

VERTICAL DISTRIBUTIONS AND PREDATION
ON PELAGIC ZOOPLANKTON
IN SHALLOW WATER BODIES

Guy Edmund Melville

A Thesis
in
The Department
of
Biology

Presented in Partial Fulfillment of the Requirements
for the degree of Master of Science at
Concordia University
Montreal, Quebec, Canada

May, 1979

© Guy Edmund Melville 1979

ABSTRACT

VERTICAL DISTRIBUTIONS AND PREDATION
ON PELAGIC ZOOPLANKTON
IN SHALLOW WATER BODIES

Guy Edmund Melville

Depth-specific sampling in a small Quebec pond from April to October 1977 revealed that instars of Daphnia pulex less than 1.41mm in length and instars of Diaptomus leptopus greater than 0.64mm in length consistently have distributions which are different from those of late instars of their predator Chaoborus americanus. Experiments were done to determine to what extent these distributions affect the rate of predation by Chaoborus. Vertical and horizontal 25 litre cages 1.4m long and small 2.5 litre cages, all containing Chaoborus-prey pairs, were introduced into a second pond for 3 day periods weekly from July to September. Predation rates in vertical cages were considerably lower than those in small and horizontal cage experiments. These results suggest that distributions of Diaptomus and small Daphnia in vertical cages reduced predation on them by Chaoborus. Where overlap of predator and prey is increased, i.e. horizontal and small cages, predation by Chaoborus is higher. Cooccurrence of a small crustacean zooplankton at low to moderate densities with a large invertebrate predator in a shallow water body may often be precarious without some degree of spatial separation of predator and prey.

ACKNOWLEDGEMENTS

To Dr. Ed Maly, my supervisor. I extend my sincerest thanks. He gave me an opportunity and his forbearance saw me through.

I thank the members of my committee, particularly Dr. E. MacLeod, for their criticism of the text of the thesis. I thank Bruce DeLong for assistance with the collection of zooplankton in Colorado.

To my wife, Cornelia, I express my most heartfelt gratitude. She willingly assisted in all phases of the project.

TABLE OF CONTENTS

	PAGE
LIST OF SYMBOLS	1
LIST OF FIGURES	2
LIST OF TABLES	3
LIST OF APPENDICES	4
INTRODUCTION	5
THEORY	7
Predation on pelagic crustacean zooplankton.	7
Predation by fish.	7
Predation by other vertebrates.	10
Predation by zooplankton.	11
Vertical distributions: effects on predation.	16
Fish	16
Zooplankton.	18
QUESTIONS ASKED	25
STUDY AREA	27
Communities.	30
MATERIALS AND METHODS	33
Sampling.	33
Field experiments.	35
Laboratory experiments.	42
Laboratory analysis.	43
Analysis of data.	44
Data comparisons.	49
<u>Diaptomus</u> copepodite population projections.	52

TABLE OF CONTENTS (cont'd)

	PAGE
RESULTS AND INTERPRETATIONS	53
Temporal relations of the pelagic zooplankton of Hill Pond.	53
Vertical distributions: day.	64
Influence of ambient light: day.	70
Vertical distributions: night	70
Long-cage predation experiments.	74
Predation rates: day versus night.	81
Predation rates: females with clutch.	83
<u>Diaptomus</u> copepodite population projections.	83
DISCUSSION	89
Vertical distributions, encounter probabilities and sampling.	91
Predation rates and impact assessments.	98
Age (size) specificity.	104
Other causes of distribution.	105
Limits to the importance of vertical separation.	107
CONCLUSIONS	110
REFERENCES	112
APPENDICES	118

1

LIST OF SYMBOLS

Symbols which are conventions are not listed here.

SYMBOL	DEFINITION
I	index of predator interest
t_1	time to 55% mortality for each immature lifestage
t_a	time to 55% mortality for adults
C1	<u>Chaoborus</u> , first instar
C2	<u>Chaoborus</u> , second instar
C3	<u>Chaoborus</u> , third instar
C4	<u>Chaoborus</u> , fourth instar
D.1.A	<u>Diaptomus leptopus</u> adults
D.1.B	<u>Diaptomus leptopus</u> copepodites IV, V
D.1.C	<u>Diaptomus leptopus</u> copepodites I, II, III
D.c.A	<u>Diaptomus coloradensis</u> adults
D.p.A	<u>Daphnia pulex</u> adult females
D.p.B	<u>Daphnia pulex</u> less than 1.41mm long
V	vertical
H	horizontal
VC	vertical control, prey, no predators
VP	vertical, prey and predators
HC	horizontal control, prey, no predators
HP	horizontal, prey and predators
S	surface
M	mid-depth
B	bottom
N_0, N_t	population densities, original and subsequent respectively
r	instantaneous rate of population growth
c	instantaneous rate of predation
P	predator density
t	time

LIST OF FIGURES

FIGURE	TITLE	PAGE
1	The study area.	28
2	Schematic representation of a long cage in a vertical position <u>in situ</u> , side view.	36
3	A standard curve for determining O_2 concentrations.	45
4	Size frequencies of the four <u>Chaoborus</u> instars.	46
5A,B	Temporal changes in each zooplankton category, over the whole water column of Hill Pond, on each sampling date in spring and summer, 1977.	54
6	The relative abundance of <u>Chaoborus</u> instars in Hill Pond on each sampling date.	60
7	Predator-prey relations confirmed in laboratory experiments.	63
8	Differences between the distributions of late instar <u>Chaoborus</u> and <u>Diaptomus leptopus</u> copepodites in Hill Pond during the day prior to August, 1977.	65
9	A comparison of the distributions of third instar <u>Chaoborus</u> and <u>Diaptomus leptopus</u> adults in Hill Pond over 24 hours (15,16 August, 1977).	73
10	The mean number of adult <u>Diaptomus leptopus</u> prey remaining in long-cage predation treatments after three days.	75
11	Long-cage predation experiments.	76
12	The mean number of immature <u>Daphnia pulex</u> prey remaining in long-cage predation treatments after three days.	79
13	Long-cage predation experiments.	80
14	Hypothetical <u>Diaptomus</u> copepodite population projections.	87
15	Surface temperature and O_2 data for Hill Pond and Lower Lake, 1977.	119

LIST OF TABLES

TABLE	TITLE	PAGE
1	The open water zooplankton community of Hill Pond.	29
2	The schedule of starting dates of long-cage replicates.	41
3	Approximate maximum size of prey that each instar of <u>Chaoborus</u> can ingest with complete success.	47
4	Codes for probability ranges.	51
5	The mean number of prey eaten per <u>Notophthalmus</u> per hour during the day in small tanks in the laboratory.	57
6	The mean number of <u>Diaptomus leptopus</u> adults eaten per fourth instar <u>Chaoborus</u> per day in small tanks in the laboratory.	62
7	A summary of t-test statistics for all Hill Pond zooplankton distribution comparisons.	67
8	Depth of the mode of the adult <u>Diaptomus leptopus</u> population under different ambient light conditions during the day.	71
9	Anova statistics from long-cage predation experiment comparisons.	77
10	The mean number of adult <u>Diaptomus coloradensis</u> eaten per fourth instar <u>Chaoborus</u> during the day and night.	82
11	The mean number of adult <u>Diaptomus coloradensis</u> (any females non-gravid) and <u>D. coloradensis</u> females with clutch eaten per fourth instar <u>Chaoborus</u> per day.	84
12	Parameters used in hypothetical <u>Diaptomus</u> copepodite population projections.	86

5

4

LIST OF APPENDICES

APPENDIX		PAGE
1	Some physical data for Hill Pond and Lower Lake.	118
2	Chemistry of the waters of Hill Pond and Lower Lake.	120
3	The main species in the zooplankton communities in the Arboretum ponds and Lower Lake.	121

INTRODUCTION

The research presented in this paper concerns mainly:

- (1) the vertical distributions of pelagic crustacean zooplankton and their main predators,
- (2) the effect of vertical distributions on rates of predation hence the abundance of prey populations,
- (3) and various consequences of (1) and (2) in terms of zooplankton community structure,

in relatively shallow water bodies. I had chosen to study predation because it is one of the functional ecological mechanisms most often considered to generate the structure and dynamics of zooplankton communities (e.g. Brooks and Dodson, 1965). I had chosen to study predation in relation to vertical distributions in relatively shallow water bodies because this aspect has not been adequately considered in them, even though most hypotheses concerning predation on zooplankton have originated from studies of it in such systems.

To orient the reader, background information on this area of study is presented under THEORY. In that section, I first present current general concepts with respect to predation (vertebrate and invertebrate) on pelagic crustacean zooplankton, mainly in terms of effects on the distribution and abundance of species of different sizes and behaviors. The aspect of vertical distributions and some effects on predator-prey relations is then introduced. After THEORY, the actual questions which I asked are presented (see QUESTIONS ASKED).

The section RESULTS AND INTERPRETATIONS is organized primarily around the answers to my questions, but the general temporal relations of the pelagic zooplankton of Hill Pond, the system which I chose to work on,

are presented first. Hopefully, these general relationships will put the answers to the questions more into perspective with respect to the zooplankton community there. The most general aspects of Hill Pond and its environs are presented beforehand under STUDY AREA.

Finally, it may help the reader if I review the basic life histories of the three main Arthropod groups: copepods, cladocerans and chaoborids, he will encounter through out this paper. Copepods generally have thirteen life stages, the first of which is the egg. Eggs are deposited in an external "sac", which may be carried and then dropped, or dropped almost immediately. The next eleven stages are larval stages. Each of the first six is termed a nauplius, and each of the last five is termed a copepodite. It is in the initial copepodite stage that the morphology of the organism first resembles that of an adult, the thirteenth stage.

The number of stages or instars, both immature and reproductive, in the Cladocera is more variable. In Daphnia there are from three to six immature instars and perhaps as many as twenty reproductive instars. All instars of Daphnia have the same general morphology. Eggs are generally carried for a time in a dorsal brood pouch, and it is here that the young may develop. Most of the information in this and the preceding paragraph comes from Hutchinson (1967).

Chaoborus usually has four larval instars and a pupal stage, all aquatic (e.g. Fedorenko and Swift, 1972). The adults, flying insects, emerge to mate and reproduce. Eggs are laid on the surface of the water. The life cycle is generally one year (the organism overwinters in the fourth larval stage), although some species e.g. C. trivittatus have been found to have a two year cycle. In the latter, the organism spends two winters (and the intervening time) as a fourth instar larvae.

THEORY

Predation on pelagic crustacean zooplankton.

Predation by fish.

In this section I concentrate on fish predation mainly in terms of its effect on the distribution and abundance of zooplankton species of different sizes and behaviors.

The work of Brooks and Dodson (1965) on the plankton of nine small Connecticut lakes and ponds provided impetus to the study of mechanisms generating the structure and dynamics of plankton communities. They found that small crustacean zooplankters such as Bosmina longirostris, rather than larger crustacean zooplankters of the genera Daphnia and Diaptomus, were the most abundant zooplankters in the presence of planktivorous alewives (Alosa aestivalis, A. pseudoharengus). Large invertebrate predators such as Leptodora kindtii, Epischura nordenskioldi and Mesocyclops edax were also among the zooplankton generally absent from lakes containing Alosa. Larger zooplankters were the most abundant in the absence of piscine planktivores. Brooks and Dodson stated that the modal size in the presence of Alosa was 0.285mm, whereas the modal size in the absence of Alosa was 0.785mm. They concluded that the absence of large zooplankters was the result of intensive predation by alewives. They also suggested that in the presence of such a predator, large zooplankters are likely to be eaten before they reach reproductive age.

Brooks and Dodson also noted that other factors must also be considered because, for example, Diaptomus minutus and not Cyclops bicuspidatus was eliminated from lakes containing Alosa, even though the smallest female instars of both species were of similar size.

Gailbraith (1967) investigated the influence of zooplankter prey

size on predation by rainbow trout (Salmo gairdneri) and yellow perch (Perca flavescens). He measured the length of the carapace of prey found in the stomachs of the fish, then compared these lengths with the size range of the zooplankters found in the two Michigan lakes from which he took the fish. He discovered that both species ate mainly Daphnia and that 96% of the Daphnia in trout guts and 82% of those in perch guts exceeded 1.3mm, even though half the Daphnia taken from the lake at the time of the comparison were less than 1.3mm in length.

Gailbraith also compared the width of the space between the gill rakers in the trout to the length of the zooplankters found in the stomachs. Although the zooplankters found in the stomach were generally greater than 1.3mm in length, approximately half of the intervals between the gill rakers were less than 1.1mm. Only Daphnia longer than 1.3mm were found in the guts of trout that had been observed feeding on Daphnia. He concluded that both species must have actively selected for large prey organisms since indiscriminate sieving would have provided the fish with a greater number of animals between 1.1 and 1.3mm in length.

Gailbraith also noted a trend towards smaller zooplankton species in Sporey Lake, Michigan, after the introduction of trout in 1959. Prior to 1960 Daphnia pulex, a relatively large zooplankter, had been abundant, but by 1961 few D. pulex attained maturity. Only a few reproducing individuals were found at that time, having a mean size of 1.2mm, just below the minimum size at which they would fully interest trout. This size was considerably smaller than 1.8mm, the mean size at maturity prior to 1960. Smaller Daphnia species appeared, but these too declined in abundance by 1964. By this time populations of the small cladoceran Bosmina and other species had become established. Some Daphnia

persisted but they were not abundant.

Brooks (1968) provided size selection data for Alosa pseudoharengus. His approach was to investigate size specific survival of zooplankters in the presence of Alosa, rather than zooplankter mortality as a result of piscine predation. Zooplankton from Bashan Lake, which did not contain alewives, were introduced into a 250 l. aquarium containing a school of young Alosa, and the remaining zooplankton were sampled at fifteen minute intervals thereafter over a one hour period. Large Daphnia were consumed immediately hence Brooks used Diaptomus minutus as his indicator species. He compared times to 55% mortality for each Diaptomus life (size) stage and found that predation was inversely proportional to length. As expected, Alosa readily ate prey which were much smaller than the smallest prey eaten by trout and perch.

Brooks then quantified further the relationship between prey size and "predator interest". He determined predator interest for trout and perch from the data of Gailbraith (1967) by comparing the number of stomachs containing various sizes of Daphnia to a standard number of stomachs containing Daphnia 1.9mm long. For Alosa (feeding on D. minutus) he used as his interest index the following relationship (my formulation):

$$I = t_i^{-1} t_a$$

where I was the index of interest and t_i and t_a were the times to 55% mortality for a particular immature lifestage and adults respectively. These comparisons were then expressed as percents. Trout and perch had much more restricted zooplankton diets (restricted interest) than Alosa (sustained interest). The use of the phrase sustained interest by Brooks was of course relative; although Salmo and Perca lost interest in prey which were less than 1.5 and 1.3mm long respectively, Alosa eventually

began to lose interest in prey which were less than 0.7mm long. If an Alosa population in a small system did not lose interest, it would probably reduce its zooplankton prey to such an extent that the Alosa population would be jeopardized by a lack of food. However, Alosa continued to take zooplankton prey down to at least 0.2mm in size in Brooks experiment, and had to do so in the Connecticut lakes of Brooks and Dodson (1965) because there was little else of larger size to sustain the Alosa population. In contrast, Salmo and Perca switched to prey other than zooplankton at zooplankton prey sizes less than 1.5 and 1.3mm respectively.

Hence, Brooks (1968) categorized species having sustained interest as obligate planktivores and those having restricted interest and the ability to quickly switch as facultative. Whereas most fresh water planktivores appear facultative, Alosa is not. Brooks (1968) attributed Alosa's obligate mode of feeding to its pelagic marine background where there was little food other than plankton. Clearly, an obligate planktivore will have the most dramatic effect on the composition of the zooplankton; only the smallest of zooplankters can survive in the proximity of such feeders, unless the system is large. Small populations of large zooplankters can persist with facultative planktivores in smaller systems.

Predation by other vertebrates.

Other vertebrates also eat zooplankton; salamanders, for example, are often important in smaller aquatic systems. Salamanders are ambush predators which wait for or slowly stalk prey, whereas fish, which are much more motile, generally search for prey. Salamanders prefer even larger prey than facultative fish planktivores.

Aquatic mammals, such as baleen whales, also eat zooplankton in the oceans, but little quantitative data exists on this subject.

The classification "vertebrate predation" may be inaccurate. Young or small cephalopods and other invertebrates with well developed eyes may prey on zooplankton, in which case the classification "visual predation" would be more appropriate.

Predation by zooplankton.

The work of Fryer (1957) on the food of certain fresh water copepods provided some of the impetus to the study of predation by zooplankton on other zooplankton. Hall (1964) did not determine rates of predation by predaceous zooplankters in Baseline Lake, but suggested that the average summer loss rate of $28\% d^{-1}$ for Daphnia galeata mendotae was primarily a result of predation. The predators Hall mentioned included Leptodora which reached densities of 13 per 100 l. in midsummer in 1961, and Chaoborus, the densities of which were not determined. The results of gut analyses showed that the fish present in Baseline Lake did not feed extensively on D. galeata. These observations formed the basis of his suggestion above.

Brooks and Dodson (1965) stated that predation by invertebrates could be significant in some lakes but they did not think it to be as important as fish predation. Hall et al. (1970) also thought fish predation to be more important than invertebrate predation. Many studies, some of which were reviewed by Hall et al. (1976), have suggested otherwise.

Anderson (1967) found that Diaptomus shoshone ate from 4 to 9 Diaptomus tyrelli predator⁻¹ d^{-1} depending on the light and temperature conditions. He did not say whether the latter were adults but did state

that only smaller D. tyrelli were taken by D. shoshone (late copepodites?) and that most eggs, and perhaps most egg-bearing females, escaped predation. Anderson (1970) found that D. shoshone could eat as many as 12.3 prey (less than 0.9mm long) predator⁻¹d⁻¹, and that D. shoshone preferred copepods to cladocerans. Maly (1976) also found D. shoshone to be a voracious predator. Copepodites IV through adult ate small diaptomid copepodites to some extent, but ate D. coloradensis nauplii at a high rate when nauplii were alone or when the nauplii were offered amongst a selection of other zooplankton. Diaptomus shoshone has also been found to be abundant. Dodson (1970) found it to be present at least part of the summer in 13 of 15 mountain ponds, and present all summer in all of 9 more ponds.

Confer (1971) found that Mesocyclops edax could eat as many as 1.30 Diaptomus floridanus copepodites predator⁻¹d⁻¹, and that Mesocyclops preferred D. floridanus to Daphnia ambigua. Mesocyclops also preyed on the smaller copepodites. No nauplii were made available to Confer's Mesocyclops, which might have selected more for nauplii than copepodites had they been present.

Like Diaptomus shoshone, both Mesocyclops edax and Cyclops bicuspidatus (another copepod predator, McQueen, 1969) have been found to be abundant. Patalas (1971) found the latter two to be among the six most widely distributed and abundant zooplankton in 45 Ontario Lakes.

Confer and Blades (1975) found that Epischura lacustris, also a wide-spread genus, could eat as many as 2.2 nauplii or 1.9 small copepodites (0.34 to 0.54mm long) of Diaptomus sicilis predator⁻¹d⁻¹.

Thus, several studies showed that predatory freshwater copepods, representative of highly motile zooplankton predators, were voracious predators and selected for the smaller life stages of their preferred prey species, often copepods. Dodson (1974a) consolidated these findings and

proposed that, in general, invertebrate predators select small prey. He found that Daphnia minnehaha was excluded from experimental cages after one month by its predator there, Diaptomus shoshone. Daphnia minnehaha, although of intermediate size, was small relative to most of the prey zooplankters that were available to D. shoshone in the cages.

Dodson (1975) found zooplankton predation to be very important in shallow arctic ponds, but that the zooplankton communities were much more complex than temperate pond zooplankton communities. The trophic structure was not hierarchical. He found that Acanthocyclops vernalis produced eggs while eating Heterocope, and a few weeks later Heterocope matured on a diet of A. vernalis nauplii.

The predators which I've discussed so far in this section have all been found to be highly motile. Diaptomus shoshone, for example, exhibited short bursts of rapid swimming with coasting between the bursts, as opposed to the smoother, slower swimming exhibited by the small herbivore Diaptomus tyrelli (Anderson, 1967)

Ambush predators e.g. the phantom midge, Chaoborus, have also been found to occur in the zooplankton. Dodson (1970) found that C. flavicans could eat as many as 4.4 small daphnids predator⁻¹d⁻¹ and C. nyblaei could eat 3.9 of the same predator⁻¹d⁻¹, although at high daphnid densities. Sprules (1972) found C. americanus to be a voracious predator, but that it preferred copepods when they were presented to Chaoborus in the same vessel.

Fedorenko (1975b) found that Chaoborus americanus and C. trivittatus were significant predators on a variety of zooplankters. For example, fourth instar Chaoborus of both species could eat over 20 small Diaptomus tyrelli predator⁻¹d⁻¹ albeit at high D. tyrelli concentrations of 60 to 80 l.⁻¹. References to Chaoborus by these and many other authors (e.g. Lance, 1974) indicated that Chaoborus were also widespread.

