
Blocks	2	443.	13.2***	1	2401.	40.6***	2	314.	1.1	2	41.3	10.8***
Species	1	417.	12.4***	1	23.8	.4	1	29977.	102.5***	1	45.6	11.9***
Density of <i>Holopedium</i>	1	82.9	2.6	1	84.8	1.4	1	343.	1.2	1	.7	.2
Density of <i>Daphnia</i>	1	410.	12.2***	1	245.	4.2*	1	1536.	5.3*	1	9.3	2.4+
Species-by-density of <i>Holopedium</i>	1	81.2	2.6	1	7.7	.1	1	1038.	3.6+	1	1.1	.3
Species-by-density of <i>Daphnia</i>	1	15.7	.5	1	2.7	.05	1	.2	.01	1	.05	.01
<i>Holopedium</i> density-by- <i>Daphnia</i> density	1	2.6	.08	1	155.	2.6	1	611.	2.1	1	.06	.02
Species-by- <i>Holopedium</i> density-by- <i>Daphnia</i> density	1	4.7	.1	1	30.3	.5	1	1105.	3.8+	1	.7	.2
Error ^e	38	33.5		39	59.2		36	292.		37	3.9	

*** = < .001 ** = < .01 * = < .05 + = < .10
^aDensities were 50 per litre versus 150 per litre. Experiment conducted July 5, 7, and 9, 1970.
^bDensities were 15 per litre versus 45 per litre. Experiment conducted July 21 and 22, 1970.
^cDensities were 50 per litre versus 150 per litre. Experiment conducted July 23, 24, and 26, 1970.
^dDensities were 50 per litre versus 150 per litre. Experiment conducted August 2, 3, and 4, 1970.
^eAll interaction terms involving blocks are pooled into the error term.

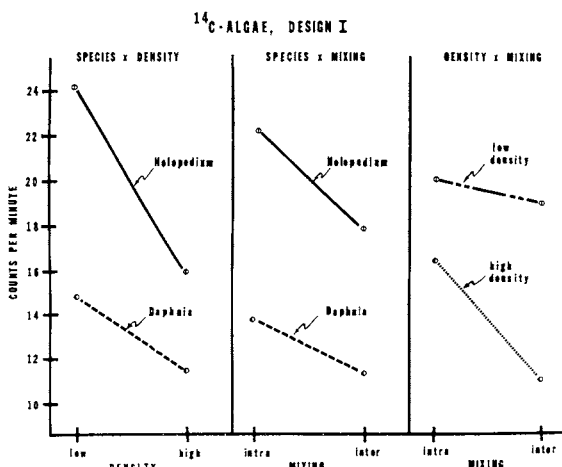


FIG. 2. Reduction in uptake of ¹⁴C-labeled algae as an index of competition. Main effects of variance analysis are species, intraspecific density, and interspecific mixing. None of the interaction terms are statistically significant, but graphical comparison of slopes allows inferences to be made about trends.

between species, and with increasing densities of *Daphnia* ($P < .025$). Again, none of the interaction terms are significant.

The experimental results are graphed (Fig. 2 and 3) as an aid in interpreting results and generating hypotheses for future experimentation. The density-by-mixing result (Fig. 2) indicates that the effect of interspecific competition is more intense at higher levels of intraspecific density. Second, the result of increased *Holopedium* density is to inhibit the uptake of labeled food by *Holopedium* but not by *Daphnia* (species-by-*Holopedium* density: Fig. 3). This indi-

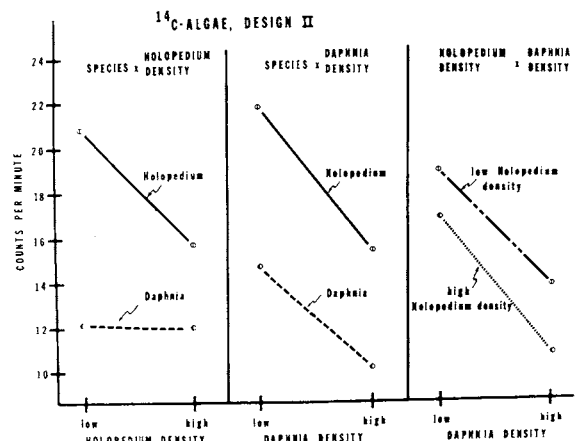


FIG. 3. Reduction in uptake of ¹⁴C-labeled algae as an index of competition. Main effects of variance analysis are species, *Daphnia* density, and *Holopedium* density.

cates some resource partitioning so that *Holopedium* may deplete algal populations unimportant to *Daphnia*.

A second set of experiments with labeled algae was conducted several weeks later and designed to ask whether the above results would occur with lower density manipulations. Therefore, densities of 15 and 45 per litre rather than 50 and 150 were selected. The results revealed high variability and fewer significant differences than with the higher density manipulations reported above. Under Design I (Table 1) only the block (among days) effect was significant, and under the interspecific design (Table 2) both blocks and the main effect of *Daphnia* density ($P < .025$) were significant. Evidently, fairly high

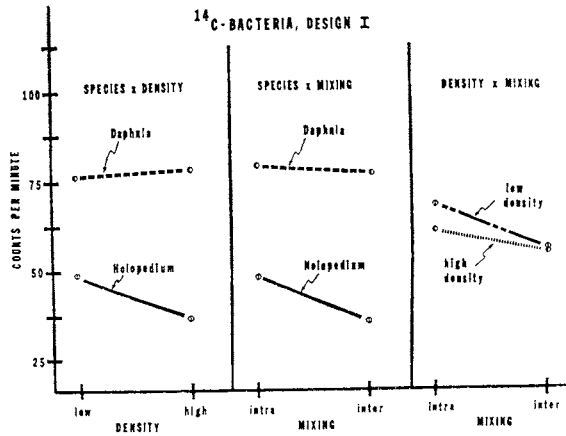


FIG. 4. Reduction in uptake of ¹⁴C-labeled bacteria as an index of competition. Main effects of variance analysis are species, intraspecific density, and interspecific mixing.

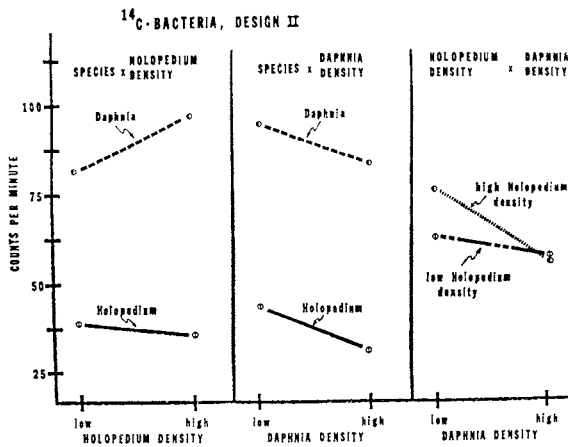


FIG. 5. Reduction in uptake of ¹⁴C-labeled bacteria as an index of competition. Main effects of variance analysis are species, *Daphnia* density, and *Holopedium* density.

densities are needed to reveal competitive interactions. As the *Daphnia* effect is still detectable at lower density levels I conclude it plays a strong role in the competitive relationships. The time difference of 2 weeks between the two sets of algal experiments did not appear to change the outcome.