Dodson (1970) proposed that an invertebrate predator in the zooplankton

was a "dependent" predator, which relied for its existence on the presence of a highly selective vertebrate predator. He suggested that the neotenic form of the salamander Ambystoma tigrinum in deep subalpine ponds excluded its preferred (larger) food items, thus favouring the presence of suboptimal (smaller) prey which were the preferred food of his dependent predator Chaoborus americanus. He also suggested that the suboptimal (to the vertebrate predator) prey species were the only suitable prey species for the dependent predator. This logic contradicted his most important findings, but the contradiction was concealed by the organisms he chose to discuss as prey to Ambystoma. In his study, which lasted ten weeks, he considered only Daphnia as prey to Ambystoma, although gut analysis showed that plankton were the major food of Ambystoma only during the first few weeks of development. After that Ambystoma ate mainly insect larvae (particularly Chaoborus larvae) and amphipods. This observation suggests that Dodson's selective predator, Ambystoma, should have eliminated Chaoborus his dependent predator. Sprules (1972) data support this contention; he found that one neotenic Ambystoma removed 8 fourth instar Chaoborus in half a day at the relatively low Chaoborus density of 0.25 l.^{-1} in 40 l. aquaria in the laboratory. However Ambystoma did not eliminate Chaoborus in the deep subalpine ponds studied by Dodson (1970) and Sprules (1972). I return to this problem in the DISCUSSION.

Reseachers have also observed Chaoborus populations in lakes without vertebrate predators. Swift and Fedorenko (1972) found populations of Chaoborus americanus and C. trivittatus in fishless Eunice Lake in British Columbia, and Pope et al. (1973) found that fishless lakes in the Matemek River systems in Quebec contained abundant Chaoborus .

Confer and Blades (1975) proposed what some people might consider an alternative to Dodson's (1970) second predatory dependency hypothesis.

"Since predacious zooplankton (also prey to fish) are much larger and more visible to the fish than their own (the fishes') prey, this more than compensates for the energy lost by the additional trophic level and the moderate ability of predacious zooplankton to elude capture."

(Confer and Blades, 1975)

Thus, the success of the vertebrate predator could depend more on the presence of an invertebrate predator. The work of Davis (1976) on Hogan's Pond supported this contention. Davis found that the 1973 year class of the stickleback in Hogan's Pond had developed when there was an unusually large standing crop of Epischura. He also concluded that the 1973-year class of the stickleback was an extremely successful one because of the number of stickleback adults taken (presumably by him) in 1974. It may have been that survival of the stickleback juveniles in 1973 was greatly enhanced because there were so many optimal prey that year.

The hypotheses of Dodson (1970) and Confer and Blades (1975) I return to in the DISCUSSION.

Gerritsen and Strickler (1977) proposed that the presence of faster-moving potential prey allowed the existence of secondary ambush predators such as Chaoborus, Diaptomus coloradensis and Daphnia rosea, both small and slow moving (relative to Diaptomus shoshone, for example), have been found to be the only prey available to Chaoborus in the deep subalpine ponds of Sprules (1972) and others. Thus, the generalization of Gerritsen and Strickler (1977) was exaggerated.

This concludes my discussion of predation per se. Again, I have restricted it mainly to the effects of predation on the distribution and abundance of crustacean zooplankton species of different sizes and behaviors. Other topics, such as cyclomorphosis and polymorphism

(including intraspecific variation in the size at which females mature) in cladoceran prey species, have been related to predation by both vertebrate and invertebrate predators but are beyond the scope of this paper (see Brooks, 1965, 1966, 1968; Jacobs, 1965, 1966; Green, 1967; Zaret, 1969, 1972a, b; Dodson, 1974b; Zaret and Kerfoot, 1975; Kerfoot, 1975, 1977a, b, 1978 and others).

Vertical distributions: effects on predation.

Spatial considerations are extremely important in dealing with aquatic systems. In the last section I introduced space in the sense of the whole system. It is possible to subdivide this system horizontally or vertically. On a horizontal plane, one can define pelagic and littoral habitats; on a vertical plane, one can define strata of water of differing physical, chemical and or biological characteristics. In this section, I discuss movement of pelagic organisms in a vertical plane.

Fish.

Vertical distributions of fish have been extensively studied, often with respect to their prey. Roger and Grandperrin (1976) considered the "space-time components" of trophic interactions in the pelagic tropical Pacific in relation to energy transfer. To do this, they examined vertical distributions, vertical migrations, stomach contents and feeding rhythms of successive links of a pelagic food chain. The problem was relatively easy to analyse because many of the species did not migrate outside certain strata, the space scale over which they worked was large (depth intervals of 450 metres), and the fact that they were only interested in the number of animals of a species eaten by a second species between each trophic level. Roger and Grandperrin

found that tuna (Thunnus alalunga, T. albacares) and their prey, micronektonic fish, were epipelagic. They remained above 450 metres, and fed only during the day. The prey of the micronektonic fish, mainly the euphausiid Stylocheiron were also epipelagic and fed during the day. Thus, this segment of the food chain did not benefit from the large biomass of the migrating micronektonic fish (e.g. Myctophidae) and euphausiids (Euphausia, Thysanopoda) which came up only at night. The latter fed on epipelagic prey, and were either nocturnal or continuous feeders (with respect to the continuous, they may have been feeding below as well). Thus, the resultant of energy transfer through this chain was towards the bottom.

Begg (1976) explored the relationship between the diurnal movements of the sardine Limnothrissa miodon and some of the zooplankton in Lake Kariba, Rhodesia. He found that the sardines spent most of the day, and the middle of the night, between 12 and 25 metres as a shoal, although they sometimes went deeper during the day if there was enough O_2 . At dusk and at dawn they scattered at the surface. Bosmina longirostris, the major prey of the sardine in Lake Kariba, spent most of the day in deep waters. Bosmina came to the surface only in the middle of the night, and descended long before dawn. When O_2 was low Bosmina stopped above the thermocline. Since Limnothrissa distributed in a manner different from Bosmina during several periods over the course of a day, migration of fish and food organisms were probably independent responses to light intensity stimuli. The fish simply fed on Bosmina whenever they met, usually at night. Although planktivorous fish were known to be visual feeders L. miodon fed on Bosmina during both the day and the night; Begg did not know how L. miodon selected Bosmina in the dark.

There are instances where vertical distributions should have been given more consideration. Brooks and Dodson (1965) emphasized that Alosa eliminated the larger zooplankton from many of the Connecticut lakes, but only gave passing reference to the continued existence of Senecella calanoides below 80 metres in Lake Cayuga, New York, which contained Alosa.

No one seems to have documented studies where the vertical distributions of fish, in relation to those of their prey, have been monitored or manipulated experimentally, probably because of the great distances over which fish can move and the speed with which they can do so.

Zooplankton.

Many investigators have found different zooplankters to have different vertical distributions in the water column (e.g. Raymont, 1963). Few investigators have incorporated consideration of vertical distributions into zooplankton predation studies. Confer (1971) stated that the predator Mesocyclops edax and its prey Diaptomus floridanus had similar distributions in the water column in Anderson-Cue Lake. Begg (1976) found Mesocyclops leukartii to be generally below 20 metres during the day in Lake Kariba, but that they rose to the surface at night where potential prey e.g. rotifers were generally found.

Pearre (1973) and Fedorenko (1975a,b) presented two of the most complete studies incorporating vertical distribution and zooplankton predation. Pearre worked with the chaetognath Sagitta elegans, an ambush predator (Gerritsen and Strickler, 1977), in Bedford Basin, Nova Scotia. From his analysis of feeding behavior Pearre concluded that Sagitta underwent extensive vertical migration and that it could not have been detected from distributional data alone. Apparently time spent in the

upper waters was only concerned with hunting and was short. Because of rapid turnover of large Sagitta in the surface waters, they never contained a large standing population. In such a case, if only a few members of the population were engaged in migratory activity at any time real migrations would appear to be essentially stationary modes and there would be no need for a significant nighttime shallow mode. Pearre's data do show a slight decrease in the depth of the mode of Sagitta at night, when more Sagitta were found with prey in the guts, most of which were surface living copepods.

Fedorenko (1975a) worked with Chaoborus americanus and C. trivittatus in Eunice Lake, British Columbia, and found that the diet was determined largely by spatial availability of prey, although prey size placed an ultimate limit on vulnerability. For, example, the most diverse diet was that of fourth instar larvae, particularly T4o (fourth instar Chaoborus trivittatus in their second year) because they could handle nearly all prey sizes and encountered all prey types in their extensive, diel vertical migrations. Also, the diel feeding activity of T4o on Diaptomus kehai and on Bosmina (the main prey of T4o) was highest at the time of maximum spatial overlap between predator and prey. This occurred at night in the case of T4o.

Fedorenko (1975b) also calculated the number of each particular prey type removed by a larval instar from any depth zone. She multiplied the density of the predator at that depth by the predator's feeding rate at the prey density found there. This calculation was done in her estimation of the predation impact of Chaoborus larvae in Lake Eunice.

Few investigators have considered vertical distributions of zooplankters in shallow waters, even though it has been known since the turn of the century (Fordyce, 1900), if not before, that zooplankton in such systems

can have particular vertical distributions. Dumont (1972) is the only investigator I know of to have considered the above with respect to functional relationships; he interpreted reverse vertical migrations of several zooplankters in Lake Donk, Belgium, to be mechanisms to avoid interspecific competition for space. More will be said of this study below. Nobody I know of has considered predation with respect to vertical distributions of zooplankton in relatively shallow systems, a serious omission. Dodson (1970, 1974a), for example, proposed two hypotheses concerning zooplankton predation in general as a result of work done on alpine and subalpine ponds. However, in both studies he took all his quantitative samples at mid-depth. With respect to the whole water column, this procedure would have been adequate only if all the animals distributed randomly (or evenly) and, within species, had similar biologies (e.g. body sizes, behaviors) throughout the column.

Dumont (1972) is the only investigator I know of who has attempted to experiment, albeit inadequately, with functional ecological mechanisms of zooplankters in relation to vertical distributions, and in artificial water columns which approached the scale of the natural water column from which the zooplankters tested were taken. Although he was concerned with competition, I deal with his study extensively here mainly because he may in fact have been studying predator-prey interactions. He first observed what appeared to be (they may not have been; see below) opposite patterns of migration in Bosmina sp. (spp?) and the rotifer Asplanchna priodonta, i.e. Bosmina seemed to migrate up at night and down during the day, while Asplanchna seemed to do the reverse, in Lake Donk (maximum depth, 3.2m) in 1964 and early 1965. He thought that by doing this the two species were avoiding competition with one another for space. In an

attempt to test his idea he built two plexiglass columns 2.5m long, which he placed in a vertical position in Lake Donk. He then enclosed a "pair" of supposedly competitive zooplankton "species" in the tubes for 24 to 48 hours on three different occasions, twice in 1966 and once in 1967. The first two pairs consisted of unidentified Daphnia and cyclopoid species, while the third pair consisted of Asplanchna priodonta and cyclopoid copepods of which the most numerous was Cyclops vicinus vicinus. The densities of experimental animals in the columns were somewhat greater than their densities in the lake (the control). The distributions of the animals were (partially; see below) monitored via sampling in both the columns and the lake over the experimental periods, and he implied that a significant difference between the (partial) vertical distributions of paired groups was proof of competition between them.

Dumont's (1972) experimental design was inadequate. An observation alone that two species may have occupied different portions of a water column was by his own admission, not enough to confirm that the species in question were competing; a difference in any one of several physical, chemical or biological factors to which one species was adapted and the other species was not could have caused a difference in distributions. However, confinement of test pairs which supposedly competed for vertical space to just a vertical column(s), as Dumont did, did not test his hypothesis. In vertical columns, the organisms could have distributed exactly as they did outside the cages (provided of course that any other environmental parameters essential to the wellbeing of the animals were not substantially altered). The animals were not placed in a situation where the availability of the resource, their space, was (more) limiting, where one might have expected one or both groups to show some adverse

effect as a result of the resource limitation if the groups were competing. Several ways in which he could have restricted the groups to the same stratum of the water column would have been to use small cages or to have placed long cages in a horizontal position (as I have done; see QUESTIONS).

Dumont increased the density of the two groups in the tubes relative to their densities in the lake, in an attempt to increase the dichotomy between the migration patterns of the groups being tested. Increasing the densities to enhance other effects of competition might have been acceptable if he had used small or horizontal cages as suggested above (provided interspecific competition was more important than intraspecific competition). Misinterpretation of results (interspecific competition for vertical space) could be the consequence of increasing animal densities in vertical cages. Since the organisms in Dumont's cages could still have migrated, animals might have aggregated mainly in their respective ends of the tubes and suffered (increased) intragroup competition.

There are many other problems with Dumont's (1972) work. As I've alluded to previously, it is not possible to form an adequate picture of the depth distributions of the animals for which results were reported. The reason: although his experimental columns were 2.50m deep, and the reported depths of sampling stations were 1.30 and 2.25m, he only sampled at points 0.20m above the bottom and 0.20m below the surface (except on one occasion, when he found a relatively uniform distribution in the cycloids present). Obviously the animals in most of the water column were unaccounted for. Apparent migrations over the period of the whole study were variable, particularly those of the cycloids. Perhaps

the inadequate sampling design was responsible for some of the variability. A second problem is that, although the apparent opposite patterns of migration observed in the field were strongest in Bosmina and Asplanchna, Bosmina was not among the species tested, and Asplanchna was used only in the last of the three experiments. A third problem is that many of the animals were not identified as to species. The use of several species in each half of a test pair may have caused some of the variability in his results. Finally, his experiments lasted only 24 to 28 hours, too short for zooplankton competition experiments even if his design had been adequate.

In Dumont's (1972) first experiment, both groups declined drastically in relative abundance over periods less than twelve hours, possibly as a result of O_2 depletion. Oxygen levels were low in the lake at the time and the solid container walls would have prevented lateral mixing of lake water, albeit poorly oxygenated, with O_2 depleted container water. Dumont used fewer animals in his second experiment because of similar O_2 conditions. In his third experiment both groups used also exhibited mortality, particularly Asplanchna. Apparently the water was well oxygenated, so asphyxia could not be used to explain the patterns and mortality there.

A fact (other than asphyxia) that could have explained Dumont's results, particularly those of his third experiment, was that all the predominant cyclopoids Dumont found in Lake Donk, hence those which he used in his experiments: Acanthocyclops robustus, Mesocyclops leukarti and Cyclops vicinus, have been described elsewhere as voracious predators of zooplankton (e.g. Fryer, 1957). Dumont did identify Cyclops vicinus as being the dominant cyclopoid in his third experiment; Oliva and Sládacek (1950; cited in Fryer, 1957) described C. vicinus as attacking

even axolotl salamanders 2.0cm long. It is inconceivable that Dumont did not recognize this fact i.e. that he was using predator-prey groups rather than competitors, especially in light of the observation below that he made in the laboratory.

"Repeatedly it was seen how some Cyclops clashed with Asplanchna. Frequently, the weak integument of the latter was hereby so damaged that death followed quickly."
(Dumont, 1972)

Other observations could have been used to support the predation conclusion. Dumont observed significant mortality, particularly of non-cyclopoids, in experiments one and three, where the densities of the zooplankters were greatest. In both cases the mortality of the non-cyclopoids preceded the mortality of the cyclopoids. In one cage in experiment three the function of the decrease in density of Asplanchna was a negative exponential, characteristic of the prey population response in some planktonic predator-prey interactions (Maly, 1976).

No one I know of has (intentionally) used full scale experimental enclosures for studies of predation (or competition) in relation to vertical distributions of zooplankters. Had Dumont (1972) realized he was using predator-prey groups and had he carried out controls in experimental columns, he could have presented predation rate data for the whole water column, but not for animals confined to the same stratum. Since he did not present the density of Cyclops vicinus in experiment three, it is not possible to calculate the rate of predation on Asplanchna.

QUESTIONS ASKED

I chose to study the vertical distributions of pelagic crustacean zooplankton in relation to the vertical distributions of potential predators in a small pond, mainly because:

- (1) such relationships had not been adequately studied in relatively shallow water bodies. Despite this fact a considerable number of hypotheses e.g. those of Dodson (1970, 1974a) have been generated concerning the general importance of predation on zooplankton from studies of it in such bodies of water.
- (2) the pelagic water column was of a scale which could be manipulated experimentally in its entirety.

With respect to vertical distribution and predation on zooplankton, the questions I asked were:

- (1) Where do the predators and their prey distribute in the water column during the day in the pond? Are the distributions separate to a significant degree? Females with clutch comprise one prey group which I mention here, and which the reader should keep in mind below, because the clutch obviously represents many vulnerable individuals in which considerable resources have been invested.
- (2) Where do both groups distribute in the water column at night? Again, is there a significant degree of spatial separation between the predator and the prey?
- (3) If there is little separation during one of these periods, when might the predators have a higher rate of predation - during the day or the night?
- (4) What proportion of females with clutch are taken with respect to their abundance?

- (5) If there is significant separation at any time, what will the rate of predation be if I enclose a water column containing a specific predator-prey pair in a vertical cage? In this cage the animals will, hopefully, distribute the way they do outside the cage in the pond. Will the rate of predation increase if I enclose the water column with animals in a similar cage in a horizontal position, confining predator and prey to the same stratum? Will the latter rate be similar to the rate of predation in small (shallow) vessels, similar to those used by other investigators (e.g. Dodson, 1970; Sprules, 1972; Allan, 1973; Fedorenko, 1975b)? Some of these investigators (e.g. Dodson, 1970; Allan, 1973) applied a single predation rate attained in small vessels to the whole water column.
- (6) If the predation rate increases with confinement to one stratum, how might this increase affect the abundance of prey over a period of time?
- 3

STUDY AREA

The work was carried out during 1977 on the zooplankton of Hill Pond (Fig. 1B), representative of three twelve year old man-made ponds (Fig. 1A) in the Morgan Arboretum on the Macdonald campus of McGill University.

The three ponds were similar to each other in most respects.

Hill Pond was situated in a clearing in mixed Hardwood forest on high ground. It had neither inlet nor outlet; precipitation, snowmelt and seepage provided the water. The shore and sediments were of grey-brown clays.

The pond was about 0.02ha in surface area and the depth, as measured in the N.E. pool, dropped from 2.5m early in the spring to 2.0m in midsummer. The minimum depth rarely fell below the latter, even during periods of no rain. The pond was ice-free by early April and frozen over by November. Temperatures reached a maximum of 28.5°C in late July, 1977.

The water was often turbid in the N.E. pool, and little vegetation covered the bottom. The N.W. shore of the pool was free of vegetation while the rest of the shore and all of the narrow, shallow S.W. arm of the pond were overgrown with Typha latifolia. Leaf litter input was relatively low in the deep N.E. pool.

A second pond, Lower Lake (Fig. 1A), was selected for cage experiments because cages placed in Hill Pond suffered vandalism and inadvertent human interference. Lower Lake was one of two man-made (1967) ponds on the same high ground as the other three ponds, but on Macdonald farm immediately south of the Arboretum. This pond was similar to Hill Pond in many physico-chemical respects, but differed from the latter in that it lay in a depression amid cornfields rather than deciduous forest,

FIG. 1. The study area. A. Arboretum and farm. a,b the other arboretum ponds. B. Hill Pond.

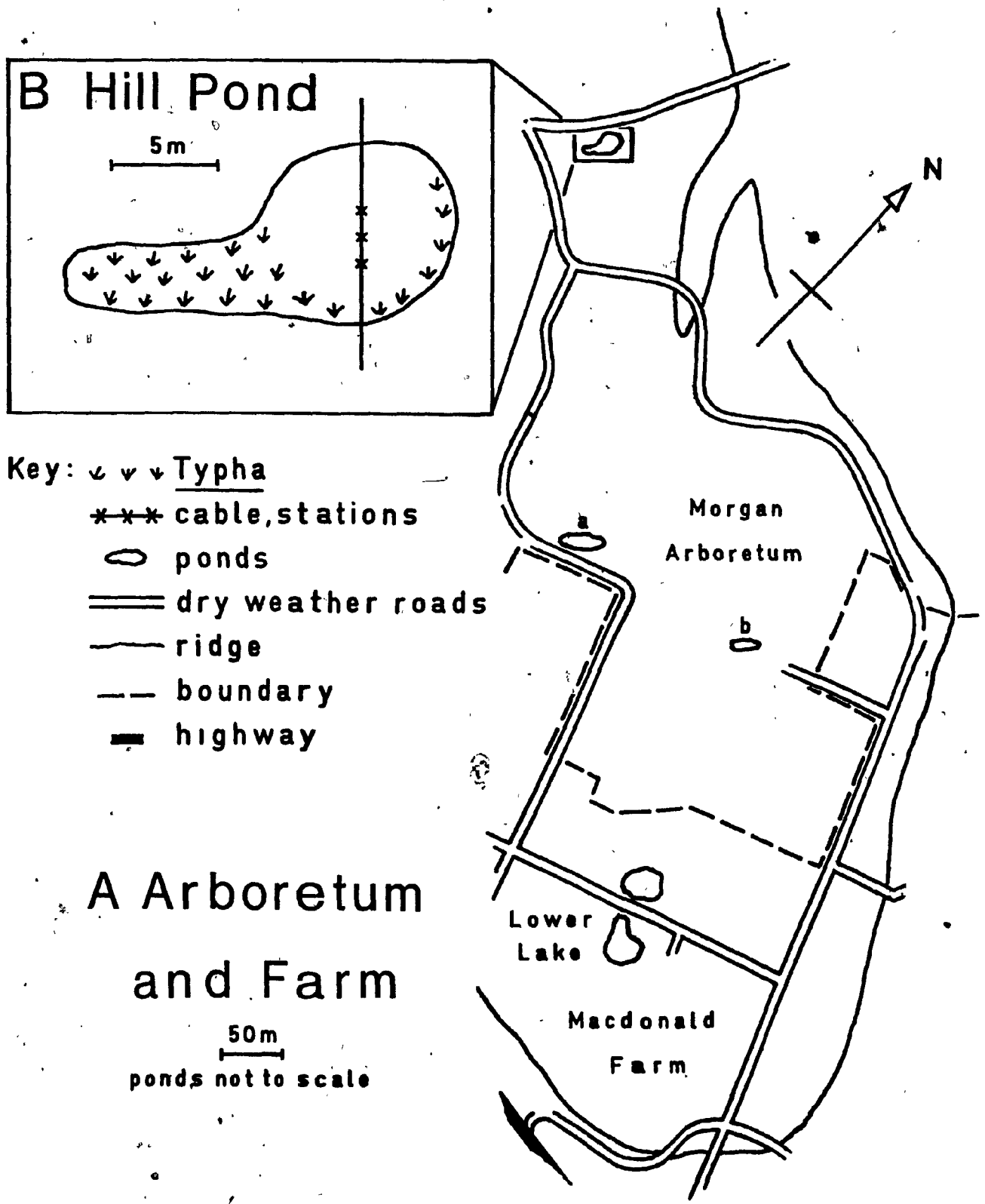


TABLE 1. The open water zooplankton community of Hill Pond.

Species	Class	Order	Trophic status
<u>Diaptomus leptopus</u>	Crustacea	Copepoda	filter feeder
<u>Daphnia pulex</u>	Crustacea	Cladocera	filter feeder
<u>Chaoborus americanus</u>	Insecta	Diptera	ambush predator
<u>Notophthalmus viridescens</u>	Amphibia	Urodela	ambush predator

Diaptomus and Daphnia classified according to Edmondson (1959), Chaoborus according to Johannsen (1970) and Notophthalmus according to Bishop (1967) and Wilt and Wessells (1967).

hence received considerable nutrient input by way of organic fertilizers applied to the fields (Ali Khan, 1971). It had approximately ten times the surface area of Hill Pond, and was less turbid, allowing greater light penetration. As a result of these factors, Lower Lake was more productive; unlike Hill Pond Cladophora insigna and other filamentous algae (Ali Khan, 1971) matted the bottom. Lower Lake received little leaf litter input. Typha had overgrown the east, N.E. and western shores.

Surface temperatures and dissolved O_2 data for 1977 are presented in Appendix 1 (includes Fig. 15). Concentrations of various chemicals in the water, as measured on 25 August, 1977, were comparable for the ponds (Appendix 2).

Communities.

The main species in the zooplankton communities described below are summarized in Appendix 3.

The open water zooplankton community of Hill Pond (Table 1) was similar to that found in the "deep" subalpine ponds 1 and 12 of Sprules (1972) and Dodson (1974a). The most abundant organisms included the large invertebrate ambush predator Chaoborus americanus Johannsen, 1903, the calanoid Diaptomus leptopus S.A. Forbes, 1882, and the cladoceran Daphnia pulex Leydig, 1860, emend. Richard, 1896, although Daphnia was abundant only for several weeks in late spring. Daphnia pulex, a filter feeder, was similar in size to the "small" Daphnia rosea and Daphnia minnehaha of Sprules (1972) and Dodson (1974a), while Diaptomus leptopus, also a filter feeder, was somewhat larger than their small Diaptomus coloradensis. The salamander Notophthalmus viridescens viridescens, a vertebrate predator, was also abundant in both adult and larval forms.

Notonectids (predatory hemipterans) were abundant near the surface,

but were rarely taken in subsurface samples in this pond. Bosmina (?) sp., Scapholeberis kingi Sars, 1903, and Simocephalus vetulus Schödler, 1858, all filter feeding cladocerans, and a few immature cyclopoid copepodites were taken occasionally on some (although not necessarily the same) sampling dates. Individuals of the Protozoa, Rotifera, Oligochaeta, Acari or Tardigrada were also occasionally taken. Other animals sighted from time to time in the open water included Rana pipiens tadpoles and predatory insects in the orders Coleoptera and Odonata.

Phytoplankton in the open water were scarce. Filamentous Spirogyra sp. and colonial Eudorina sp., both chlorophytes, were the most common but numbered only a few thousand units l^{-1} in the samples analyzed.

The animal community in the Typha was much more complex, containing all of the above species, except the main pelagic zooplankters, in greater abundance. Chaoborus and late instars of Daphnia were rare there, and Diaptomus was less abundant. Young instars of Daphnia were abundant, but again only for a short time. Amphipods and various molluscs, not found in the open waters, were found in Typha. Since the area overgrown with vegetation supported a community that was essentially different from that in the open water, I only deal with it peripherally.

Open water communities in the two other Arboretum ponds (Fig. 1A) were similar to that of Hill Pond except that Scapholeberis was present instead of Diaptomus as the smaller of the two main filter feeding species in one of the ponds. There appeared to be only one plankton community in each of these ponds since neither was overgrown to a great extent by Typha.

The open water zooplankton community in Lower Lake during the period of cage experiments was generally similar to that in Hill Pond. At mid-summer late instars of Chaoborus and their prey, Daphnia, were few

in number. Two other small herbivores, Ceriodaphnia and Bosmina, rather than Diaptomus, were present. Both cladocerans were minor species in Hill Pond and one of the Arboretum ponds as well.

The main representative vertebrate predator in Lower Lake was the yellow perch (Perca flavescens), introduced there in 1971 (R. Watson, personal communication). According to Brooks (1968) and others such an introduction could have accounted for the low abundance of Daphnia and Chaoborus, the absence of Diaptomus and the abundance of such very small crustaceans as Ceriodaphnia and Bosmina. Diaptomus leptopus was present in Upper Lake, which was adjacent but not connected to Lower Lake. I saw no fish in Upper Lake.

Certain small animals which were occasionally present in Hill Pond were much more abundant in Lower Lake; these animals included various representatives of the Protozoa, Rotifera, Cyclopoda, Oligochaeta, Acari and Tendipedidae.

The phytoplankton in Lower Lake was much more diverse than that in Hill Pond. The chlorophytes Scenedesmus sp. and Cosmarium sp. were abundant, as was the chrysophyte Chrysophærella sp..

MATERIALS AND METHODS

Sampling.

Comparisons among zooplankton communities from the Arboretum ponds were based on the data from qualitative plankton tows taken in June, July and August 1976, while the community in Lower Lake was established from data obtained in similar fashion in the summer of 1977.

Quantitative sampling of Hill Pond was done between 10:00 and 16:00h, weekly, from 01 April to 27 September, 1977, for a total of 23 sampling dates. Samples were taken with a 2.1 l. ⁻¹ Van Dorn bottle from a dinghy moored to a cable suspended N.W. to S.E. over the center of the N.E. pool (Fig. 1B), perpendicular to the long axis of the pond. Samples were taken at the surface, middle, and bottom (0.20, 1.2 and 2.0m respectively), at points 3.0 (prior to 20 July), 4.0 and 5.0m from the N.W. shore along the cable. If sampling was done before 13:00h, sampling was started from the S.E. This schedule prevented shading of the sampling station by the dinghy until the sampling was finished.

At each depth the open Van Dorn bottle was moved horizontally through a distance twice its length, parallel to its long axis (also perpendicular to the direction of the sun) before the messenger was released. Thus the bottle was given no chance to wobble nor to rotate.

Also, a diel series consisting of five sets of samples was taken, the first set at 19:00h on 15 August and one set every six hours thereafter. Each set consisted of six samples, one from each depth at 4.0 and 5.0m from the N.W. shore along the cable. At night no lights were used until after all six samples were taken.

Each sample was concentrated when transferred from the Van Dorn

bottle to a small vial via a nylon net with 50 μ mesh (all mesh sizes mentioned below are 50 μ , except where otherwise noted). Each sample was transferred again to a large vial, and anything remaining on the net and small vial was washed into the large vial with filtered pond water. The net was checked immediately after sampling, particularly after sampling in the dark; rarely had animals not been washed off. Samples were preserved in 70% ethanol and 2% glycerin in the large vial.

Densities of adult Notophthalmus in Hill Pond were estimated by marking the north bank at 1.0m intervals and, when the water was clear, counting the number of salamanders per interval to a distance 2.0m from shore in each case. Since Notophthalmus were red and often sat motionless on the bottom, here devoid of vegetation, they were easy to count. This method revealed little about the density of adults in the deep water and in the Typha, where they could not be seen, and little about the density of larvae, many of which were small enough to escape notice in such a count. However, adults frequently came to the surface in the deep water and in the Typha. No Notophthalmus were removed permanently because the total population in the pond was not great. Frequent removal over a relatively short period of time would have depleted the salamander population, in turn which would have altered the structure of the zooplankton community in Hill Pond.

Water temperature, light penetration, prevailing weather conditions and O₂ content were monitored, all at the time of sampling on each sampling date. The water temperature at 0.30m was recorded with a hand held Canlab thermometer. Light penetration was gauged using a Secchi disc. Oxygen content was determined in the following manner: water samples were collected in 300ml D.O. bottles at a depth of 0.30m, fixed (including the addition of sulfuric acid) within two minutes using the Winkler

method (Cox, 1976), wrapped in dark paper and refrigerated until analysis could be completed in the lab (within 48 hours). Water temperatures and O_2 concentrations are presented in Appendix 1.

Chemical analyses of Hill Pond and Lower Lake were carried out with a Lamotte Co. water test kit on 25 August, 1977 (see Appendix 2).

Field experiments.

Six 25 l. cages were constructed, each consisting of a cylindrical sock of commercial nylon mesh 1.4m long by 0.16m in diameter fastened to a wooden frame with Lepage's Contact Cement (Fig. 2). The length of the cages was chosen to approximately coincide with the minimum mid-summer depth (2.0m) of Hill Pond; 1.4m of height kept cages placed in a vertical position 0.30m above the bottom and 0.30m below the surface. The former eliminated interference from sharp projections on the bottom which might have damaged the mesh, and the latter reduced cage visibility to passers-by to some extent. A container diameter of 0.16m was found by observation in the lab to have little effect on the relative small-scale horizontal movements of the experimental organisms. The cylindrical shape eliminated corners in which animals might have concentrated.

The mesh was of consistent size i.e. each aperture was pentagonal in shape and had a long diagonal of 300 μ . The next largest dimension was just over half the latter. Thus free interchange of water, small particulate matter and small or vermiform organisms such as rotifers, nauplii, young *Bosmina*, and oligochaetes could take place, while large test organisms could not pass through.

One end of each cage was bounded by a canvas funnel, rather than mesh, with a hole 2.0cm in diameter at the apex through which test organisms were introduced or removed. During experiments this port was

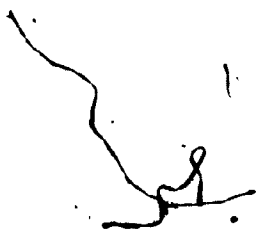
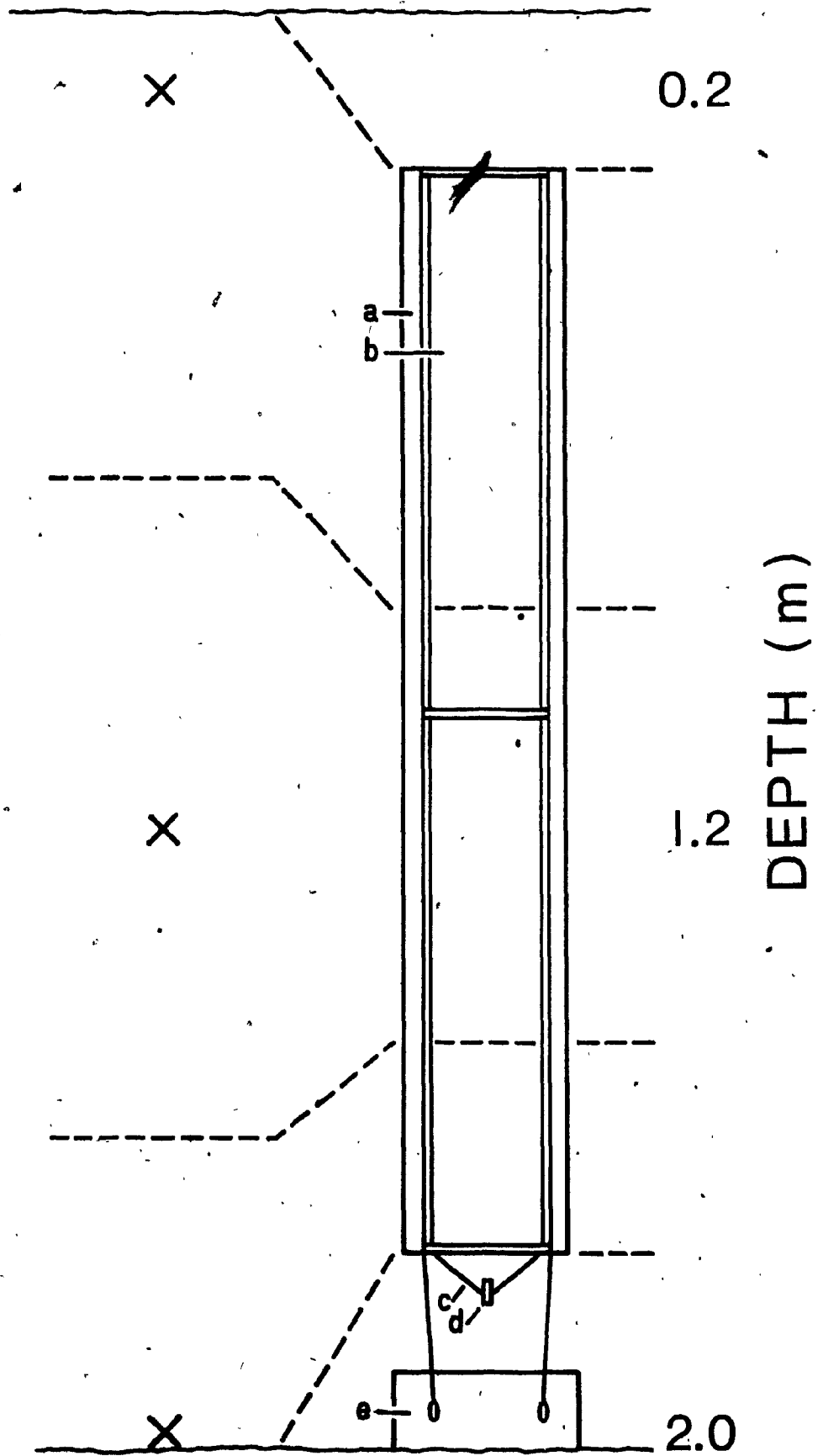


FIG. 2. Schematic representation of a long cage in a vertical position in situ, side view. (a) wooden frame, (b) mesh cylinder, (c) canvas funnel, (d) cork plug, (e) anchor, (X) depths sampled, (---) boundaries of arbitrary zones for long-cage experiment density determinations (see Analysis of data)



plugged with a cork, and the cork was secured with an elastic band wrapped around both the end of the funnel and the cork.

Cages were held in place in the pond by anchors, vertical cages by an anchor fastened to the funnel end and horizontal cages by anchors from both ends. The wooden cage frames were buoyant, hence the cages needed no added flotation to keep them up in the water column.

Cylindrical, opaque polyethylene 2.5 l. cages, 0.14m deep and similar in diameter to the long cages, were also built. Each cage had five windows 39.7cm^2 of the same mesh used in the long cages, three at equal intervals around the equator of the cage, and one in the middle of both the bottom and the lid of the cage. These cages were suspended from styrofoam floats and held in place by anchors.

Diaptomus adults (D.1.A) and fourth instars of Chaoborus (C4) to be used in the cage experiments were collected by net from Hill Pond within one week prior to the start of each set of experiments. Early instars of Daphnia (D.p.B) were raised in an artificial pond in the laboratory at ambient Hill Pond temperatures and a 12:12::L:D light cycle. Predators and prey were held in separate aquaria, containing filtered pond water, in the shade under conditions of natural light and temperature. Predator tanks were stocked with low densities of small prey for predator maintenance while prey were fed from mixed green algae cultures every other day.

Sorting of prey species for experiments was begun approximately thirty hours before the experiments were to start for early instars of Daphnia (D.p.B) and four hours before for Diaptomus adults (D.1.A). Water containing prey was siphoned from a holding tank into a large petri dish and individual prey, picked randomly, were pipetted into clear plastic containers, one container per treatment or cage to be

placed on that date. Containers received one animal at a time, i.e. no container received a second until one animal had been added to each of the others, to assure equal overall animal handling time to each treatment. Once the required number of prey had been allotted to each of the latter, fourth instar Chaoborus (C4), the predator, was sorted in the same way. Most C4 had some digested prey material in the hind gut.

The method used to justify animal densities used in all experiments is detailed under Analysis of data.

To initiate a long-cage treatment, the cage was submerged horizontally below the surface of the water, except for the open funnel end, and the prey introduced via plastic funnel and hose through the opening. The empty prey container, funnel and hose were washed with filtered pond water and this rinse water was then added to the cage. Each cage was oscillated end to end slightly to distribute prey organisms, then the predators were introduced in the same fashion. The cage was stoppered, an anchor attached, and the cage slowly sunk. Any trapped air was forced out by applying mild pressure to the bubble caught under the mesh.

Cages were arranged randomly on an east-west axis, parallel to the long axis of Hill Pond. Vertical cages were positioned with mid-cage at mid-depth, and small and horizontal cages at mid-depth. The horizontal cages were marked with a small cork on a chord, and the study site was marked with a float offset to the N.W.

Treatments were terminated in the order they had been set up. To terminate a long-cage treatment, the cage was brought to just below the surface, and the anchor(s) removed. The cage was positioned vertically with the funnel end down, then it was slowly brought out of the water which concentrated the remaining organisms in the funnel. The mesh was washed with pond water as the cage was drawn out. The contents

concentrated in the funnel were poured into a container, the funnel washed with filtered pond water, the predator(s) (if present) removed from the container (were kept for other experiments), and any prey remaining in the container preserved with 4% formalin if Diaptomus, 70% ethanol and 2% glycerin if Daphnia.

All experiments were of three days duration since relatively severe changes in the density of prey enclosed with predators occurred over longer time periods in preliminary test.

Four replicates of each long-cage treatment were done using Diaptomus adults (D.l.A) as prey (no females with clutch), and two replicates were done using early instar Daphnia (D.p.B) as prey. The schedule of starting dates of long-cage replicates is presented in Table 2. The symbols VP and VC represent cages which were placed vertically and contained prey with and without fourth instar Chaoborus (C4) respectively. The symbols HP and HC represent cages which were placed horizontally and contained prey with and without C4 respectively. No replicates are indicated for some treatments on some dates (Table 2). Each of these replicates had been interfered with and lost. A lost replicate was redone on a subsequent date along with the replicate scheduled for that date. This is why there are two replicates for one treatment on some dates in Table 2.

In the small-cage experiment (similar in depth to the cages of Sprules (1972) and others), Diaptomus adults (D.l.A) were used as prey for fourth instar Chaoborus (C4). Three controls containing D.l.A alone, and three replicates containing both D.l.A and C4 were used; starting 31 August, 1977.

All cage experiments from which results could be obtained were carried out in Lower Lake. Experiments attempted in Hill Pond in early

TABLE 2. The schedule of starting dates of long-cage replicates.

Week beginning	Prey category	No. replicates				
		VC	VP	HP	HC	
August	1	D.1.A	1	1	1	1
	8	D.1.A	1	1	1	1
	22	D.1.A	1	-	-	1
	29	D.1.A	1	2	2	1
September	5	D.p.B	-	1	1	1
	12	D.p.B	2	1	1	1

summer were lost through human interference.

Laboratory experiments.

All laboratory experiments were done in 2.5 l. aquaria having the same dimensions as the small cages used in the field. Collection, maintenance, and sorting of the animals used in the experiments were the same as for the field experiments, except for Notophthalmus. The latter were trapped in the field the day before the experiments, and were not fed between the time of capture and the start of the experiments.

To determine whether Chaoborus had a higher feeding rate during the day or the night, Diaptomus coloradensis adults (D.c.A) were used as prey for fourth instar Chaoborus americanus (C4). These animals were obtained from pond 12 of Sprules (1972) and Dodson (1974) in July, 1978. The treatments during the day lasted from dawn (06:00h) to dusk (21:00h), a total of 15 hours, while the treatments at night lasted from dusk to dawn, a total of nine hours. Two controls, each containing 25 D.c.A alone, and two replicates, each containing 25 D.c.A and 5 C4, were done during each of two time periods. Water temperatures fluctuated from a minimum of 11°C at 06:00h to 15°C at 21:00h.

To determine what proportion of female Diaptomus with clutch were taken with respect to their abundance, Diaptomus coloradensis adults (D.c.A) were again used as prey for fourth instar Chaoborus (C4). Two controls were done, each containing 12 D.c.A (any females were non-gravid) and 12 D.c.A females with clutch, but no C4. Two replicates, each containing the same complement of Diaptomus as the controls plus 5 C4, were also done. The experiment lasted 24 hours, and the water temperatures were the same as those in the experiment described previously.