Bacteria.—Under Design I (Table 1) strong differences emerged between blocks and between species for uptake of labeled bacteria. No other effects were significant. Under Design II (Table 2) the significant results are between species, and the *Daphnia* main effect ($P < .025$).

The graphed results (Fig. 4 and 5) bear out the inhibiting effect on both species of increased *Daphnia* density. Other results, however, are rather erratic. The tendency towards a species-by-*Holopedium* interaction (Fig. 5) is due to *Daphnia*'s increased uptake of tracer at higher densities of *Holopedium*, contradicting expectations of a competitive reduc-

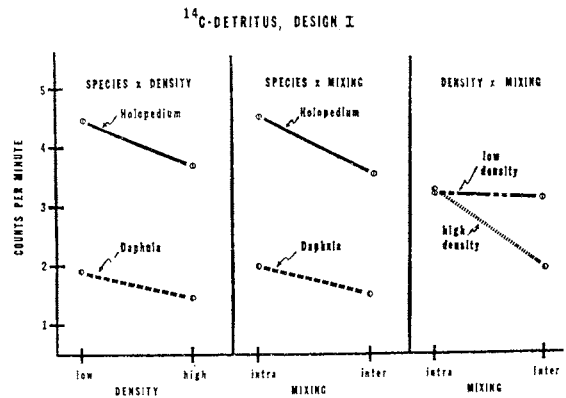


FIG. 6. Reduction in uptake of ¹⁴C-labeled detritus as an index of competition. Main effects of variance analysis are species, intraspecific density, and interspecific mixing.

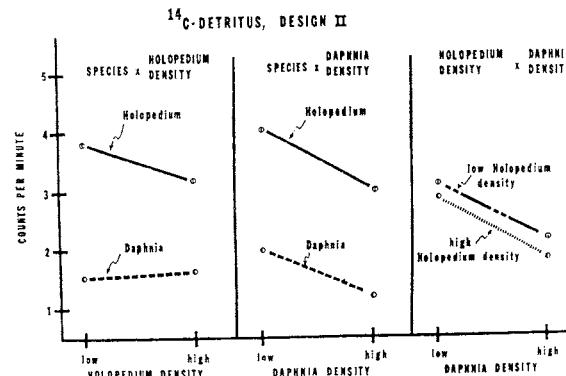


FIG. 7. Reduction in uptake of ¹⁴C-labeled detritus as an index of competition. Main effects of variance analysis are species, *Daphnia* density, and *Holopedium* density.

tion. In the absence of any information on the activity of different bacteria species or possible mixing among compartments it is difficult to pursue these data further.

Detritus.—Under both designs (Tables 1 and 2) the only significant differences are blocks and species. Graphical examination (Fig. 6 and 7) suggests a strong similarity between the detritus and the algae results. Only the *Daphnia* density effect is at all pronounced ($P < .10$), but the resemblance between algal and detrital results suggests that the same interpretation of main effects and interaction terms will hold for both. That is, *Daphnia* exerts a strong effect on both species; increasing densities of *Holopedium* affect primarily conspecifics; and the effect of mixing is more pronounced at higher densities. Taken together, these results specify certain characteristics of niche overlap.

BIRTHS AND DEATHS IN NATURAL POPULATIONS

Changes in the densities of species populations may be combined with fecundity information derived from the highly visible eggs of brooding micro-

crustaceans to allow evaluation of the birth and death components of population change. Techniques introduced by Edmondson (1960) and Hall (1964) provide reasonable estimates of the population parameters b , instantaneous birth rate and d , instantaneous death rate. These may be coupled with predictions of relative abundances based on the competition experiments so that, where observed abundances of *Daphnia* and *Holopedium* differ from expectations, we may examine changes in births and deaths as a clue to causal factors.

Methods

Population densities of the dominant zooplankters were estimated throughout the summer study periods of 1969 and 1970. Four equidistant sampling stations were established in a transect across Hummingbird Lake. The stations at either side were located in the littoral zone approximately 3 m from the bog mat where the water was 1.5 m deep. The two central stations were located one-third of the distance across the lake at points where the depth was approximately 5 m. Two samples were collected at each station at 0.5 m depth with a 1-litre kemmerer bottle. An additional two samples were collected at the central stations from a depth of 2.5 m. Weekly population estimates were made by pooling all 12 samples, and separate estimates could also be made of the littoral zone (side stations), open water (central stations, 0.5 m), and deep open water (central stations, 2.5 m) to gain some insight into spatial distributions. All collections were made at midday to minimize the effects of vertical migration patterns on weekly sample variance. Samples were filtered onto a disc of 20 μ Nytex netting and counted under a dissecting microscope. Population estimates of *Holopedium gibberum*, *Daphnia parvula*, *D. catawba*, *Bosmina longirostris*, and *Cyclops sp.* were made from May 31 to August 11, 1969, and from June 18 to August 13, 1970. Most of the data presented in this paper are from the 1970 study.

To estimate birth and death rates I obtained measures of egg production in *Daphnia* and *Holopedium*. The lengths of all individuals were measured and the number of eggs in the brood pouch recorded. Ephyrial eggs were recorded separately. The number of adults was calculated as all individuals larger than the smallest size of first reproduction, which proved to be constant throughout the study period. Mean brood size per adult is simply total eggs divided by the number of adults in the sample.

Analysis

The calculations of rates of increase, modified from Edmondson (1960) and Hall (1964), require the following information over a time series: total population size, number of adults, mean brood size,

and egg developmental rates. The first three are estimated for the populations of Hummingbird Lake, and the data for egg development rates are taken from Hall's (1964) temperature-dependent measures on *D. galeata mendotae* and my own temperature data. Other estimates of development rates for *D. g. mendotae* (Jacobs 1961), *D. magna* (Anderson and Jenkins 1942, Green 1956, Obreskove and Fraser 1940), for *Ceriodaphnia reticulata* (Hall et al. 1970) and for *Bosmina longirostris* (Kerfoot, personal communication) are sufficiently similar to allow confidence in the applicability of these data to *Holopedium* and *Daphnia*. In subsequent calculations it will be necessary to assume that eggs are produced and hatched continuously, and that the population age distribution approximates the stable form.