In experiments to establish trophic relationships, early and late instar Daphnia (D.p.B and D.p.A respectively), both alone and mixed, were used as prey for single adult Notophthalmus. Mixed Daphnia and adult Diaptomus (D.l.A) were also used as prey for single larval Notophthalmus. Prey densities varied. These experiments were carried out for one hour at 20°C.

An experiment in which D.l.A were used as prey for C4 was also done; it duplicated in the laboratory the small-cage field experiment. Three replicates of both treatments were included. This experiment lasted three days and was done at a water temperature of 20°C and a 12:12::L:D cycle.

Laboratory analysis.

Individuals of all species except Chaoborus and Notophthalmus were identified using Edmondson (1959). Characters by which the species were classified were viewed at different magnifications on a Wild M5 stereo-microscope. Chaoborus was identified first by Dr. P.J. Albert using Johannsen (1970), and Notophthalmus was keyed using Bishop (1967) and Wilt and Wessells (1967).

All individuals from field samples and experiments, except Notophthalmus, were counted and measured under a Jena binocular dissecting microscope, Chaoborus at 12.50 magnification and all other zooplankters at 31.25 magnification. Each animal was placed on its side and the antenna removed the animal did not lie flat. An ocular grid was used to measure the animals e.g. the metasome of the copepods and the carapace, from the tip of the helmet to the base of the tail spine, for cladocerans. Measurements were accurate to the nearest 0.01mm. The Wild M5 stereo-microscope was used to observe the algal contents of guts

of Diaptomus leptopus copepodites.

Analysis of the fixed O_2 samples was completed by measuring the percent transmittance of the sample at 450um on a Bausch and Lomb Spectrometer 20, then interpolating from these readings to $mg\ O_2\ l^{-1}$ on a standard curve (Fig.3), a semilogarithmic plot of percent transmittance against O_2 concentration. Standards were determined at $11.0^\circ C$ and $28.5^\circ C$ (the former by N.J. Hibberd, and the latter by D. Galley and S. Cheng). These temperatures were the limits between which organisms were sampled from Hill Pond; $11.0^\circ C$ coincided with the temperature at which organisms were first encountered, and $28.5^\circ C$ was the highest temperature recorded in 1977. Since these plots were linear and essentially parallel, and all O_2 samples were taken at temperatures within this range all O_2 concentrations were derived by interpolation using the $11.0^\circ C$ plot.

Analysis of data.

Categorization of Chaoborus americanus into instars was achieved by measuring the length, less the lengths of the antennae and anal papillae, of all Chaoborus on the date that a particular instar reached peak abundance. Size frequency histograms were formed for the Chaoborus taken on these days, and the size distribution for the instar that had reached peak abundance in each case was truncated at the middle of the bottom of the deepest depression on either side of the peak. The four truncated peaks, representing the four instars, were put together into a final size frequency histogram (Fig.4). Peaks for C1, C2, C3 and C4 were taken from data obtained on 29, 03, and 16 June and 25 May respectively. Body lengths were rounded to the nearest 0.5mm.

Prey were categorized (Table 3) as to the approximate maximum size of prey that each instar of Chaoborus americanus can ingest with complete

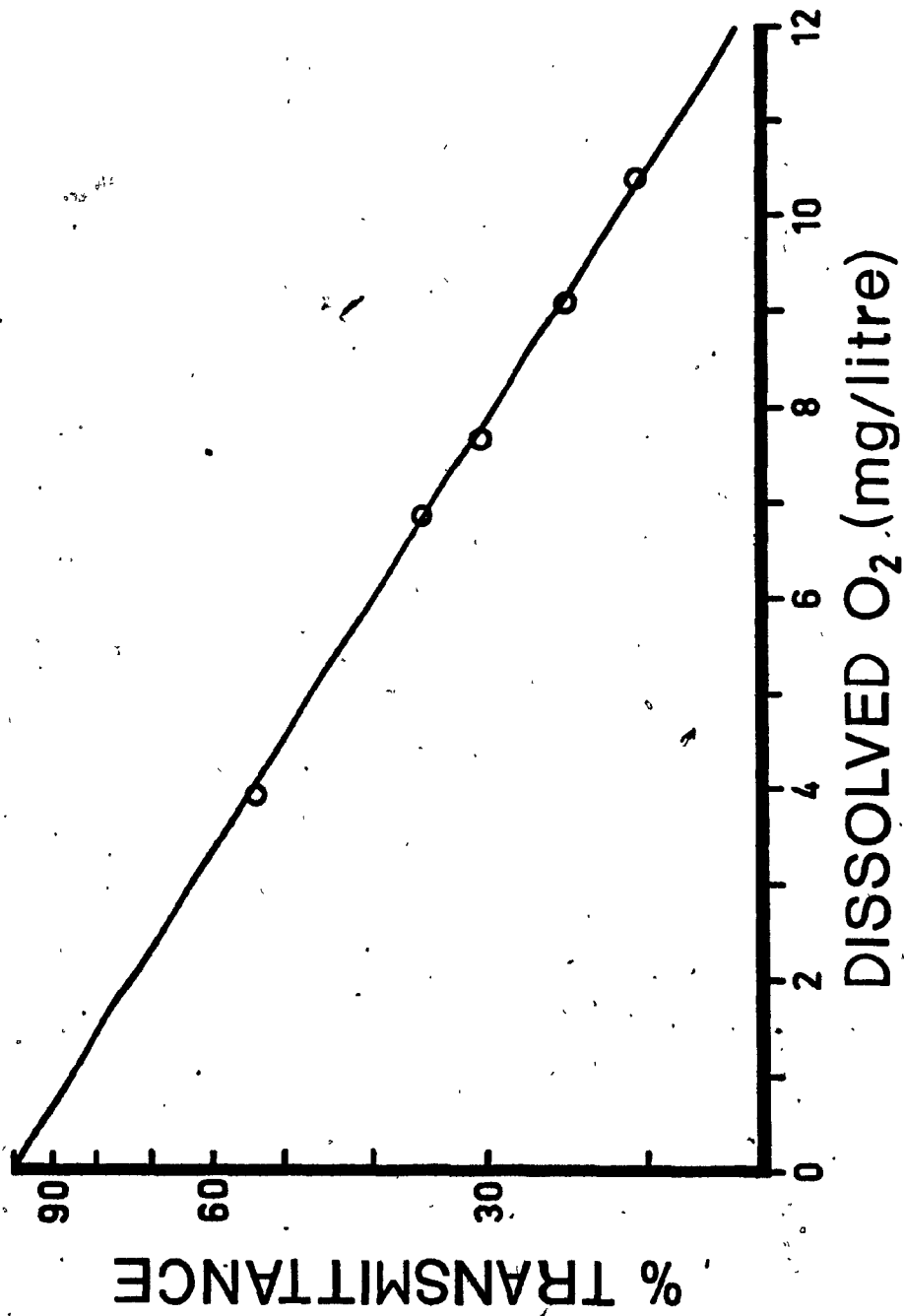


FIG. 3. A standard curve for determining O₂ concentrations.

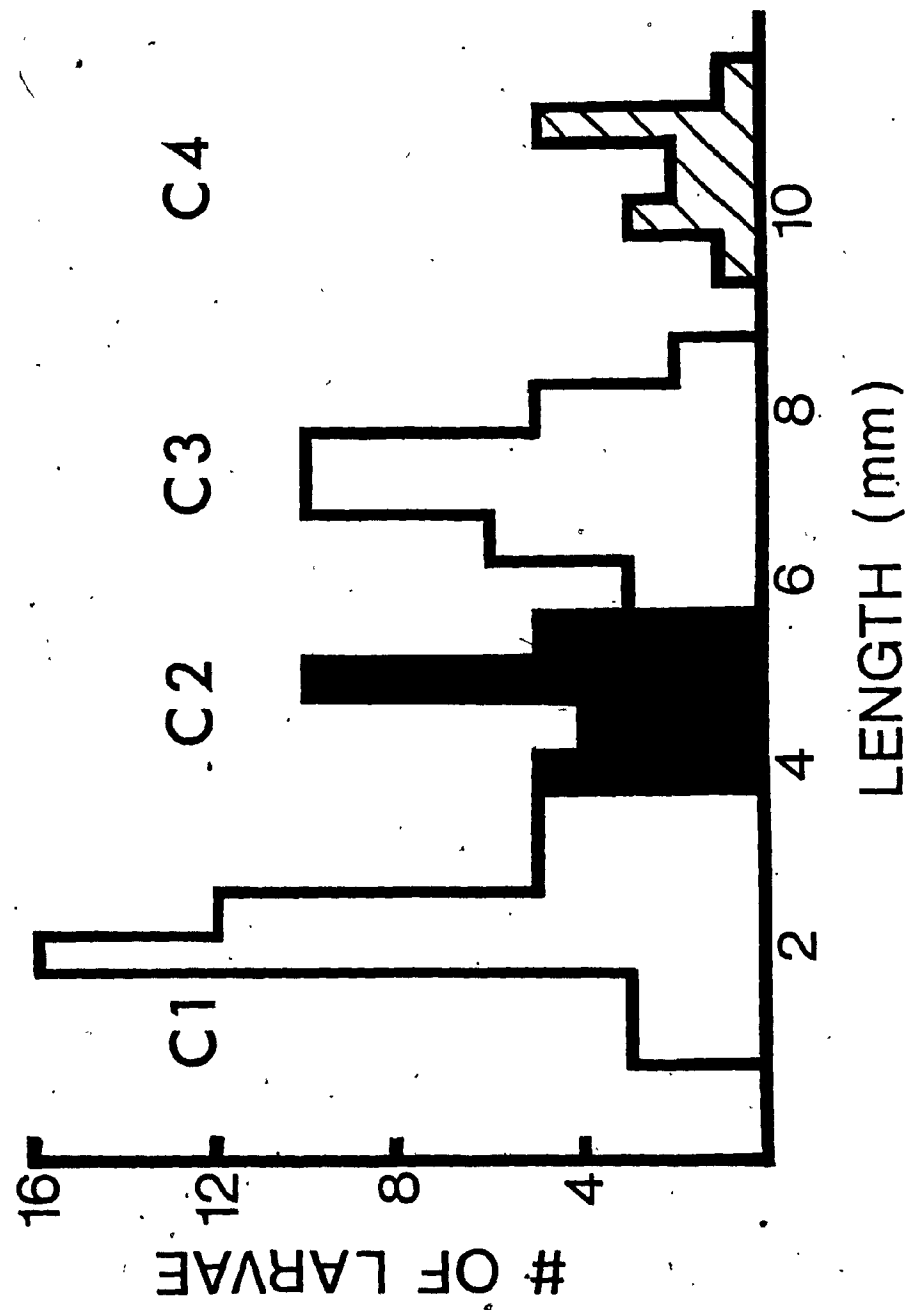


FIG. 4. Size frequencies of the four Chaoborus instars. See text for further explanation.

TABLE 3. Approximate maximum size of prey that each instar of Chaoborus can ingest with complete success.

instar	<u>Chaoborus</u>				Prey			
	code	body lengths (mm)	mouth gape ^x (mm ± 1SD; n=30)	species	stage	code	body thickness (mm ± 1SD; n=10)	body lengths (gt or lt;mm) ^z
4	C4	9.0-12.0	0.71±0.06	<u>Daphnia pulex</u>	immature	D.p.B	0.48±0.05	lt 1.41
3	C3	6.0- 8.5	0.43±0.04	<u>Diaptomus leptopus</u>	all adults	D.1.A	0.47±0.03 (females)	gt 1.00
				<u>Diaptomus leptopus</u>	copepodites IV, V	D.1.B	0.39±0.05 (V; females)	0.65 -1.00
2	C2	4.0- 5.5	0.30±0.02	<u>Diaptomus leptopus</u>	copepodites I, II, III	D.1.C	0.22±0.02 (111)y	0.30 -0.64

x from Fedorenko, 1975a.

y n = 5.

z gt = greater than; lt = less than.

success, based primarily on the data of Feorenko (1975a) and Swift and Fedorenko (1975).

The method used to calculate the depth intervals for the zones of different zooplankter densities was as follows. Based on the three sampling depths S, M, and B, the water column in the ponds was divided into three corresponding zones for which horizontal boundaries were set at depths roughly halfway between each sampling depth (Fig.2). Thus, a depth of 0.8m approximated the boundary between the zones S and M, while 1.6m represented the boundary between M and B, hence zones S and M both had a depth interval of 0.8m. This interval, divided by the pond depth 2.0m, equaled 40% of the water column. The remaining zone, B (1.6 to 2.0m) represented 20% of the 2.0m water column. These same zones e.g. S=40% were applied to vertical cages. The mean density of a particular species, derived from the samples taken within the zone in the pond, was then extrapolated to represent the density of that species within the zone, whether a zone in the pond or its counterpart in a vertical cage.

The number of Diaptomus adults (D.l.A) used in vertical cages (treatments) was determined from the data for 13 July, 1977. Overall Diaptomus abundance on this date was typical of the early summer period when late instar Chaoborus were relatively abundant and Diaptomus copepodites were not. The volume of each zone in a 25 l. cage (i.e. S=10.00 l., M=10.00 l., B=5.00 l.), multiplied by the density D.l.A l.⁻¹ found in that zone on 13 July (i.e. S= 1.27, M=1.43, B=0.32, all in units of D.l.A l.⁻¹), set the total number of D.l.A at 28.6 animals vertical cage⁻¹ [i.e. (10.00 x 1.27) + (10.00 x 1.43) + (5.00 x 0.32) = 28.6]. This total was increased to 67 D.l.A vertical cage⁻¹ so that losses to C4 predation would have less influence on the density dependent capture rate during short-term enclosure experiments.

The number of early instar Daphnia (D.p.B) used vertical cage⁻¹ was determined from the data of 29 July, 1977 by the same method. Unlike Diaptomus, Daphnia were usually taken in abundance or not at all. The use of the densities $S=0.48$, $M=26.0$, and $B=0.63$, all in units of D.p.B l.⁻¹, provided for a total of 278 D.p.B cage⁻¹. To offset potential mortality as a result of handling this total was increased to 300 D.p.B vertical cage⁻¹.

Fourth instar Chaoborus (C4) numbers were determined from data taken the same day from which densities of its particular experimental prey were taken. This provided for 4 C4 cage⁻¹ containing D.l.A, and 6 cage⁻¹ containing D.p.B. These totals were increased to 6 and 9 C4 respectively to compensate for 33% pupation over the course of three day experiments. This value was determined from preliminary enclosure experiments in the field.

The number of animals of each species category used in horizontal cages was the same as that used in vertical cages in each case. It was assumed that the horizontal cages prevented vertical separation of predators and prey, hence animal densities in horizontal cages could be represented by mean densities for the water column i.e. the number of animals in the cage divided by 25 l., the volume of the cage. These were the densities used in the 2.5 l. cages as well.

The initial number of a species category cage⁻¹ was held constant for successive sets of treatments, even though the density of that species may have changed in Hill Pond.

Data comparisons.

The mean density of each group of animals, whether predator, prey or sex (prey) at each depth on each sampling date was converted to a

percentage of the sum of the mean densities, one from each depth, on that date for the group in question. The proportion of each particular animal group taken from mid-depth over the period of low Diaptomus abundance was then compared to the proportion of the same group taken at the bottom over the same period. A similar comparison for each group was also done for the whole season. A t-test for the means of the arcsine transformations of the proportions was used for the above comparison. Actual densities could not be used because the means were often positively correlated with the variance. The use of proportions best mirrored the pattern inherent in the raw data, eliminating variability resulting from seasonal changes in overall abundance. As proportions, all values were finitely bounded between 0 and 1.00.

A rows by columns test of independence using the G-statistic was used to test whether the location of the population mode of an indicator group, D.I.A, in the water column was independent of the ambient daytime light conditions.

A Model 1 single classification anova (equal n) was used for all comparisons involving cage experiments. The ratio of the variance was used to show the homogeneity between variances for the total number of animals eaten in vertical and horizontal predator-prey treatments. From this it was assumed that the variances were homogeneous for all cage experiment anova comparisons.

Sokal and Rohlf (1969) was used as a reference for all of the statistical tests documented above. In all cases, P less than 0.100 was accepted as the level of significant difference. Codes for the different probability ranges used are summarized in Table 4.

TABLE 4. Codes for probability ranges.

Code	Probability ranges ^x	
	lt	gt
*	0.100	0.050
**	0.050	0.010
***	0.010	0.001
****	0.001	-

x lt less than

gt greater than

Diaptomus copepodite population projections.

The instantaneous feeding rates, c , of fourth instar Chaoborus (C4) feeding on adult Diaptomus (D.l.A) in vertical and horizontal cages were calculated using the formula:

$$N_t / N_0 = e^{-cPt}$$

where N_0 and N_t were the mean densities l^{-1} of D.l.A in a particular set of similar treatments at times 0 and t (3 days), or the beginning and the end of the long-cage predation experiments, respectively. Here P was the mean density of C4 in a particular set of similar treatments over the duration of the cage experiment.

Hypothetical Diaptomus copepodite population projections for two situations were calculated using the formula:

$$N_t = N_0 e^{(r-cP)t}$$

Here, c and P were as above, t was time over three day intervals and r , N_0 and N_t were the rate of population change and the initial and subsequent densities l^{-1} of Diaptomus copepodites respectively. Further elaboration of these situations is inappropriate here; values of these parameters are given where the hypothetical situations are presented.

RESULTS AND INTERPRETATIONS

Temporal relations of the pelagic zooplankton of Hill Pond.

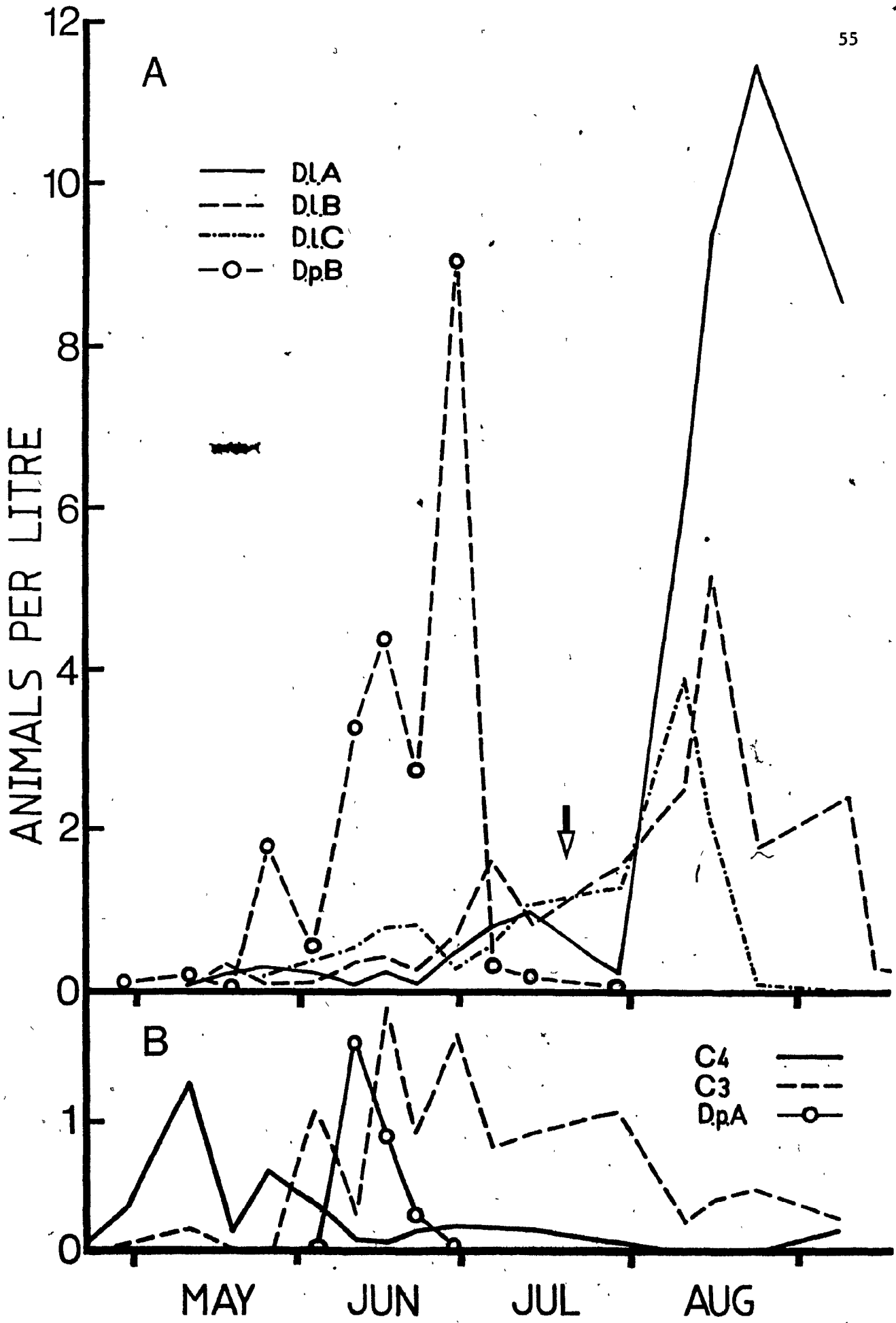
Although the material in this section does not answer any of the questions put forth under QUESTIONS ASKED, I have included it as a preliminary to the answers to my questions for several reasons. First, to put the answers into perspective it is necessary to have an overall picture of the temporal abundance patterns of predators and prey. Second, it was desirable to ascertain whether certain predator-prey relationships existed, and to quantify them if they did.

In this and subsequent sections, categories of animals are often referred to only by their respective codes, most of which are described in Table 3. Adult Daphnia pulex and first instar Chaoborus americanus are not presented in Table 3, but are often described hereafter as D.p.A and C1 respectively. Also, no statistics were necessary in the analysis of any of the experiments presented in this section. No animals died in controls in any of the laboratory experiments presented here or subsequently.

The temporal changes in the pelagic zooplankton of Hill Pond, over the course of spring and summer, 1977, are shown in Figures 5 and 6. In Fig. 5, the ordinate represents the mean number of animals $l.^{-1}$ in each category over the whole water column on each sampling date.

Certain observations and results suggest that Notophthalmus might have eliminated Daphnia from Hill Pond. The D.p.A category peaked in early June at only 1.59 animals $l.^{-1}$ (Fig. 5B). Then, within 11 days it declined to just 0.26 animals $l.^{-1}$. The new generation of Notophthalmus was then present and abundant, although the larvae could not be accurately

FIG. 5 A,B. Temporal changes in each zooplankton category, over the whole water column of Hill Pond, on each sampling date in spring and summer, 1977. Arrow; for an explanation, see text.



enumerated (see METHODS). Also, adult Notophthalmus numbered more than 0.5 adults m^{-2} (as they did over the whole summer). Therefore, given:

- (1) the low abundance of Daphnia in June,
- (2) the number of Daphnia Notophthalmus can eat in a short period of time (Table 5), and
- (3) the abundance of Notophthalmus in June,

Notophthalmus might have eliminated Daphnia:

Other observations also support this contention. The only alternate prey for Notophthalmus in June was the new generation of Chaoborus, C3 in particular (maximum 1.90 $l.^{-1}$; Fig 5B). However C3 remained relatively abundant until August, long after mature Daphnia had disappeared. When a mixture of Daphnia and C2 and C3 from Hill Pond was presented to two larval newts, each in a separate small aquarium in the laboratory, some Chaoborus still remained after several days, but all the mature Daphnia and most of the immature Daphnia had been consumed. The population of Daphnia in the control increased, while that of Chaoborus remained the same (Chaoborus could not of course increase because it has a generation time of one year). These observations suggest that larval Notophthalmus selected Daphnia over Chaoborus.

There is cursory evidence that D.p.A were food limited to some extent in Hill Pond in June, because the mean clutch size declined from 17.00 eggs female $^{-1}$ (n=2) on 3 June to 2.33 eggs female $^{-1}$ (n=3) on 21 June. However, it is unlikely that lack of food caused D.p.A to decline to extinction. For example, on 21 June D.p.A numbered just 0.26 animals $l.^{-1}$, and the mean clutch size of those carrying clutch (n=3) was only 2.33 eggs female $^{-1}$. However the D.p.A category increased from 2.75 animals $l.^{-1}$ on 21 June to 9.05 $l.^{-1}$ on 29 June. The most probable effect of food

TABLE 5. The mean number of prey eaten per Notophthalmus per hour during the day in small tanks in the laboratory. Two replicates per treatment. Temperatures 20 - 23.5° C.

Prey	Prey eaten <u>Notophthalmus</u> $^{-1} \text{ h}^{-1}$		Initial prey $l.^{-1}$
	adults (87mm)	larvae (39mm)	
D.p.A	31.00	-	16.00
D.p.B	36.00	-	15.20
D.p.A/D.p.B	20.00/9.00	-	8.00/8.00
	-	7.00/3.00	
D.1.A	-	0.00	4.00

limitation would have been to increase the relative impact of Notophthalmus predation, because D.l.A would have been eaten faster than the Daphnia population could have replaced them.

Although it is possible that Notophthalmus eliminated Daphnia from Hill Pond, one further question must be answered before this claim can be made with reasonable certainty. Both Notophthalmus in Hill Pond and another salamander, Ambystoma tigrinum, in subalpine ponds in Colorado spend most of their time during the day (when these salamanders do most of their feeding; Attar and Maly, submitted; Dodson, 1970) on or near the bottom. If D.p.A spent most of their time during the day off the bottom in Hill Pond it is unlikely that Notophthalmus could have eliminated Daphnia. Thus, the question one must answer is whether or not D.p.A were concentrating near the bottom in Hill Pond. This I answer under the section Vertical distributions: day.

Several observations also suggest that Notophthalmus reduced the abundance of late instar Chaoborus in Hill Pond over the course of the summer. Although C3 remained relatively abundant until late July, the C3 category declined somewhat during this period and more so thereafter, until the end of August (Fig. 5B). The C4 category had disappeared in early August (partly because individuals pupated and emerged) hence C3 individuals must have died or have been eaten as soon as they metamorphosed into the C4 stage. In the absence of mortality the C3 category would have increased in abundance via the development of younger instars. Given that Notophthalmus was abundant in Hill Pond over the summer, and that Notophthalmus ate C3 in the laboratory, Notophthalmus might have reduced the abundance of late instar Chaoborus.

By eating late instar Chaoborus, Notophthalmus might also have delayed

the appearance of the new generation of C4. The relative (percent) abundance of Chaoborus instars on each sampling date is presented in Fig. 6. Rather than a pattern of appearance: C4,1,2,3,4, the pattern of major peaks was: C4,1,2,3,1,2,3,4. Clearly, the appearance of the new generation of Chaoborus was delayed. It is unlikely that there were two generations because no major increase in the relative abundance of C4 occurred between C3 and C1. An increase in abundance of C4 would have been necessary for the production of the adults required to produce a second Chaoborus generation. If this were the case, the second peak of C1 must be accounted for. It may have been that C1 were simply cannibalized by late instar Chaoborus (see Vertical distributions: day); when the former hatched C4 were relatively abundant (Fig. 6). Chaoborus surviving through to their cannibalistic C3 stage would have helped suppress the (continuously recruiting) C1 stage until the middle of June when C3 started to decline. It was then that C1 increased for the second time.

Since the overall densities of D.p.A and C3 were similar in Hill Pond in June (Fig. 5B) one might ask why Notophthalmus might have eliminated D.p.A and not late instar Chaoborus. Notophthalmus selected D.p.A over C3 when they were offered to Notophthalmus in the same vessel, therefore C3 must have escaped predation by some means other than a distribution different from that of Notophthalmus. This problem I return to in the DISCUSSION.

Temporal changes in the different prey categories of Diaptomus are presented in Fig. 5A. Copepodites I through VI were present throughout the summer. Prior to June, when C4 were abundant (maximum 1.32 l.^{-1}), Diaptomus was present at very low densities. Adults were the most abundant (maximum 0.32 l.^{-1}) of the Diaptomus stages present during this period. During June and July each category became slightly more abundant

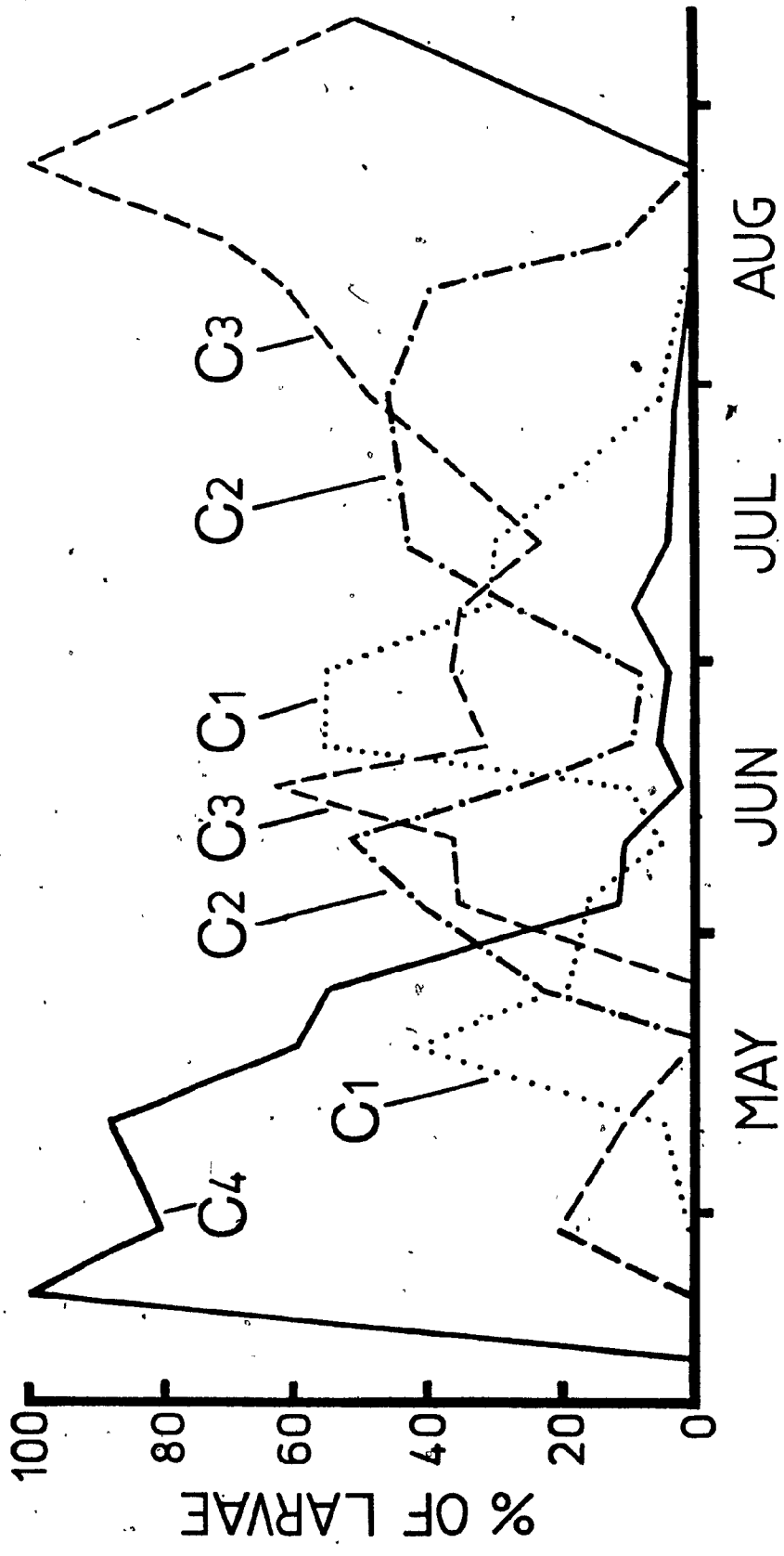


FIG. 6. The relative abundance of Chaoborus instars in Hill Pond on each sampling date.

in the succession D.1.C, D.1.B, D.1.A. However, the peaks of the abundance in July were still relatively low; D.1.B were the most abundant Diaptomus (maximum 1.64 l.^{-1}) at this time.

Certain observations and results suggest that Chaoborus had the capacity to reduce the abundance of, possibly eliminate, Diaptomus in July (Fig. 5, region marked by the arrow). Chaoborus was the only species present which might have affected Diaptomus; no D.1.A were taken by larval salamanders in the laboratory (Table 5). Also, Chaoborus were relatively abundant (between 1.01 and 1.91 l.^{-1} , C3 plus C4; Fig. 5B) whereas Diaptomus were not; the Diaptomus population varied between just 3.01 and 3.10 individuals l.^{-1} , all copepodites included (Fig. 5A). At such densities in the laboratory, late instar Chaoborus can eat all the Diaptomus copepodites present in several days. For example, C4 (0.40 l.^{-1}) ate a mean of $2.33 \text{ D.1.A predator}^{-1} \text{ d}^{-1}$ (initial density 4.00 l.^{-1}) (Table 6). Except for the occasional cyclopoid copepodite, there were no alternate prey for Chaoborus in Hill Pond in July. Diaptomus did not appear to be food limited during July because clutch sizes were as large ($28 \text{ eggs female}^{-1}$, $n=6$) as they were at any other time in 1977.

However, Chaoborus did not eliminate Diaptomus from Hill Pond, although it was in early August that Diaptomus started to increase in overall abundance, after the C3 and C2 categories had decreased dramatically (from 2.13 l.^{-1} , C3 plus C2, on 29 July to 0.40 l.^{-1} on 10 August). Thus, one might ask if there was a particular mechanism, e.g. a significant degree of vertical separation, by which Diaptomus copepodites persisted in the presence of late instar Chaoborus in July. I return to this question in the section Vertical distributions: day.

TABLE 6. The mean number of Diaptomus leptopus adults eaten per fourth instar Chaoborus per day in small tanks in the laboratory. Three replicates per treatment. Temperatures 20 - 21.5° C.

Initial D.l.A l. ⁻¹	C4 l ⁻¹	D.l.A eaten C4 ⁻¹ d ⁻¹
4.00	0.40	2.33
5.00	1.00	3.50

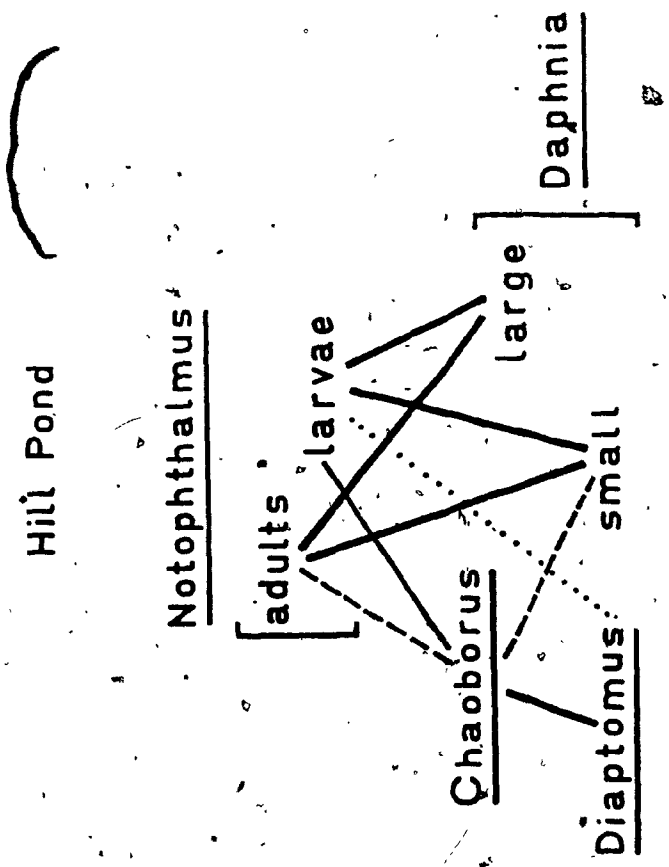


FIG. 7. Predator-prey relations confirmed in laboratory experiments. See text.

In summary, I have attempted to show that, in a water body as shallow as several metres, the relationships between the pelagic zooplankters and their main predators cannot always be explained by just gross temporal patterns. Three specific questions that arose out of the consideration of such patterns and which remain to be answered are:

- (a) Did D.p.A concentrate near the bottom in Hill Pond, hence increase the possibility of elimination from predation by Notophthalmus ?
- (b) By what means, if any, did C3 escape predation by Notophthalmus ?
- (c) Could Diaptomus copepodites have co-occurred with late instar Chaoborus in July by way of a significant degree of vertical separation ?

Figure 7 depicts by solid line the predator-prey relations confirmed in the laboratory experiments presented above. The thickness of the solid line indicates the relative intensity of the relationship. The dashed lines represent probable relations (see THEORY), which have been added for completeness. These relations are probably intense as well. The dotted line indicates that the relationship is uncertain, having been tested only at low prey densities.

Vertical distributions: day.

Generally, the pelagic zooplankters which persisted in the presence of their main predators in Hill Pond had day distributions which were significantly different from those of the predators (answers question (1) QUESTIONS ASKED). Some of these differences in distribution are depicted in Fig. 8 and the statistics for all comparisons are summarized in Table 7. Over the whole season, the category modes for C4 and C3 occurred at the bottom (2.0m) whereas the category modes for their main prey: D.1.A (including females with clutch), D.1.B, D.1.C and D.p.B, were found at mid-depth (1.2m). For example, 73% of C4 were taken at the bottom and

FIG. 8. Differences between the distributions of late instar Chaoborus and Diaptomus leptopus copepodites in Hill Pond during the day prior to August, 1977. S = Surface (0.2m), M = mid-depth (1.2m), B = bottom (2.0m).

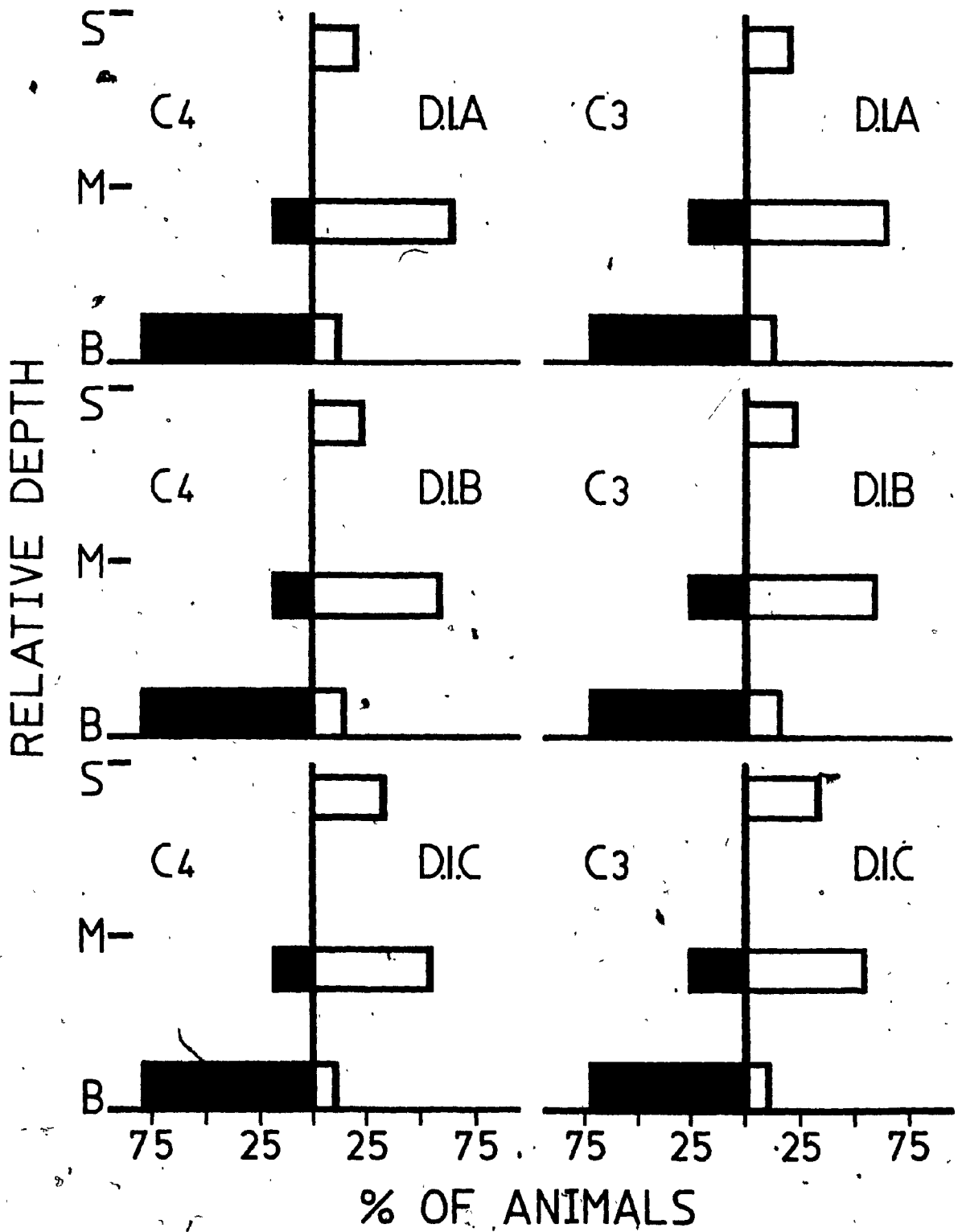


TABLE 7. A summary of t-test statistics for all Hill Pond zooplankton distribution comparisons.

Category	Depth* of Mode	Year			To 29 July		
		t observed	df	P	t observed	df	P
C4	B	1.8214	22	0.100	2.6428	20	0.020
C3	B	1.8869	30	0.100	2.6533	16	0.020
C2	B	1.4320	26	0.250	0.7422	16	0.500
C1	M	1.9886	26	0.001	7.0948	14	0.005
D.1.A	M	3.3220	36	0.005	2.6055	18	0.020
D.1.A ^x	M	4.3699	22	0.001	-	-	-
D.1.B	M	2.5858	32	0.020	2.0089	16	0.100
D.1.C	M	4.6377	30	0.001	3.8962	16	0.020
D.p.A	B	8.0924	6	0.001	-	-	-
D.p.B	M	3.4867	20	0.005	-	-	-

* B bottom

M middle, mid-depth

^x only females with clutch

only 26% at mid-depth, while 58% of D.1.A were taken at mid-depth and only 17% at the bottom (both significantly different; Table 7, Year). Less than one percent of C4 were taken at the surface, where 25% of D.1.A were taken, virtually free of C4 predation during the day.