We first derive an estimate of per capita rate of changes in density as follows:

$$\text{per capita rate of change} = dN/Ndt \text{ in units } 1/t \quad (1)$$

$$\text{and } dN/Ndt = \frac{d(\log_e N)}{dt} \quad (2)$$

$$\cong \frac{\log_e N_{t+\Delta t} - \log_e N_t}{\Delta t} \quad (3)$$

$$\begin{aligned} N_{t+\Delta t} &= \text{numbers at time } t + \Delta t \\ N_t &= \text{numbers at time } t \end{aligned}$$

This is the average derivative between the two points in time chosen for its calculation and, plotted at the midpoint, represents the rate of change at that instant in time.

An estimate of birth rate may be derived (from Hall 1964) as

$$\text{birth rate} = \frac{N_a \cdot \bar{E} \cdot 1/D}{N_t} \text{ in units } 1/t \quad (4)$$

where N_a = number of adults

\bar{E} = average brood size per adult

$1/D$ = fraction of egg development per day
(D = mean time required for egg development)

N_t = total population size

since the use of $1/D$ assumes a uniform egg age distribution, whereas a growing population has a skewed egg age distribution, a correction is necessary. Edmondson (1968) offers an estimator F that is the corrected fraction of egg development per day.

$$F = \frac{e^{-rD} - e^{-r(D-1)}}{e^{-rD} - 1} \quad (5)$$

Thus equation (4) becomes (Allan 1971)

$$\text{birth rate} = \frac{N_a \cdot \bar{E}}{N_t} \cdot F \quad (6)$$

We may now plot against time the estimates of population growth rate dN/Ndt and birth rate b ; then by interpolating to a common point in time and subtracting growth rate from birth rate, we obtain death rates at various points in time. This refers to an instant in time and may appropriately be termed d .

In estimating these population parameters we are implicitly assuming exponential growth over the specified time interval. Essentially, this forces any inhibiting effects of the approach to environmental carrying capacity ($1 - N/K$ of the logistic) into either the birth term or the death term. This is biologically reasonable as the feedback of $(K - N)/K$ can be expressed only as changes in b or d . Because b and d are formally defined for age-specific data from exponentially-growing populations with stable-age properties, I prefer to use the notation \hat{b} and \hat{d} to emphasize their nature as approximations to the true parameters.

Historically, there has been considerable confusion in the literature over the relationship between finite birth rates and instantaneous rates. The controversy arises when, in the field, birth rates are derived from a count of the number of births over a finite time interval, say $t \rightarrow t + \Delta t$. Then the issue reduces to determining the N which produced the births. This is because some newborn will be the progeny of females reproductive at time t , and some will result from females accruing to the population during the interval $t \rightarrow t + \Delta t$ because of population growth. Demographers approximate the birth rate by choosing the population density at the midpoint of the

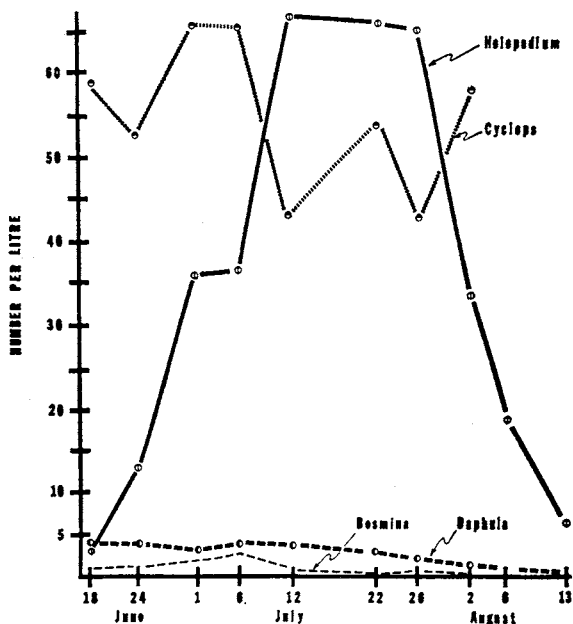


FIG. 8. Population densities of predominant zooplankters in Hummingbird Lake, 1970. Each point is based on two 1-litre samples from each of 6 sampling stations.

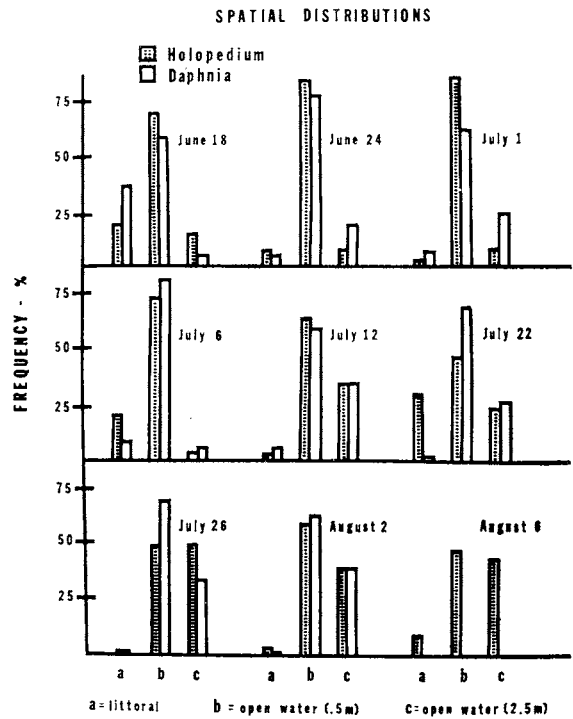


FIG. 9. Spatial distributions of *Daphnia parvula* and *Holopedium gibberum* in Hummingbird Lake, 1970. The percentage of total numbers represented in each of three spatial zones (littoral, shallow open water, deep open water) is plotted on the ordinate.

time interval as their estimate of N , although life table data are used to provide the more exact estimate (cf. Keyfitz 1968). This is a reasonable approximation for human populations, where the rate of population growth is generally less than 0.03, but becomes increasingly suspect for larger values.

However, the birth rate estimate in (6) derives from a single point in time. Converted to daily units of newborn by the factor F , it is an estimate of the instantaneous rate \hat{b} and requires no further manipulation. The assumptions involved in utilizing \hat{b} and dN/Ndt are continuous hatching of eggs and a stable age distribution. However, the error introduced is small and the results demonstrate reasonable behavior of these population parameters.