Differences between the distributions of predators and prey were even more significant for the period prior to August when prey, particularly Diaptomus, were generally few and late instar Chaoborus were relatively abundant. Here 81% of C4 were taken at the bottom (B) and only 18% at mid-depth (M), while 65% of D.1.A were taken at mid-depth and only 13% at the bottom (Fig. 8; both significantly different, Table 7, To 29 July). Many Diaptomus (22%) were still at the surface (S), which was free of C4 predation during the day. Reported as densities, the significance of the different distributions is equally apparent; on 29 July the densities of C4 and C3 at the bottom were 0.48 and 3.49 animals l^{-1} respectively, while the densities of C4 and C3 at mid-depth were 0.16 and 1.59 animals l^{-1} respectively. No Diaptomus and only 0.63 D.p.B l^{-1} were taken at the bottom, but 3.97 D.1.C l^{-1} and 26.00 D.p.B l^{-1} were taken at mid-depth.

This information is evidence for for the suggestion that Diaptomus copepodites might have persisted in the presence of late instar Chaoborus in July by way of a significant degree of vertical separation (partially answers question (c), Temporal relations). Significant vertical separation during the day might also have reduced predation by the latter on Diaptomus copepodites at other times in the season, and reduced predation by late instar Chaoborus and Notophthalmus on D.p.B when the latter were present.

The vertical distribution of C2 during the day was different from those of the older instars; C2 was evenly distributed over the middle

and the bottom ($t_{s(26)} = 1.432$ n.s., Table 7, Year). This distribution still favoured Diaptomus copepodites and D.p.B since they were found more at mid-depth. Also, C2 are not as voracious as C4 and C3 (e.g. Table 3). First instar Chaoborus distributed primarily at mid-depth (M) rather than the bottom (B) ($t_{s(26)} = 1.989$ ****, Table 7, Year). However C1 have the least impact on the prey I have considered.

Vertical separation from Chaoborus during the day might have contributed to the survival of some Diaptomus nauplii in Hill Pond. Few nauplii were taken at any time in plankton samples from Hill Pond, however when some were taken during the day they were generally taken at the surface. Few Chaoborus were taken there during the day. Nauplii are most vulnerable to predation by Chaoborus because of the small naupliar body size. Fedorenko (1975b), for example, found C2 to eat 20 nauplii $C2^{-1} d^{-1}$, albeit at a high naupliar density.

A significant degree of vertical separation during the day would have reduced the incidence of cannibalism among Chaoborus instars. In Hill Pond C1 were found mainly at mid-depth (M) while C3 and C4 were found mainly at the bottom (B) (Table 7). In the shallow Chaoborus tanks in the laboratory, which contained a mixture of all four instars, C4 and larger C3 were occasionally observed ingesting C1 and smaller C2. Also, the remains of many partially digested smaller instars were removed from the air-water interface.

All D.p.A were taken at the bottom (B) in Hill Pond (Table 7), where they were extremely vulnerable to Notophthalmus predation. Thus Notophthalmus could have been responsible for eliminating Daphnia in Hill Pond (answers question (a), Temporal relations). Third instar Chaoborus were also distributed mainly at the bottom (B), but were not eliminated. This supports

the idea that C3 must have escaped predation by some means other than a day distribution different from that of Notophthalmus (see question (b), Temporal relations). However, the observation does support the contention that Notophthalmus delayed the appearance of the new generation of C4.

Influence of ambient light: day.

The location of the mode of the indicator (D.l.A) category, almost always found at mid-depth, was significantly independent of the ambient light conditions during the day ($G_{s(3)} = 1.648$ n.s.). The data for D.l.A are presented in Table 8. The numbers under "Middle" and "Bottom" represent the number of dates on which the mode was found at that depth. Light conditions are listed in order of decreasing relative light intensity; the categories also represent variable light quality. The symbols "lt m" and "gt m" indicate whether the Secchi disc disappeared above or below 1.00m respectively. The two categories were distinct; at "gt m" the Secchi disc disappeared between 1.25 and 2.00m (mean 1.58m) while at "lt m", the disc disappeared between 0.60 and 0.75m (mean 0.64m). Included with "sun" were days with occasional cloud; "no sun" included overcast days and rain. It is probable that the distributions of the other animal groups were also independent of ambient light conditions during the day, because their distributions were significantly consistent (Table 7).

Vertical distributions: night.

A comparison of the distributions of C3 and D.l.A over the course of 24h is presented in Fig. 9. During the day, both groups distributed

TABLE 8. Depth of the mode of the adult Diaptomus leptopus population under different ambient light conditions during the day. See text.

Light conditions ^x	Middle	Bottom
gt m, sun	4	1
gt m, no sun	1	0
lt m, sun	5	1
lt m, no sun	4	0

$$G_{(3)} = 1.648 \text{ n.s. } (\chi^2_{0.500(3)} = 2.366, P \text{ gt } 0.500)$$

x gt. greater than

lt less than

as I've described above i.e. they were separate to some extent.

At night both C3 and D.1.A migrated. The night samples were taken between 01:00 and 02:00 h, the period when one might expect a midnight "sink" in species which initially migrate up in the water column (Cushing's paradigm; Hutchinson, 1967). During a sink the animals do distribute at random. Therefore one would expect overlap between distributions to increase during a sink period.

Redistribution of C3 and D.1.A occurred, but some degree of separation was maintained between them during this period as well as during the day. The D.1.A category was found to have two modes of abundance; 39% of the animals were taken at the surface (S) and 36% were taken at the bottom (B) (Fig. 9). Only 25% of the D.1.A were found at mid-depth (M), where 50% of the C3 were taken. Of the remaining C3, 25% were taken at each of the surface and the bottom. The only other prey category present when night samples were taken was D.1.B, and its distribution was similar to that for D.1.A. Obviously, C3 and Diaptomus must have passed each other sometime after sunset and again before dawn. Although this would have increased the probability that Diaptomus be taken as prey, time spent in passing represented only a small portion of the 24 h day.

Thus, the information in this section is further evidence for the suggestion that Diaptomus copepodites might have persisted in the presence of late instar Chaoborus in July by way of significant vertical separation (answers question (2), QUESTIONS ASKED, and answers further question (c), Temporal relations). No statistics were done on these data because not enough samples were taken since access to the Arboretum at night was limited. However, preliminary analysis of samples taken at night from a similar system, the subalpine pond 12 of Sprules (1972)

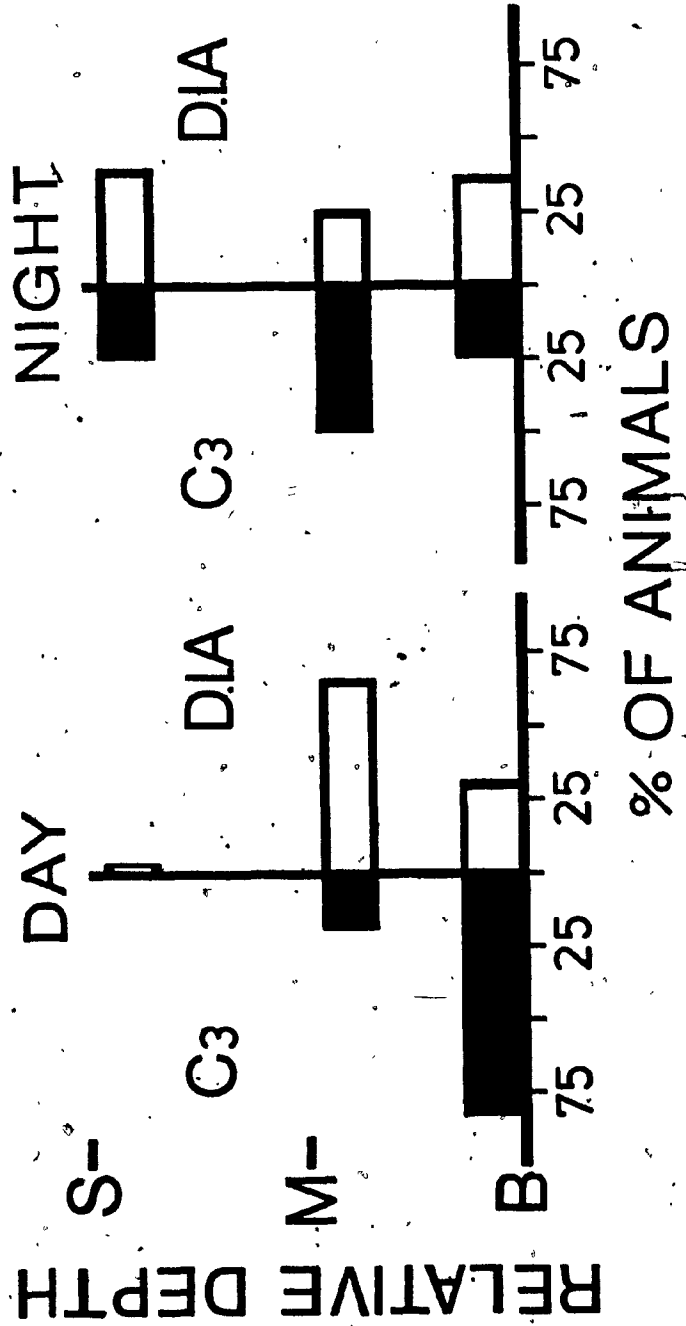


FIG. 9. A comparison of the distributions of third instar Chaoborus and Diaptomus leptopus adults in Hill Pond over 24 hours (15, 16 August, 1977). See text. S, M, and B as in FIG. 8.

and Dodson (1974a), indicates that the distribution of late instar Chaoborus americanus and Diaptomus coloradensis copepodites were separate there at night.

It is probable that there was no stratum where nauplii could have been relatively free of Chaoborus predation at night. Although no nauplii were found when night samples were taken, this assumption would be accurate if, when nauplii were present, Chaoborus distributed as they did at night in August (e.g. C3 in Fig. 9). Either the separation of nauplii and Chaoborus during the day was enough to allow some nauplii to survive, or some other mechanism was responsible, possibly in conjunction with day separation. Nauplii that weren't eaten might have developed quickly such that there was never a large standing crop.

Long - cage predation experiments.

In Figures 10 and 12 I present the mean number of prey which remained in each treatment (cage) after three days. The number of prey eaten vertical replicate⁻¹ 3d⁻¹ was determined by subtracting the number of prey remaining after three days in a vertical replicate with C4 (VP) from the number of prey remaining after three days in the corresponding vertical replicate without C4 (VC). A similar procedure was repeated for horizontal replicates. The treatment means were calculated simply by combining replicate data and dividing by 4 (the number of replicates). Data for the mean number of prey eaten are presented in Figures 11 and 13, and statistics for all comparisons made in this section are summarized in Table 11.

While a mean of 6.75 D.l.A was eaten vertical treatment⁻¹ 3d⁻¹ (V) almost three times as many D.l.A (19.75) were eaten horizontal treatment⁻¹ 3d⁻¹ (H) (Fig. 11A; $F_{s(1,6)} = 36.42$ ****, Table 11). With respect to

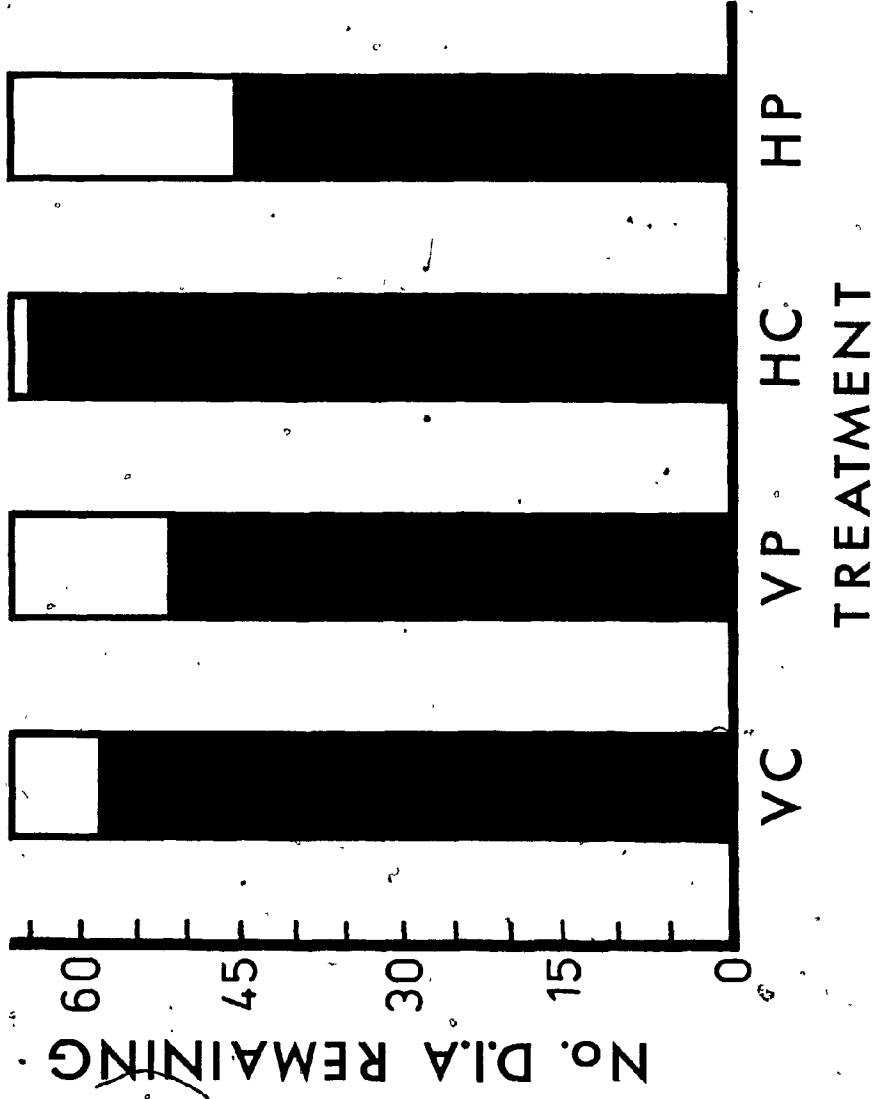


FIG. 10. The mean number of adult *Diaptomus leptopus* prey remaining in long-cage predation treatments after three days. Four replicates per treatment. See text for an explanation of treatment symbols.

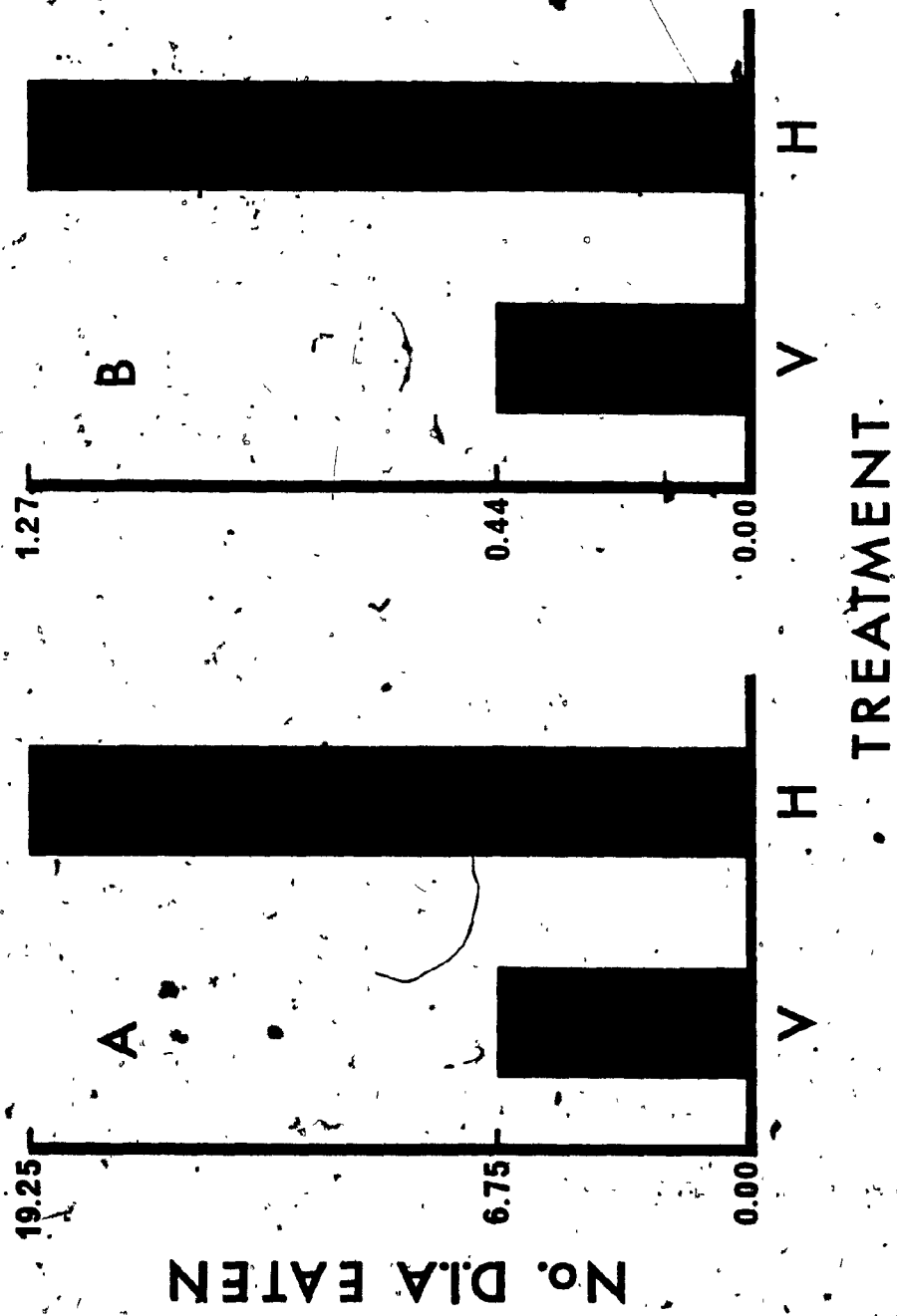


FIG. 11. Long-cage predation experiments. A. The mean number of adult *Diaptomus leptonus* prey eaten in vertical (V) and horizontal (H) treatments by fourth instar *Chaoborus* over three days. B. A similar comparison: the mean number of *D. leptonus* adults eaten per fourth instar *Chaoborus* per day. Four replicates per treatment.

TABLE 9. Anova statistics from long - cage predation experiment comparisons.

Prey-predator combination	Units	Comparison	Greater	F _s observed	df	P
D.l.A - C4	D.l.A,x	VP with VC	VC	5.77	(1,6)	0.100
		HP with HC	HC	29.11	(1,6)	0.005
		HC with VC	HC	8.26	(1,6)	0.050
	D.l.A,y	H with V	H	36.42	(1,6)	0.001
	D.l.A,z	H with V	H	5.71	(1,6)	0.100
	C4,x	H with V	H	0.00	(1,6)	1.000
D.p.B - C4	D.p.B,z	H with V	H	38.25	(1,2)	0.025

x mean # remaining cage⁻¹ 3 days⁻¹

y mean # eaten cage⁻¹ 3 days⁻¹

z mean # eaten C4⁻¹ day⁻¹

individual predators a mean of 0.44 D.l.A was eaten $C4^{-1} d^{-1}$ in vertical treatments (V) whereas a mean of 1.27 D.l.A was eaten $C4^{-1} d^{-1}$ in horizontal treatments (H) (Fig. 11B; $F_{s(1,6)} = 5.71 *$, Table 11). Some of the C4 pupated during the D.l.A experiment, but the small difference (0.25 C4) between the number remaining in the vertical and horizontal treatments was not significant ($F_{s(1,6)} = 0.000$ n.s., Table 11). A mean of only 0.085 D.p.B was consumed $C4^{-1} d^{-1}$ in vertical treatments (V), whereas a mean of 3.95 D.p.B was consumed $C4^{-1} d^{-1}$ in horizontal treatments (H) (Fig. 13; $F_{s(1,2)} = 38.25 **$, Table 11). These D.p.B were 3 days old or less. Since Daphnia were found not to reproduce before they were 7 days old in the laboratory under conditions of similar temperatures and unlimited algal food, there was little chance that the D.p.B category would increase during the enclosure period.