Results

During the study period *Holopedium* showed a pronounced increase with a peak throughout mid-July; *Daphnia* showed little population change (Fig. 8). In all cases there was little between-replicate variability, indicating that reasonable precision was obtained. The breakdown of population estimates by spatial regions (littoral zone, surface open water, deep open water) indicated that both species possess similar distributions (Fig. 9), and so are not escaping competition by habitat selection at that general

HOLOPEDIDIUM

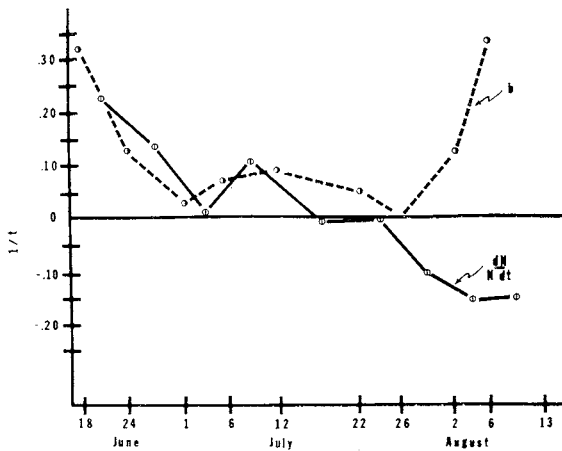


FIG. 10. Per capita rate of population growth (dN/Ndt) and birth rate (\hat{b}) for *Holopedium gibberum* in Hummingbird Lake, 1970. Rates are per day.

DAPHNIA

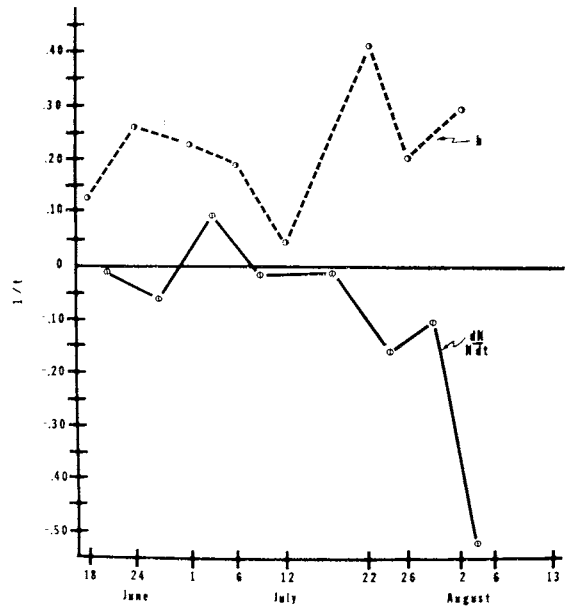


FIG. 11. Per capita rate of population growth (dN/Ndt) and birth rate (\hat{b}) for *Daphnia parvula* in Hummingbird Lake, 1970. Rates are per day.

level. There may be habitat partitioning on a finer scale or by differing vertical migration patterns; however, I have no data on this.

Census information is integrated in the estimates of dN/Ndt and \hat{b} . *Holopedium* has a high value of per capita population growth early in the study, followed by a fairly steady decrease (Fig. 10); this corresponds to the population's unimodal increase and decline. Instantaneous birth rate follows closely, and the smooth decline in \hat{b} indicates that *Holopedium* is approaching its environmental carrying capacity. Birth rate then increases sharply as the population reaches low levels in August. *Daphnia* shows quite the opposite dynamics (Fig. 11). Population growth rate is low and variable until turning sharply negative in early August, while \hat{b} remains high and variable. By subtraction, we may obtain the curves for death rates \hat{d} for each species (Fig. 12).

From the analysis of population phenomena we may state with confidence that *Holopedium* was relatively free from mortality until late July, when death rates rose from 0% to 15% per day. Conversely, *Daphnia* suffered high mortality throughout (20% per day), increasing to about 40% by late July. These values are within the range of those calculated by Edmondson (1960), Hall (1964), and Tappa (1965). The consistently high birth rate of *Daphnia* in Hummingbird Lake suggests that its resources remained plentiful throughout the study. Contrarily, *Holopedium* seems to have severely cropped its resource supply in the course of its burst of growth. Further, there is no evidence that *Daphnia*'s birth rate (and therefore resources) was affected by *Holopedium*'s increase (see Fig. 11). There appears to

DEATH RATES

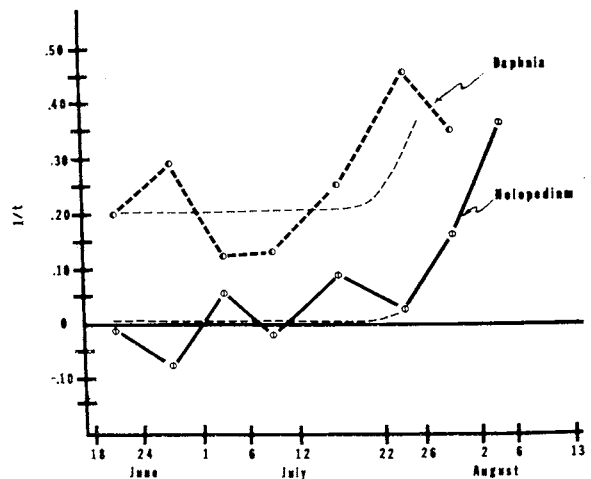


FIG. 12. Per capita death rate (\hat{d}) per day for *Daphnia parvula* and *Holopedium gibberum* in Hummingbird Lake, 1970. The smooth lines are fitted by eye. *Daphnia* suffers high mortality throughout the study.

be no significant competition between the lake populations for shared resources. The substantial discrepancy between *Holopedium*'s abundance and *Daphnia*'s low and declining population would not have been predicted on the basis of the competition experiments. From this analysis it is clear that the two populations behave quite independently of one another.

PREDATOR SELECTIVITY FOR *Daphnia* AND *Holopedium*

Previous results revealed that *Daphnia* suffered substantially higher mortality than did *Holopedium*. To evaluate the importance of mortality through predation in determining the relative abundances of *Daphnia* and *Holopedium*, I investigated phantom midge larvae (*Chaoborus* spp.) and perch (*Perca flavescens*) during 1969 and 1970. The only other likely predator, the cladoceran *Polyphemus*, was observed only occasionally, in the littoral zone, and since it occurred infrequently in samples probably did not constitute a significant source of mortality. The copepod (*Cyclops* sp.) was judged to be herbivorous on the basis of its morphology; this was verified in later experiments.

Perch

Methods.—Investigations of perch predation were based upon a pen enclosure experiment and on stomach samples. Adult perch (10 to 20 cm in length) were collected for stomach analysis by gill net in early August of 1969 and 1970; in each case 10 stomachs were examined for the presence of zooplankton prey. The pen enclosure was constructed out of nylon window screening (1 mm mesh) with a perimeter of 3 m by 5 m and placed in 3 m of water. The bottom was securely anchored in the soft mud bottom. All fish were removed and zooplankton populations were estimated inside and outside the pen from August 9 to September 10, 1969. The predominant zooplankters were *Daphnia parvula*, *Bosmina longirostris*, and *Cyclops* sp., but not *Holopedium gibberum*. Some zooplankton migration through the 1-mm mesh could presumably occur, but there is no a priori reason to expect a difference between immigration and emigration.

Results.—A comparison of zooplankton population densities inside and outside the perch enclosure from August 9 to September 10, 1969 gave no indication that reduced fish predation allowed increases in the number of zooplankters. Densities inside the pen mimicked outside densities well (Fig. 13); the only exception was the higher outside estimates of August 28 for *Cyclops*. Had the removal of planktivorous fish significantly reduced predation, populations should have increased inside the pen instead. It appears that perch predation had little if any impact on the populations of *Daphnia*, *Bosmina*, and *Cyclops*.

Stomach samples analyses corroborate the results of the pen experiment. Ten perch collected August 7, 1969, contained only *Chaoborus*. As *Holopedium* was absent from the plankton in 1969, these results emphasize only the absence of *Daphnia parvula* from perch stomachs. Examination of 10 more perch collected August 4, 1970, revealed large numbers of *Holopedium* mixed with *Chaoborus* in two stomachs

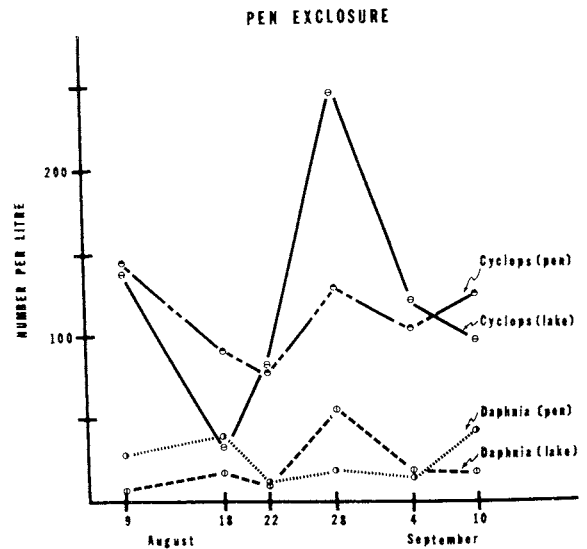


FIG. 13. Zooplankton densities inside and outside a fish enclosure, 1969. *Bosmina longirostris* was present at trace densities both inside and outside. No increase in density inside the pen was observed.

only; the remaining eight contained *Chaoborus*, and *Daphnia parvula* was rarely observed. It is of at least incidental interest that the larger *D. catawba*, which appeared very rarely in Hummingbird Lake in the August samplings, was observed in stomach samples far more frequently than its extremely low densities in the lake would have suggested. As Galbraith (1967) has demonstrated a sharp decline of perch interest in zooplankters under 1.3 mm, and, since both *Holopedium* and *D. parvula* average 1 mm or less, these results conform well to previous work.

Chaoborus

Methods.—*Chaoborus* densities are notoriously difficult to estimate as they are able to escape nets and traps by their rapid swimming movements and because they spend the day either in the mud zone or next to it. The third and fourth instar larvae (Fig. 1), which are the zooplankton-predatory stages (Berg 1937), show the strongest migration patterns (Teraguchi and Northcote 1966). Furthermore, at one particular time only one-sixth to two-thirds are out of the mud zone and represented in the density census (Berg 1937, Stahl 1966). On the basis of one all-night sampling sequence it was established that peak densities occurred at midnight. All subsequent sampling was conducted at that time. Three vertical hauls with an 0.22 m² plankton net were made from a depth of 5 m and at a point half-way between the two open-water stations. These samples were counted using the procedure described above for microcrustacea. Measurements were made of head length and inter-bladder length using the procedure of Teraguchi and Northcote (1966).

TABLE 3. Predation rates of the invertebrate predator *Chaoborus*, in numbers of prey items of *Bosmina*, *Cyclops*, *Daphnia*, and *Holopedium* consumed per predator per day. Data represent decrease in zooplankton density in experimental bottles with *Chaoborus* compared to control bottles

Date	Duration of experiment	Prey	<i>Chaoborus punctipennis</i> ^a	<i>Chaoborus nyblaei</i> ^a
August 9-11, 1969	59 hr	<i>Bosmina</i> ^b	3.99	Not tested
		<i>Daphnia</i>	0.88	Not tested
August 16-18, 1969	38 hr	<i>Bosmina</i>	Not tested	3.13
		<i>Daphnia</i>	Not tested	3.41
June 20-22, 1970	48 hr	<i>Holopedium</i> ^b	1.81	0.78
		<i>Daphnia</i>	3.12	1.74
		<i>Cyclops</i>	2.75	0.99
		<i>Holopedium</i>	0.64	0.22
July 5-7, 1970	48 hr	<i>Daphnia</i>	1.26	1.81
		<i>Holopedium</i>	0.43	0.88
July 13-14, 1970	24 hr	<i>Daphnia</i>	1.96	1.25
		<i>Cyclops</i>	0.26	1.34
		<i>Holopedium</i>	0.96 ± 1.01	0.63 ± 0.35
Mean, 1970		<i>Daphnia</i>	2.13 ± 1.21	1.60 ± 0.53
		<i>Cyclops</i>	1.51 ± 1.28	1.17 ± 1.30

^a20 individual predators were used in 1969; 10 were used in 1970.

^b100 individuals of each prey were used in 1969; 50 were used in 1970.

All predation experiments were conducted in 1-litre cylindrical bottles suspended in the lake at approximately 0.2 m depth for a given time interval (generally 48 hours). The bottles were filled with lake water first sieved through 220 μ bolting silk; then a predetermined number of zooplankters collected by townet was added to each. The experimental systems were randomly divided into lots, one left as a control and *Chaoborus* added to the other. In the 1969 experiments 100 *Bosmina* and 100 *Daphnia* were the prey items, and 20 individuals of either *C. nyblaei* or *C. punctipennis* were added to the predator treatment bottles. In the 1970 experiments 50 each of *Cyclops*, *Daphnia*, and *Holopedium* were added as prey and 10 individuals of either *C. nyblaei* or *C. punctipennis* as predators. The basic design consisted of 3 predation treatments by 3 prey items, with 4 replicates of each. Number of prey items remaining and the size frequencies remaining provided the basic data for analysis.

Results.—From the number of prey items remaining compared to controls, and from the number of predators, we may calculate a predation rate on each prey species per 24 hours. Size data comparing prey size distributions after predation to the control allow us to examine size-selectivity by *Chaoborus*. Finally, the predation rate information may be combined with the population density statistics of *Chaoborus* to estimate an expected death rate per day for each cladoceran. This is compared to the observed death rate calculated in the previous section to determine the contribution of *Chaoborus* predation to the total mortality rate.