These results suggest that if pelagic zooplankton and their main predators are prevented from separating vertically to the extent that they do in nature, predation rates are increased. In this experiment the horizontal treatments confined predators and potential prey to the same shallow stratum and predation rates increased substantially. The vertical treatments provided a water column, although this experiment does not tell us if the animals distributed in them as they did when they were free in the water column of Hill Pond. However, the substantial difference in predation rates leads me to believe that some vertical separation was occurring. The difference in predation rates also suggests that if vertical separation decreased at any time e.g. when predators and prey passed each other at night, any increases in the predation rates were not nearly as great as they would have been if predators and prey occupied the same stratum all day. Thus we have yet further evidence

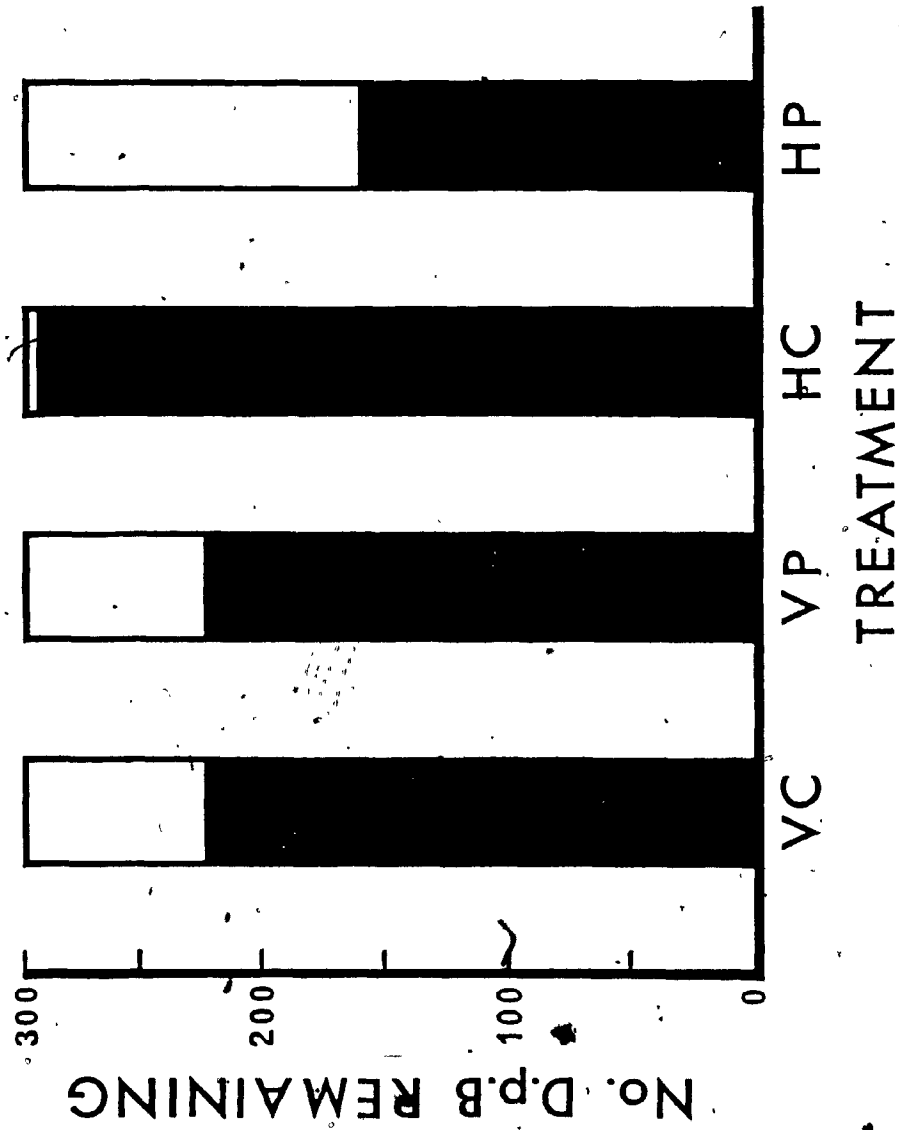


FIG. 12. The mean number of immature *Daphnia pulex* prey remaining in long-cage predation treatments after three days. Two replicates per treatment. See text for an explanation of treatment symbols.

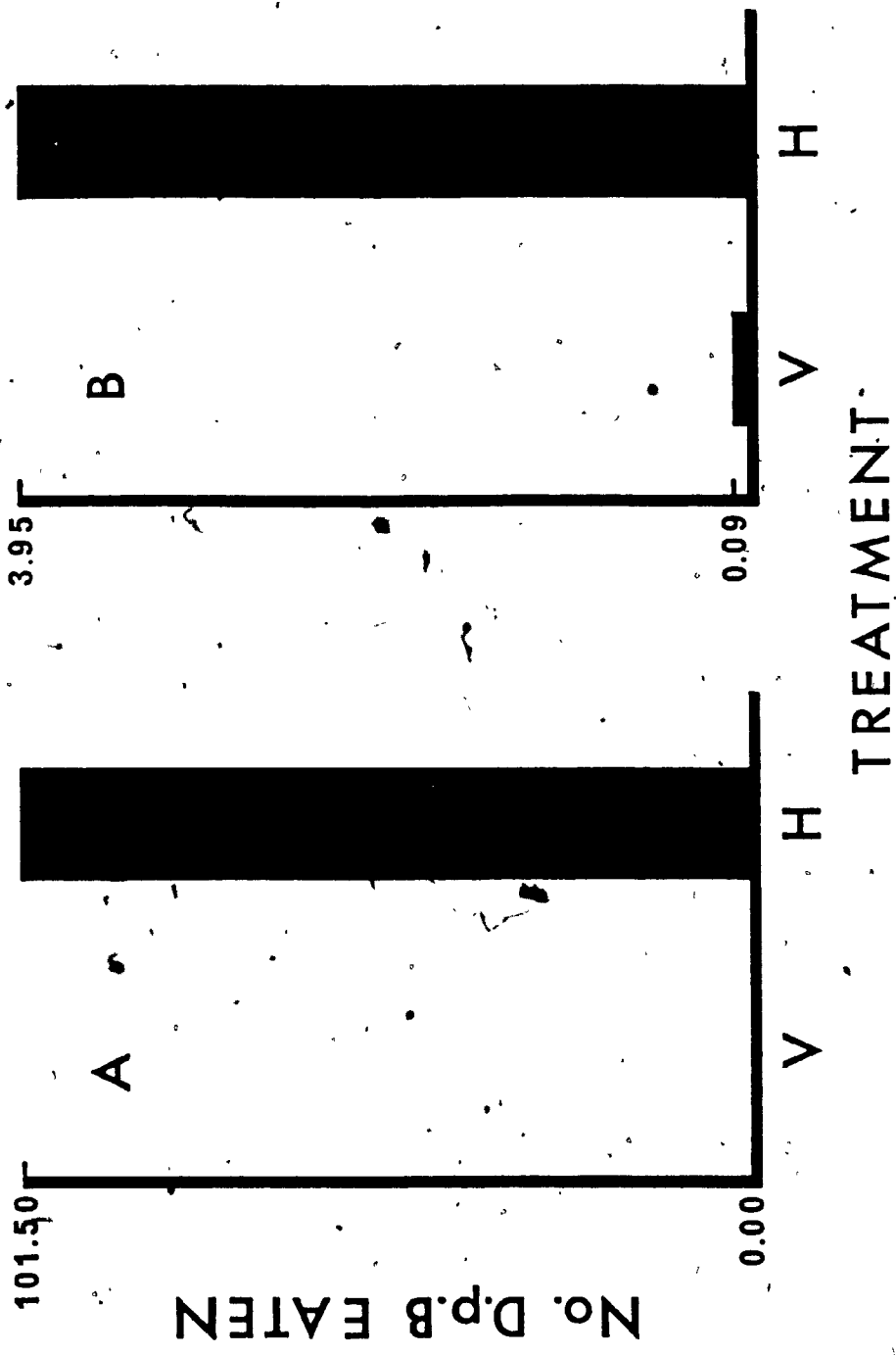


FIG. 13. Long-cage predation experiments. A. The mean number of immature *Daphnia pulex* eaten in-vertical (V) and horizontal (H) treatments by fourth instar *Chaoborus* over three days. B. A similar comparison: the mean number of immature *D. pulex* eaten per fourth instar *Chaoborus* per day. Two replicates per treatment.

for the hypothesis that Diaptomus copepodites, cooccurred with late instar Chaoborus in July by way of a significant degree of vertical separation. We also have more evidence that without vertical separation the D.p.B category in Hill Pond would have suffered severe predation by both late instar Chaoborus and Notophthalmus, while Diaptomus copepodites would have suffered more predation from the former at other times in the season.

Some mortality of prey groups occurred in vertical control treatments, but I do not believe that this fact invalidates the experiments. I return to this problem in the DISCUSSION.

In small - cage predation experiments, a mean of 1.00 D.1.A was eaten $C4^{-1} d^{-1}$. All D.1.A were recovered from controls. Although no statistics were done, this result is similar to that obtained from horizontal long-cage treatments. There a mean of 1.27 D.1.A was eaten $C4^{-1} d^{-1}$. Clearly it would not be valid to relate such a result obtained in either way to a predator-prey pair which separates to a significant degree in the water column.

Predation rates: day versus night.

In this and the following section D.c.A represents Diaptomus coloradensis adults.

The mean number of D.c.A eaten $C4^{-1} h^{-1}$ at night ($t_{s(4)} = 0.0012$ n.s., Table 10) (answers question (3), QUESTIONS ASKED). Since the day is longer than the night in the temperate zones in the summer, significantly more D.c.A were eaten $C4^{-1}$ during the day (15h) than during the night (9h) ($t_{s(4)} = 3.131$ **, Table 10). During the day a mean of 2.40 D.c.A $C4^{-1}$ was consumed while a mean of 1.70 D.c.A $C4^{-1}$ was eaten at night. However, it was during the day in Hill Pond that the degree of vertical separation

TABLE 10. The mean number of adult Diaptomus coloradensis eaten per fourth instar Chaoborus during the day and night. Experiments were done in small tanks in the laboratory. Two replicates per treatment. Temperatures 11° - 15° C.

Initial D.c.A l^{-1}	C4 l^{-1}	D.c.A eaten $C4^{-1} 15h^{-1}, x$		D.c.A eaten $C4^{-1} h^{-1}, y$	
		day	night	day	night
10.00	2.00	2.40	1.70	0.16	0.19

$$x \cdot t_{s(4)} = 3.131 \text{ ** } (t_{0.050(4)} = 2.776, P \text{ lt } 0.050)$$

$$y \cdot t_{s(4)} = 0.001 \text{ n.s. } (t_{0.200(4)} = 1.533, P \text{ gt } 0.200)$$

of late instar Chaoborus and Diaptomus copepodites was greatest. Therefore, it is probable that vertical separation was most effective during the day in reducing the number of Diaptomus eaten by late instar Chaoborus. Since some degree of vertical separation might have occurred at night, the number of Diaptomus eaten during this period might have been reduced as well.

The numbers of D.c.A eaten $C4^{-1}$ during the day and the night presented here are not additive, because different predators were used in each set of treatments and the two treatments were done one immediately after the other.

Predation rates: females with clutch.

The mean number of females with clutch eaten $C4^{-1} d^{-1}$ was not significantly different from the mean number of D.c.A eaten $C4^{-1} d^{-1}$ in the same treatments ($t_{S(4)} = 0.277$ n.s. Table 11) (answers question (4), QUESTIONS ASKED). This result suggests that Diaptomus females with clutch are eaten by larger late instar Chaoborus in proportion to their abundance, hence are no less susceptible to predation by larger late instar Chaoborus than other Diaptomus copepodites. Diaptomus females with clutch distributed the same way as other Diaptomus copepodites, therefore the significant degree of vertical separation between them and late instar Chaoborus probably reduced predation on them by these Chaoborus.

Diaptomus copepodite population projections.

In this section I contrast the growth of two hypothetical pelagic Diaptomus copepodite populations living in shallow water bodies. One population (a) has a significantly different vertical distribution from

TABLE 11. The mean number of adult Diaptomus coloradensis (any females non-gravid) and D. coloradensis females with clutch eaten per fourth instar Chaoborus per day. Experiments were done in small tanks in the laboratory. Two replicates per treatment. Temperatures 11 - 15° C.

Initial D.c.A ^y l. ⁻¹	C4 l. ⁻¹	D.c.A ^y eaten C4 ⁻¹ d ⁻¹
4.80 / 4.80	1.80	0.89 ^x / 1.00 ^x

^x $t_{s(4)} = 0.277$ n.s. ($t_{0.200(4)} = 1.533$, P gt 0.200)

y clutch / no clutch

that of a Chaoborus (C4) population, and one (b) does not. The population parameters used are presented in Table 12. The formula used to calculate projected population levels (N_t) was described under METHODS.

The numerical values of N_0 (initial number of Diaptomus copepodites l^{-1}) and P (number of C4 l^{-1}) were taken from field and long - cage experiment data. The value of N_0 for both populations I set equal to the overall density of Diaptomus copepodites on 13 July, 1977 in Hill Pond (Fig. 5A), the period when Diaptomus was low in abundance. This value is also similar to the overall initial density of D.I.A (2.68 l^{-1}) used in the long - cage experiments. These values are similar to the overall density that was found for C4 in Hill Pond on 13 July.

The formula for the calculation of feeding rates, c , was described under METHODS. The values for c for population (a) and (b) were determined from vertical and horizontal treatment data respectively (Fig. 11), because vertical treatments did not prevent vertical separation whereas horizontal treatments did. Also, the cages in these treatments were of the same scale as the water column for which the predation rates were determined.

The value of r (the rate of increase of the Diaptomus population) was arbitrarily set equal to 0.070 (individuals individual⁻¹ 3d⁻¹) for both (a) and (b). Although arbitrary, it is probably within the range of the same parameter for natural populations. McNaught (1975) presents data which convert to a value of 0.120 (individuals individual⁻¹ 3d⁻¹) for r_{max} (intrinsic rate of increase) for Diaptomus.

The population projections are presented in Fig. 14, and the implications are clear. Although both populations have been given what may be a moderate rate of increase the population which does not separate

TABLE 12. Parameters used in hypothetical
Diaptomus copepodite population projections

Graph	N_0	r	c	P	N_{15}
a	3.010	0.070	0.194	0.215	4.581
b	3.010	0.070	0.546	0.210	1.533

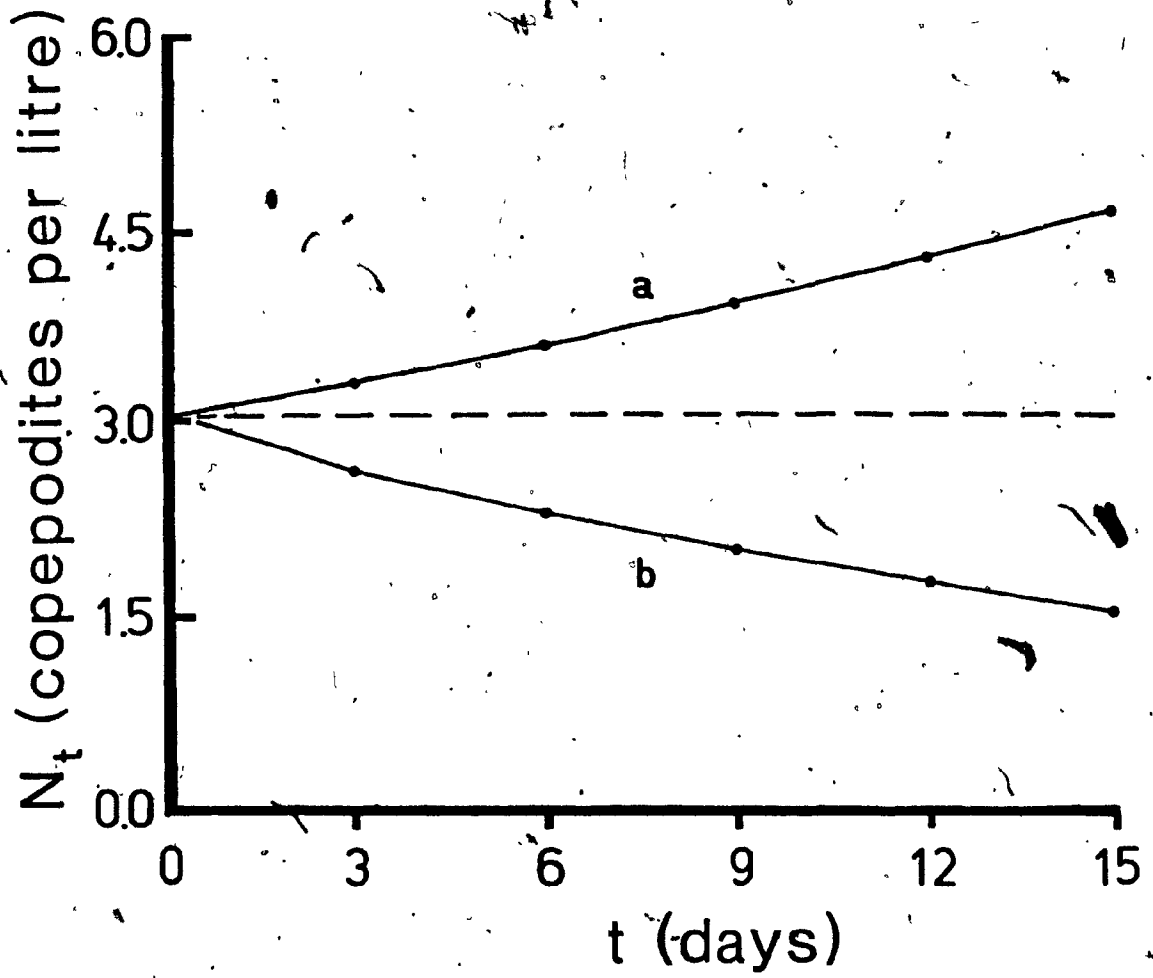


FIG. 14. Hypothetical Diaptomus copepodite population projections. See text.

80

vertically from its predators declines significantly, while the population which does separate to some extent continues to increase. One might also achieve a graph such as (b) (Fig. 14) if a single feeding rate, determined in shallow vessels, was applied to predator-prey densities in a system where they had significantly different vertical distributions. This would be the result if c was high, which is usually the case with laboratory determinations of finite feeding rates.

If the Diaptomus copepodite population in Hill Pond was a type (b) (no separation) population, and if one were to project its growth, the decline in abundance would be greater than the decline that I've shown for (b) in Fig. 14. While I've used the overall density for Diaptomus in Hill Pond on 13 July as the value of N_0 above, I considered only the C4 population there. The overall density of C3 in Hill Pond on 13 July was 0.90 C3 l.^{-1} (Fig. 5B). General predation pressure would also have been increased by C2, which varied between 0.63 C2 l.^{-1} and 1.59 C2 l.^{-1} . Also, the overall density of late instar Chaoborus did not change much in July. In such a case (constant predator density), the feeding rate would probably increase exponentially as the abundance of prey declined. Maly (1978) found that the function of the feeding rate of Didinium on Paramecium was a negative exponential when plotted against increasing initial Paramecium density.

In conclusion, the Diaptomus population in Hill Pond in July would have been in a precarious position with respect to extinction without some significant degree of vertical separation.

DISCUSSION

This study suggests that there are four important aspects of vertical distribution with respect to predation in shallow water zooplankton communities:

(1) Pelagic zooplankton groups (including females carrying clutch) and their main predators may often have significantly different vertical distributions in relatively shallow bodies of water. In such systems, pelagic zooplankton groups may be much less abundant if they do not have such vertical distributions when their predators are abundant. Immature Daphnia pulex in Hill Pond had a distribution during the day which was significantly different from those of their main predators, late instar Chaoborus americanus and predatory larvae (and adults) of the salamander Notophthalmus viridescens (e.g. Table 7). For a time immature Daphnia became relatively abundant when the most voracious groups of both predator species were abundant. Late instar Chaoborus in Hill Pond did not separate from their predator Notophthalmus and were reduced in abundance.

Significant differences may also occur between the vertical distributions of predator groups belonging to the same species but of different age in relatively shallow systems. Such differences in distribution may reduce the incidence of cannibalism by older groups on younger groups when both are present together. First instar Chaoborus, vulnerable to cannibalism by late instar Chaoborus, had a vertical distribution during the day in Hill Pond which was significantly different from those of late instars (e.g. Table 7).

(2) If predators and main prey do not separate vertically when they are together in relatively shallow systems, the former may delay the

appearance of those prey, hence give rise to unusual patterns in the appearance of various prey life stages. Late instar Chaoborus did not separate from their predator Notophthalmus during the day (when the latter feed; Attar and Maly, submitted) and the pattern of appearance of instars was: C4,1,2,3,1,2,3,4. (Fig. 6; % composition reflected density changes).

(3) If a pelagic zooplankton group in a shallow system does not have a vertical distribution which is significantly different from those of its main predators, the species to which the group belongs might even be eliminated from the system. Significant separation may be particularly important at times when the potential prey species is present at low to moderate densities and its predators are relatively abundant, and may also be particularly important (but not restricted) to mature females carrying clutch. Diaptomus leptopus would probably have been eliminated from Hill Pond by Chaoborus, if Diaptomus life stages, particularly copepodites, had not had vertical distributions which were significantly different from those of the appropriate instars of Chaoborus. This would have occurred during periods when Chaoborus was abundant and Diaptomus was not. Mature Daphnia pulex in Hill Pond did not have a day distribution which was different from that of Notophthalmus, and Daphnia pulex was eliminated there. It is probable that the effect of predation on mature Daphnia by Notophthalmus was heightened by food limitation.