The predation rates for each predator on each prey item are presented in Table 3 for all experiments. Based on the 1969 data, it appears that *C.*

nyblaei selected *Bosmina* and *Daphnia* equally, whereas *C. punctipennis* exhibits a strong preference for *Bosmina*. From the 1970 experiments, however, with a different plankton composition, strong preferences emerge for both predators over all prey items. The order of preference *Daphnia* > *Cyclops* > *Holopedium* holds for *C. punctipennis* in each experiment and for *C. nyblaei* in two out of three. The exception is July 13-14, when a slightly higher preference is shown for *Cyclops* than for *Daphnia*; *Holopedium* remains lowest in preference. The mean rate of removal of *Daphnia* is more than twice that of *Holopedium*, indicating that selective *Chaoborus* predation may explain the wide difference in observed mortality rates. Capture rates of from one to four prey items per predator per day seem reasonably high, and correspond well to the estimates of Dodson (1970) using *C. nyblaei* and *C. flavicans* as predators and *D. pulex* as prey.

Analysis of variance for the 1969 data with *Bosmina* and *Daphnia* bears out the significant effect of selection for *Bosmina* by *C. punctipennis* ($P < .001$). Separate analysis of each of the three 1970 experiments reveals highly significant differences ($P < .01$) between prey items chosen (Allan 1971).

The prey selection results with *Bosmina* and *Daphnia* suggested that selection could be based upon size, as *Bosmina* averaged only 0.33 mm to the latter's 0.79 mm. The role of size-selectivity was further considered by comparisons of prey size frequencies in the control and experimental bottles. The results of the 1970 experiments where all individuals were measured support the hypothesis of selection for smaller prey items (Table 4). In almost every case, the mean size was increased by the predation process; that is, predation was concentration upon

TABLE 4. Size-selection by the invertebrate predator *Chaoborus*, 1970 predation experiments. Data represent mean size of prey populations in experimental bottles with *Chaoborus* compared to control bottles

(a) Mean size of prey population (in mm) remaining after predation.						
Date	<i>nyblaei</i>	prey = <i>Holopedium punctipennis</i>	control	<i>nyblaei</i>	prey = <i>Daphnia punctipennis</i>	control
June 20	.791	.687	.648	.894	.846	.771
July 5	.496	.482 ^a	.486	.554 ^a	.667	.619
July 13	.468	.473	.447	.661	.694	.651

(b) Significant differences determined by the Mann-Whitney U-test.						
Date	N-C ^b	prey = <i>Holopedium</i> P-C ^c	N-P ^d	N-C	prey = <i>Daphnia</i> P-C	N-P
June 20	<.001	—	<.025	<.10	<.10	—
July 5	—	—	—	<.001 ^a	<.10	<.001
July 13	—	<.05	—	—	<.025	—

^aIn 2 cases out of 12, mean size decreased with predation. Only 1 is statistically significant.

^b= *C. nyblaei* compared to the control.

^c= *C. punctipennis* compared to the control.

^d= *C. nyblaei* compared to *C. punctipennis*.

smaller individuals. The only clear exception was *C. nyblaei* on *Daphnia*, July 5–7.

The size-selection emerged most strongly in the June 20–22 experiments in which the mean size of control individuals was high. On subsequent dates smaller prey items were used, particularly *Holopedium*. The selection effect was slight or non-existent with very small *Holopedium* (July 5–7, 13–14), suggesting that the mean size of these individuals approached the size of prey item selected by *Chaoborus*. With *Daphnia* the effect was never as strong, suggesting that a wider range of body sizes may have been taken. These data are based upon total length (excluding tail spine) and as *Holopedium*'s gelatinous sheath lends it a much larger volume for a given length (Fig. 1), these results are consistent with the overall hypothesis that *Chaoborus* selects smaller prey items. We may also note that even when the carapace plus sheath length of *Holopedium* averages less than *Daphnia* (July 5–7, 13–14), more of the latter are taken.

Prey selection in my experiments appears to be based upon at least two factors. Selection for smaller prey was suggested by the higher predation rates on *Bosmina* and by examination of size distributions remaining after predation. Size selection does not explain, however, why *Cyclops*, with an average size of 0.4 mm does not suffer higher mortality than *Daphnia*, nor why *Holopedium* does not sustain higher mortality in the July 5–7 and 13–14 experiments when its average size was considerably smaller than *Daphnia*'s. *Cyclops* was observed to swim faster than the cladocerans studied, suggesting one reason why its capture may be more difficult. Swimming behavior may affect visibility as well. *Holopedium* possesses the structural adaptation of an enlarged gelatinous sheath to increase its buoyancy (Hamilton 1958); possibly this makes it difficult to grasp.

Analysis.—The predation information may now be used to predict mortality in *Daphnia* and *Holopedium*. From estimated predation rates (Table 3) and predator density statistics (Table 5) we may calculate the expected daily death rate of the zooplankters due to *Chaoborus* predation (Table 6). As only a fraction of the larvae are represented in the density census at any one time, these expected death rates may be an underestimate.

Based on the expected and observed mortality rates, we may draw two conclusions. First, the estimates of percent mortality per day due to *Chaoborus* predation indicate mortality concentrated from two to several times as strongly on *Daphnia*, although the expected rates considerably underestimate the observed values. This discrepancy probably may be attributed to the anticipated underestimation of *Chaoborus* densities. Second, *Chaoborus* predation is a declining function over the summer because of the decline in its numbers, while total mortality is increasing (Table 6). Clearly additional predation pressure must account for this increase. The sampled perch did prey upon *Holopedium*, but based on evidence from gut samples did not take *Daphnia*. However, young of the year perch would not have been sampled by the gill net used because of their small size (35 to 55 mm by the first of August). As young perch of that size feed rather unselectively on cladocerans and copepods (Pycha and Smith 1954), this is a significant potential for mortality that was not investigated. Alternatively, freshwater planktivores (e.g., *Perca*, *Salmo*, *Coregonus*) generally switch their preferences as particular prey populations become abundant or rare (Brooks 1968). As the adult *Holopedium* population had increased from 1 or 2/litre to 24/litre by August 2 while *Chaoborus* (the primary food item observed in perch stomachs) had declined considerably, we may plausibly suggest

TABLE 5. *Chaoborus* densities, 1970. Each estimate is the mean of three vertical hauls taken at 12 AM. Numbers are per cubic meter

Date	<i>Chaoborus nyblaei</i>		<i>Chaoborus punctipennis</i>	
	\bar{x}	s	\bar{x}	s
June 22	39.7	13.3	40.0	1.0
July 6	25.0	1.7	34.3	21.2
July 23	36.3	2.5	4.7	2.9
August 4	19.0	9.5	2.0	2.7

TABLE 6. Expected mortality is the product of *Chaoborus* densities and mean predation rates, divided by observed prey densities. Observed mortality is the difference between birth rate (\dot{b}) and growth rate (dN/Nat). Note that expected mortality is several times higher on *Daphnia* than *Holopedium*. Data are percent mortality per day

Date	Expected mortality/day		Observed mortality/day	
	<i>Daphnia</i>	<i>Holopedium</i>	<i>Daphnia</i>	<i>Holopedium</i>
June 22	4.25	1.92	22.5	0.0
July 6	3.30	0.14	12.5	0.0
July 23	2.60	0.04	42.5	3.5
August 4	4.30	0.05	50.0	36.5

a change in perch feeding behavior towards cladocerans, accounting for the unexplained rise in mortality after late July.

Holopedium's declining birth rate could suggest starvation as an explanation for increasing death rate. However, a falling birth rate demonstrates only that the population is approaching its environmental carrying capacity, not that it is starving. *Daphnia*'s death rate rise parallels *Holopedium*'s and mean longevity in cladocerans is 8 to 10 weeks. Thus, increased predation is the logical explanation.

DISCUSSION

Plankton are widely acknowledged as a puzzling contradiction to competitive exclusion theory. Copepods illustrate some of the size-related feeding specializations familiar to terrestrial ecologists (Hutchinson 1951) and are known to feed selectively (Parsons and LeBrasseur 1970), but neither phytoplankton (Hutchinson 1961) nor cladocerans (Brooks and Dodson 1965) may be so easily resolved. Current theory of zooplankton population regulation holds that all zooplankton are equally adept at capturing small particles, but large zooplankters sustain higher filtering rates and may consume larger foods as well. Fish predation selective for larger zooplankters offsets the competitive advantage of large size (Brooks and Dodson 1965). Much of this has been documented (Brooks 1968, Burns 1969b, Dodson 1970, Galbraith 1967), and

graphical models based on these data provide reasonable predictions.

Resource partitioning would reduce competition and further complicate this model; at present, the evidence indicates some food selection may occur. Mechanisms of selection could involve chemical factors, particle shape as well as size, and the behavior of the grazer, where and how it feeds (Burns 1969a). As *Holopedium* tends to stay higher in the water column because of its gelatinous sheath, and was observed to do so in the competition bottles, this habitat differentiation may be one component of resource partitioning. Direct observations by Burns (1968) indicated qualitative differences in algal selection among daphniids. Using beads in suspension with two daphniids of the same size. Burns (1969a) found differences in size of particles consumed. Clearly the existence of particle selection is highly probable, although we understand little of the mechanisms. Finally, these grazers are known to differ in their ingestion and assimilation efficiencies on various foods (Schlindler 1969) and thus may show different dependencies on various algae even if they are equally adept at capturing particles.

In essence, the feeding relations among cladocerans are of unknown complexity. Opportunities exist for resource subdivision on the basis of habitat differences between *Daphnia* and *Holopedium* and possibly also through selective particle retention, although this point remains poorly understood. As to the relative importance of each resource compartment, we need not belabor the crucial role of algae. It appears that detritus rather than bacteria is likely to be next in importance (Jørgensen 1966, Riley 1970, Saunders 1969). *Daphnia* and *Holopedium*, as similar-sized filter feeders, should not differ greatly in their food potentialities. Yet the complexity of the feeding relations is sufficient to allow considerable partitioning. Thus the question as to what degree these two species may share resources is unanswerable without direct experimentation.

Niche overlap

Results of the competition experiments enable us to construct a simple model of niche overlap for *Daphnia parvula* and *Holopedium gibberum*. Although the coexistence of two species in nature need not invoke a competitive equilibrium explanation, bottle experiments provide an estimate of competitive relations based upon natural food resources. This independent assessment of competitive relations then may be compared with observed population abundances.

Experiments with labeled algae revealed that both intraspecific and interspecific competition are signif-

icant. Further, the effect of adding interspecific competition to the intraspecific component is equivalent for both species (note the lack of a species-by-mixing interaction in Fig. 2) implying that the overall impact of interspecific competition is to reduce the food acquisition of each population to the same extent. Considering each species separately, it appears that increasing *Daphnia* density exerts a strong negative effect on both species, whereas *Holopedium*'s effect is concentrated primarily upon its own population (Fig. 3: species-by-*Holopedium* density versus species-by-*Daphnia* density). Clearly, then, competition does occur and *Daphnia* is at an advantage with respect to the shared resources.

This information on competitive relationships allows the construction of a simple model of niche overlap for *Daphnia* and *Holopedium* based on the results with labeled algae, but which seems applicable to the detritus compartment as well. The lack of a species-by-mixing interaction (Fig. 2) indicated that each species suffers the same proportionate reduction in food uptake when subjected to interspecific competition. In the set theoretic notation for niches introduced by Hutchinson (1957), Fig. 14a is our first approximation, assuming the niches are of similar size.

The interspecific design, however, revealed a strong effect of *Daphnia* on both species, whereas *Holopedium* affected primarily itself. At first glance this contradicts our previous interpretation, suggesting that *Daphnia* should be the superior competitor. If, however, we consider that the impact of interspecific competition depends both on the competitive interactions within the zone of overlap and upon the relative importance of the zone of overlap (i.e., the relative sizes of nonoverlap regions to the overlap region), then the results become consistent. We simply require the non-overlap areas to be unequal in size.

This may be illustrated with a numerical example. Let $K_1 = 100$ and $K_2 = 50$, and let the two species utilize the shared resources in exactly the same manner. Then if all resources are shared, an individual of species 2 has twice the effect in utilizing resources as does an individual of species 1 (i.e., $\alpha_{12} = 2$), and conversely ($\alpha_{21} = 0.5$). Rather than assume complete resource sharing, let us suppose each species has some resources not available to the other, but maintain the proportionality between competitive ability and carrying capacity. Then $\alpha_{12} = c \cdot K_1/K_2$, $\alpha_{21} = c \cdot K_2/K_1$; for example, suppose $\alpha_{12} = 1$ and $\alpha_{21} = 0.25$. Solving the competition equations at equilibrium, we find $N_1 = 66.66$, $N_2 = 33.33$. Each species suffers a reduction of one-third of its potential population size in attaining equilibrium, but the competition coefficient of the rarer species is four times that of the commoner species. Although this simplistic example



FIG. 14. Venn diagrams of *Daphnia* and *Holopedium* niches. (a) First approximation: each species is equally affected by interspecific competition, suggesting some niche overlap and equivalent niche dimensions. (b) Second approximation: *Daphnia*'s superior ability to capture shared resources suggests that it is competitively superior in the zone of overlap. Thus for each species to be equally affected by interspecific competition, *Daphnia* must possess a smaller niche.

is fraught with assumptions, it serves to illustrate a basic point. Identity of competitive effects under Design I does not imply identity of competition coefficients unless the carrying capacities are equal. As Design II indicated that one species had a greater inhibitory effect in interspecific competition, a difference in carrying capacities is implicated.

More generally, if two species are conceptualized as sharing some resources and not others, then it is conceivable that one species may be less adept at capturing the shared resources but possess a broader niche. It appears that *Daphnia* is competitively superior in the zone of overlap as it affects *Holopedium* uptake but is not affected in return. Therefore *Daphnia* must have a relatively high dependence upon the overlap region; that is, the ratio area of niche overlap/non-overlap area must be high. And for *Holopedium* the converse should be true, generating the following model of niche relationships (Fig. 14b). If this is the case it would appear that the species with the broader niche is the poorer interspecific competitor, as Miller (1964) found in his study of four species of pocket gopher.

THE RELATIVE ABUNDANCES OF

Daphnia AND *Holopedium*

The niche overlap model based upon competition for ^{14}C -labeled food predicts that *Daphnia* and *Holopedium* should coexist in Hummingbird Lake, and that *Holopedium* should be somewhat more abundant than *Daphnia* (Fig. 14). As *Holopedium* exhibited a pronounced burst of growth while *Daphnia* remained low and declining, population abundances clearly do not support these predictions. Simply observing the density changes, we may postulate that in mid-June the environment changed, either becoming favorable solely to *Holopedium*, or becoming favorable to both but with *Daphnia* failing to compete successfully. However, neither view is consonant with the competition experiments.

The population analysis also revealed that *Daphnia*'s low densities do not reflect an inability to compete successfully. Rather, the high birth death rates indicate that *Daphnia* was too constrained by predation to develop the larger population its resource base would support. Substantially higher predation rates owing to prey selection by *Chaoborus* resulted in *Daphnia* mortality of 20% per day or higher in the June–July period of *Holopedium*'s burst of growth. However, the increased mortality later in the summer was not attributable to *Chaoborus* and may only speculatively be assigned to perch.

The theory advanced by Brooks and Dodson (1965) that larger zooplankters are better competitors but also are selectively cropped by vertebrate predators has received strong support for fish (Galbraith 1967, Brooks 1968) and salamanders (Dodson 1970). The size-selectivity of *Chaoborus* for smaller zooplankters suggests an additional factor to be considered in predicting plankton composition. Presumably *Chaoborus* will not find sufficient populations of suitable size prey in lakes where a vertebrate predator is absent, as was indeed the case in the study of Dodson (1970). The perch in Hummingbird Lake, although severe predators upon *Chaoborus*, are evidently of considerable importance in maintaining the latter's food supply by excluding the larger components of the zooplankton community.

To ask what the role of competition is in determining species abundances assigns considerable importance to competitive relations in nature, for it attributes to competition the controlling role in the system. It is hardly surprising, then, that in Hummingbird Lake competition did not play a deciding role in determining relative abundances. Analysis of population processes corroborated by studies of predator selectivity explains the discrepancy between field populations and the competition model. *Chaoborus* mortality concentrated on *Daphnia* places a severe constrain upon its potential population in-

crease. Although *Chaoborus* is selective for smaller sizes, the two zooplankters are sufficiently similar in length so that *Holopedium*'s gelatinous sheath may well be the major determinant of relative predation rates and relative abundances.

ACKNOWLEDGMENTS

This study benefited from the many helpful suggestions of my doctoral committee, consisting of F. F. Hooper, N. G. Hairston, J. T. McFadden, and D. Woodring. I am also indebted to Frederick Smith, John Vandermeer, and the members of the University of Michigan ecology group for sound advice on various phases of my research. Monte Lloyd was especially helpful in preparing the manuscript. Susan Allan shared in the field work and contributed much to the study.

This research was supported by National Science Foundation grants GB 5306 and GB 7840. I was supported by a fellowship from the Institute for Environmental Quality during 1970–1971.

LITERATURE CITED

- Allan, J. D. 1971. Competition and the relative abundance of two cladocerans. Ph.D. Thesis. Univ. of Michigan, Ann Arbor. 110 p.
- Anderson, B. G., and J. C. Jenkins. 1942. A time study of events in the life span of *Daphnia magna*. Biol. Bull. (Woods Hole) **83**: 260–272.
- Beauchamp, R. S. A., and P. Ullyot. 1932. Competitive relationships between certain species of fresh-water triclads. Jour Ecol. **20**: 200–208.
- Berg, Kaj. 1937. Contributions to the biology of *Corethra* Meigen (*Chaoborus* Lichtenstein). Det. Dan. Vidensk. Selsk. Biol. Medd. **13**: 1–101.
- Brooks, J. L. 1968. The effects of prey-size selection by lake planktivores. Syst. Zool. **17**: 272–291.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150**: 28–35.
- Burns, C. W. 1968. Direct observations of mechanisms regulating feeding behavior of *Daphnia*, in lake water. Int. Rev. Gesamten Hydrobiol. **53**: 83–100.
- . 1969a. Particle size and sedimentation in the feeding behavior of two species of *Daphnia*. Limnol. Oceanogr. **14**: 693–700.
- . 1969b. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. Limnol. Oceanogr. **14**: 492–502.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**: 392–402.
- Dodson, S. I. 1970. Complementary feeding niche sustained by size-selective predation. Limnol. Oceanogr. **15**: 131–137.
- Edmondson, W. T. 1960. Reproductive rates of rotifers in natural populations. Mem. Ist. Ital. Idrobiol. **12**: 21–27.
- . 1968. A graphical population model for evaluating the use of the egg ratio method for measuring birth and death rates. Oecologia **1**: 1–37.
- Galbraith, M. G. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. **96**: 1–10.
- Green, J. 1956. Growth, size and reproduction in *Daphnia magna* (Crustacea: Cladocera). Proc. Zool. Soc. Lond. **126**: 173–204.

- Hall, D. W. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. *Ecology* **45**: 94-112.
- Hall, D. W., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* **15**: 839-928.
- Hamilton, J. D. 1958. On the biology of *Holopedium gibberum* Zaddach. *Verh. int. Ver. Limnol.* **XII**: 785-788.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* **32**: 571-577.
- . 1957. Concluding remarks. Cold Spring Harbor. *Symp. Quant. Biol.* **22**: 415-427.
- . 1961. The paradox of the plankton. *Am. Nat.* **95**: 137-145.
- . 1967. A treatise on limnology. Vol. II. Wiley, New York. 1115 p.
- Jacobs, J. 1961. Cyclomorphosis in *Daphnia galeata mendotae* Birge, a case of environmentally controlled allometry. *Arch. Hydrobiol.* **58**: 7-71.
- Jørgensen, C. B. 1966. Biology of suspension feeding. Pergamon, London. 357 p.
- Keyfitz, N. 1968. Introduction to the mathematics of population. Addison-Wesley, Reading, Mass. 450 p.
- Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. *Ecology* **45**: 256-272.