(4) Thus, vertical structure may often be an integral component of pelagic zooplankton communities in relatively shallow bodies of water. Further, the vertical structure may be complex even if there are but a few species in the community (four, in Hill Pond). Much of the complexity can be explained by way of age differences within species, as I've alluded to

above. One such difference is obviously body size. An increase in body size may, for example, make a particular life stage of a species less susceptible than a previous life stage to predation by a certain category of predator, hence allow the larger life stage to distribute (for whatever reason) with that category of predator. In Hill Pond immature Daphnia pulex had a distribution significantly different from those of two of their main predators there, both late instars of Chaoborus. Mature Daphnia, which are less vulnerable to predation by late instar Chaoborus (e.g. Dodson, 1970; Sprules, 1972) mainly because of their size and shape, did not separate vertically from that predator group.

Vertical distributions, encounter probabilities and sampling.

Generally, investigators have either ignored or given token consideration to the aspect of vertical structure in studies of pelagic zooplankton communities in relatively shallow bodies of water, particularly with respect to functional relationships. Dodson (1970) attempted to quantify the impact of predation by Chaoborus americanus and Ambystoma tigrinum on Daphnia spp. in the whole of Leechmere Pond in Colorado. However, no consideration was given to where the animals were in the water column and any changes thereof which might have occurred between day and night. All his samples were taken at mid-depth and only during the day. With respect to the whole water column, the assumption inherent in his procedure was that the animals distributed randomly (or uniformly) throughout the column at all times. Also implicit with respect to the procedure was the assumption that Daphnia had an equal probability of being encountered throughout the water column and at any time. Since the zooplankton community in Leechmere is similar to that in Hill Pond

(this study) perhaps stages of Daphnia and their main predators in the former had vertical distributions which were significantly different, at least during the day. If this was the case Daphnia in Leechmere did not have an equal probability of being encountered throughout the water column nor at all times. Indeed, Dodson's zooplankton population estimates for the whole of Leechmere would also have been inaccurate.

Predation was one of several mechanisms considered by Sprules (1972) in his attempt to define the factors controlling the presence or absence of species in zooplankton communities in subalpine ponds. The depths of these ponds ranged from 0.5 to 3.0m. However, no consideration was given in his analyses to where the animals were in the water column and any changes thereof which might have occurred between day and night. He realized that animals might have had different distributions, at least during the day, but he combined the quantitative samples (surface and bottom) which he took during the day. The middle of the water column in the deeper ponds was not sampled. The zooplankton community in the deeper pond was similar to that in Hill Pond, hence it is probable that predators and their main prey in them had in most cases significantly different distributions, at least during the day. Therefore the only additional information (relative to that attained by Dodson, 1970: see above) which he might have gained after combining samples would have been more accurate population estimates for the whole water column in the shallower ponds. Consideration of differences between vertical distributions might not have changed most of Sprules' (1972) conclusions, but would have provided a more complete understanding of how community compositions were determined. Consideration of distributional differences may not have mattered in the most shallow of these ponds (but see end of

DISCUSSION), but this possibility could have been explored by Sprules.

Allan (1973) attempted to quantify the impact of predation by Chaoborus nyblaei and C. punctipennis on a population of Daphnia parvula (among other species) in Hummingbird Lake (maximum depth 5.5m) in Michigan. He too gave no consideration in his analyses to where the animals were in the water column. He realized that zooplankters in the Lake had different distributions; he even sampled for Daphnia at two depths (0.5 and 2.5m) during the day,

"... to gain some insight into spatial distributions."
(Allan, 1973)

Although most of the Daphnia distributed at 0.5m during the day, it appears that the Daphnia population estimates, which he used in assessing Chaoborus predation, were calculated by pooling data from the samples taken at different depths. Allan did not determine the distribution of Daphnia at night nor did he determine Chaoborus distributions for the day or night. The Chaoborus densities which he used in his predation assessments were those for the whole water column. The tacit assumption in the predation aspect of his work was that Daphnia had an equal probability of being encountered throughout the water column, and at any time. If Chaoborus and Daphnia there distributed in a manner similar to the way the same genera did in Hill Pond, at least during the day, it can be concluded that the assumption was not valid.

Other investigators (e.g. McQueen, 1969; Confer and Cooley, 1977) have examined the impact of predation on zooplankton populations in shallow lakes, but it appears that they did not consider depth distributions in their analyses. McQueen (1969) studied predation by the copepod Cyclops bicuspidatus thomasi on its own nauplii and the nauplii

and copepodites of Diaptomus oregonensis and D. hesperus in Marion Lake (maximum depth approximately 5.0m) in British Columbia. Confer and Cooley (1977; using Cooley's data, 1973) studied predation by Mesocyclops edax and Epischura nordenskioldi on Diaptomus minutus nauplii in Bluff Lake (maximum depth 7.0m) in Nova Scotia. In both cases samples from different depths were combined to calculate standing stocks. Also, the water column had been adequately sampled (in terms of the number of depths) only for either the day or the night. Since no data on vertical distributions were presented it is difficult to analyse these situations further.

McQueen (1969) did state that vertical separation (during the day) reduced the possibility of predation on nauplii from 15 April to about 15 June, 1967. However, it is probable that separation was not important during the latter half of this period because his data show that the predaceous late copepodites of C.b. thomasi that he was considering were not abundant (maximum 2.64 l.^{-1}) relative to the standing crop of all the nauplii (maximum about 40 l.^{-1}). The reason there were so few C.b. thomasi copepodites at that time was of course that the bulk of the nauplii then present were those of C.b. thomasi; the new generation of late instar copepodites simply hadn't developed. There is a more fundamental problem with McQueen's study, which I return to below.

Confer (1971; using the data of Maslin, 1969) examined the impact of predation by Mesocyclops edax on Diaptomus floridanus copepodites in Anderson - Cue and McCloud Lakes in Florida, the depths of which were not mentioned. Since no data on distributions, including sampling intervals, were presented, further evaluation is not possible. He did state that for most days (24 hours?) predators and prey had about the same

vertical distributions. He also stated that at any particular time more than half the animals were in a third of the water column.

I know of no studies of competition in shallow water bodies where vertical distributions have been adequately considered. For example, Hammer and Sawchyn (1968) studied congeneric associations of copepodites (including adults) of seven Diaptomus spp. in some deep (about 1.2-2.5m) Saskatchewan ponds (as well as ephemeral ponds), and acknowledged that,

"Microhabitats probably existed and vertical segregation could occur."
(Hammer and Sawchyn, 1968)

but took samples only immediately below the surface. Dumont's (1972) study of what he thought were competitors has already been discussed (see THEORY). Ironically, it appears that the animals he chose to work with were predators and prey. Other investigators have made similar errors; Hammer and Sawchyn (1968) mistook late copepodites of the large Diaptomus (Hesperodiaptomus) arcticus as competitors of other diatomids they were studying. They have been found to be predators (e.g. Anderson, 1970) and probably ate the nauplii of other diatomids in their study ponds. Late copepodites of the large, closely related D. (Hesperodiaptomus) kiseri in their study may also have been predators; late copepodites of large hesperodiaptomids e.g. D. shoshone (Anderson, 1967) for which feeding has been investigated have been found to be predators.

Certain investigators (e.g. Fordyce, 1900; Teraguchi and Northcote, 1966; LaRow, 1971) had presented evidence that particular zooplankton groups can have specific distributions and migrations in relatively shallow waters. These investigators were not concerned with functional ecological relationships. Fordyce (1900) found that Leydigia fimbriata migrated up to the surface of a Nebraska pond late in the day, but were not to be found there at mid-day. Unidentified copepods spent most of

their time nearer the surface. The pond was less than 1.0m deep.

Teraguchi and Northcote (1966) observed the distributions and migrations of fourth instar Chaoborus flavicans in experimental columns 2.0m deep (inside diameter 0.145m). For most of the day and during the middle of the night they concentrated mainly below about 1.4m, migrating towards the surface late in the afternoon or early evening and early in the morning to some extent. This pattern was that of Cushing's paradigm (Hutchinson, 1967; see Vertical distributions: night).

LaRow (1971) used somewhat smaller columns (1.5m deep X 0.10m inside diameter) to examine the effects of various O_2 concentrations, temperature and the presence or absence of zooplankton food on the vertical migration by Chaoborus punctipennis. No data were presented for day distributions, but presumably they were all at the bottom in the mud (e.g. LaRow, 1968, 1969). Even at night, most Chaoborus were below 1.20m and almost all were below 0.90m, except when O_2 concentrations were low. Even at an O_2 concentration of 4.14ppm ($mg\ l^{-1}$), comparable to O_2 concentrations in Hill Pond, no more than about 15% of the Chaoborus population was above 0.90m. The pattern of migration was usually a single maximum at 23:00h under conditions of low O_2 , although on one occasion it followed Cushing's paradigm (two maxima). LaRow did not consider where the zooplankton food was in the columns, but the Chaoborus generally responded in similar fashion whether food was present or absent.

There is of course abundant evidence that zooplankton groups have particular distributions and or migrations in deeper lakes (e.g. Teraguchi and Northcote, 1966; Rigler and Langford, 1967; Sandercock, 1967; Roth, 1968; Carter, 1969; Fedorenko and Swift, 1972; Hart and Allanson, 1976; Carter and Kwik, 1977; Lewis, 1977). However, in some studies of this kind the nature

of the distributions and migrations particularly of smaller zooplankters could not have been detected because the sampling interval was too great. For example, Wilson and Roff (1973) attempted to define the depth distributions and migrations for all crustaceans including Diaptomus minutus taken in vertical tow samples over 20m intervals in Lake Ontario. Carter (1969) took samples over 3.0m intervals from the surface to 15m of depth in Parry Sound, Georgian Bay, and found a significant proportion of D. minutus to concentrate within one 3.0m stratum (at the surface) in the summer. Obviously there is some question as to the accuracy of the distributions and migrations depicted by Wilson and Roff (1973) for the smaller zooplankters. The data of Teraguchi and Northcote (1966), Sandercock (1967), Roth (1968), Fedorenko and Swift (1972) and Carter and Kwik (1977) also show that significant population maxima can occur within strata or several metres deep.

Generally, samples should also be taken at least every half metre in water bodies having a maximum depth less than 7.0 - 8.0m, as Confer and Cooley (1977) did. For lakes about 20m deep, I recommend that samples be taken at half metre intervals for about the first 5.0m, 1.0m intervals for the next 5.0m and at 2.0 - 3.0m intervals thereafter. For larger lakes greater intervals would be satisfactory for deeper samples e.g. Carter (1969), but the half metre sampling intervals should be used for the first 5.0m. For great lakes an interval of 1.0m might be adequate near the surface. Even in large lakes small zooplankters might have definite distributions in response to surface water movements, such as those that Stavn (1971) found for Daphnia magna in response to Langmuir circulations in laboratory tanks. Sampling should also be done at least once during both the day and the night to monitor any changes in distri-

butions of populations which might occur between them.

In summary, most investigators of Chaoborus predation in relatively shallow systems have not adequately considered the vertical distributions and migrations of predators and prey. Consequently, these investigators have probably overestimated encounter probabilities. Investigators of predation by both zooplankters (copepods) in such systems have at times considered the above, but have not presented their data therefore it is not possible to evaluate their studies. Data exists which demonstrates relatively specific distributions for many zooplankters, particularly in relation to other zooplankters. Minimum sampling programs for lakes of various depths are recommended.

Predation rates and impact assessments.

Generally, investigators appear to have misused experimentally determined rates of predation in their assessments of the impact of invertebrate predation. Both Dodson (1970) and Allan (1973) determined mean predation rates (e.g. Daphnia eaten predator⁻¹d⁻¹) in small vessels (0.30 to 1.00 l.), at only one or two high prey densities (50 to 170 individuals l.⁻¹), and only for fourth instars of each Chaoborus species. The rates of predation on Daphnia varied from 0.88 to 4.40 Daphnia eaten predator⁻¹d⁻¹, depending on the species used and the set of replicates considered. These rates were then applied to the whole of the water columns in question. All prey instars e.g. of Daphnia were placed in the same prey category, and both late instars of Chaoborus were placed into the predator category. The assumption inherent in this procedure was that all prey, e.g. Daphnia, had a high and equal probability of being eaten, throughout the water column, and at any time, by both late instars of

Chaoborus.

Since the systems studied by Dodson (1970) and Allan (1973) appear to have been similar to Hill Pond, their assumption was most likely not valid. In Hill Pond those prey which cooccurred with their main predators generally had significantly different distributions, which would reduce encounter probabilities. The predation rates that they found were comparable to that which I found in horizontal treatments (3.95 immature Daphnia eaten predator⁻¹d⁻¹) which prevented vertical separation. It is probable that Allan (1973) significantly overestimated the impact of Chaoborus predation on the prey populations he was studying. Dodson (1970) may have done the same thing, although it is difficult to evaluate his assessment because his overall density estimates were probably inaccurate (see previous section). However, on some dates (13, 28 August 1968) his Chaoborus - Daphnia densities at mid-depth, which he assumed were representative of the whole water column, were similar to the densities of animals I used in the long-cage experiments. Chaoborus was a voracious predator in the experiments of both investigators, but significant vertical separation would have prevented it from being one to a significant extent in situ.

Sprules (1972) found similar rates of predation for fourth instar Chaoborus at high densities (25 Daphnia rosea plus 25 Diaptomus coloradensis l.⁻¹) of similar sized prey. The former ate 3.5 zooplankters predator⁻¹d⁻¹ in this particular experiment. Sprules did not apply his data to populations in situ.

McQueen's (1969) estimates of predation by Cyclops bicuspidatus thomasi on its own nauplii and the nauplii of Diaptomus oregonensis and D. hesperus in Marion Lake may also be significant overestimates, but for reasons other than those discussed above. There appears to be a discrepancy in

his analysis of data. On July 06, 1967, for example, there were about 33.0 nauplii l^{-1} (all species) and abundant predaceous C.b.thomasi copepodites ($24.4 l^{-1}$) over the whole water column. For this date his estimated proportion of nauplii (all species) removed d^{-1} by late C.b.thomasi copepodites was about 13%. There were of course other potential prey present. However, if the straight line representing the number of nauplii (all species) eaten predator $^{-1}d^{-1}$ plotted against the number of nauplii l^{-1} (when offered in a mixture of possible prey) in his Fig.4 was continued to the abscissa, it would have intercepted the abscissa at a point about or above 33.0 nauplii l^{-1} and where the number of nauplii eaten predator $^{-1}d^{-1}$ was 0.0. The standard deviations at the same end of the graph, although large relative to their means, were exceedingly small in absolute terms; for example, at a density of about 90.0 nauplii l^{-1} , the number eaten predator $^{-1}d^{-1}$ was approximately 0.25 ± 0.05 . Nauplii may not have been the main prey to C.b.thomasi copepodites.

If one accepts McQueen's (1969) analysis, the copepodites of C.b.thomasi in Marion Lake must have eaten something else there. Rotifers could have been their main prey; he found for example, that Keratella cochlearis was eaten at the relative high rate of about 0.50 predator $^{-1}d^{-1}$ at a Keratella density of about 50 l^{-1} in the laboratory. Few Keratella were eaten when they were included in a mixture of prey, so if rotifers were the main prey the former probably weren't among them. That Keratella weren't eaten was not unusual. Gilbert and Williamson (1978) found that Mesocyclops edax ate the rotifers Asplanchna girodi and Polyarthra vulgaris, but could not penetrate the loricae of Keratella cochlearis hence released them unharmed.

The difficulty with the suggestion that rotifers might have been the

main prey to C.b.thomasi is that McQueen does not report which rotifers were taken in samples, nor how abundant they were, in 1966 and 1967. He used Keratella as prey because its remains (loricea?) were among the identifiable matter in the guts of C.b.thomasi. Since much of the gut matter in zooplankters has been found to be unidentifiable, including that in Chaoborus which eat largely definable items (e.g. Fedorenko, 1975a; Lewis, 1977) as opposed to detritus. it is unlikely that the remains of many rotifer species would have been identifiable even if they had been abundant in the guts of C.b.thomasi. Lewis (1977) found that the remains of Keratella cochlearis and others were identifiable whereas those of Polyarthra vulgaris and Hexarthra intermedia were not, in the guts of Chaoborus after only moderate maceration.

Confer's (1971) procedure suggests that the impact of predation by Mesocyclops edax on Diaptomus floridanus copepodites in several Florida lakes was not as great as he suggested (1.1 and 5.6% of the standing crops d^{-1}). He set the prey densities which Mesocyclops might have encountered 50% above their estimated overall densities in the lakes. He did this in an attempt to compensate for the fact that half the animals (both species) were concentrated in one third of the water column rather than randomly (or evenly) throughout it. He stated that the species had similar distributions; if this was the case a 1:1 relationship between the number of prey eaten predator⁻¹ d^{-1} and prey density would be necessary if the impact of predation there was to be similar to the impact if the animals were distributed randomly (or evenly) throughout the water column. A larger ratio would be necessary to warrant the 50% increase. However, his data show that the ratio was much smaller than 1:1. Confer overestimated the impact, hence the significance, of predation by Mesocyclops on copepodites of D. floridanus by at least 50%.

Confer and Cooley's (1977) data show that exceedingly high predation rates would have been necessary if predation by Epischura nordenskioldi and Mesocyclops edax were to account for significant mortality to nauplii of Diaptomus minutus. They concluded that such predation could account for most of the naupliar mortality, but they took their rates of predation from the literature. Most of these rates were unusually high because they had been determined at prey densities which were abnormally high. Confer and Cooley (1977) may also have overestimated predation by the two copepods on D. minutus.

Fedorenko (1975b) appears to have given relatively complete consideration to encounter probabilities in her assessment of the impact of Chaoborus predation on the zooplankton of Eunice Lake, British Columbia. This lake is as far as I know a much deeper system than the others I've discussed above. She, for example, multiplied the density of a particular category of predator by the predators feeding rate at the prey density found there. Although she has not stated it as such, she seems to imply that the above was done for both the day and the night, and that final estimates were averages of the two.

Fedorenko (1975b) may still have overestimated the effects of predation, because she assumed that the presence of one prey population did not affect Chaoborus predation on other prey populations. Presumably this was based on her observation that prey densities in Eunice Lake were well below those required for maximum Chaoborus feeding. However, her assumption is questionable. For, example, Sprules (1972) found fourth instar Chaoborus americanus to eat a mean of 3.5 zooplankters predator⁻¹ d⁻¹ (my calculations) from a mixture of Daphnia rosea and Diaptomus coloradensis (approximately equal numbers of each), while I found the same category of predators to eat a mean of 3.95 Daphnia pulex predator⁻¹

d^{-1} in horizontal long-cage treatments. Daphnia were presented alone as prey in the latter case, and at lower densities.

Although rates of cannibalism by Chaoborus have not been reported in the literature, there is evidence that they can be significant in nature. For example, in Sept., 1972, Chaoborus remains made up more than 50% of the biomass found in crops of C. trivittatus in Eunice Lake (Fedorenko, 1975a). Rates of Chaoborus cannibalism may primarily be a response to the presence of vulnerable individuals (Fox, 1975). She stated that, for some species, rates of cannibalism were consistent with simple encounter models in which the probability of attack was proportional to the probability of encountering a vulnerable individual.

In summary, investigators generally appear to have overestimated the impact of zooplankton predation on other zooplankton in nature. This resulted from the use of feeding rates which were, for whatever reason, too high. Some of them, particularly for relatively shallow chaoborid systems, were high because differences between the vertical distributions of Chaoborus and prey, hence differences in encounter probabilities, were not considered. In this study, fourth instar Chaoborus were voracious predators on particular categories of zooplankton in small aquaria, which prevented separation between them and their prey, but significant vertical separation in situ reduced the number of prey eaten.

Many of the copepod predators for which predation rates were determined might have been eating prey in nature other than those considered in the studies. The reason: predation rates were very low at prey densities similar to those found in nature, even if the predators and prey appeared to have similar distributions. If this was the case, the

potential for differences between the distributions of the predators and the other prey would have to be considered in assessments of the impact of predation on such prey. Differences between the distributions of predators and less significant prey (those studied in the above reports) would have been less, if at all, important.

Other factors must have caused a significant porportion of the mortality to prey if population estimates of the latter in some of the copepod predator studies were accurate. This aspect I return to in the section Other causes of distributions.

Age (size) specificity.

Authors of the shallowwater studies discussed above should also have given more consideration to age (size) differences within species, as I have alluded to in the two previous sections. Allan (1973), for example, did not consider differences between the vertical distributions of predators and prey in his analysis, let alone whether different life-stages had different distributions. Also, neither predators nor prey were divided up into age or size categories within species in his determination of predation rates. The other authors (e.g. McQueen, 1969; Dodson, 1970; Confer, 1971; Confer and Cooley, 1977) could also have made similar considerations in various aspects of their work.

It is important that all life stages of a species be considered in at least the preliminary portions of predation assessment studies. Some investigators have mistakenly concluded otherwise e.g.

"A study of mortality in the adult (Diaptomus) instar would be of little consequence since minimal predation occurs on individuals in this stage. Investigations into causes of mortality should be centered on the early naupliar stages..."

(Gehrs and Robertson, 1975)

There must have been a reason(s) why predation on adults was minimal, and it might have accounted for the very success of the species they were studying. For example, the survival of adults through mating, and the subsequent survival of gravid females (until the eggs have been released) are obviously necessary to perpetuate Diaptomus populations. However, in chaoborid systems Diaptomus copepodites (including adults), when present, are often the most important component of the biomass of the diet of late instar Chaoborus (e.g. Fedorenko, 1975a). In Hill Pond (this study) significant vertical separation (at least during the day) between late instar Chaoborus and Diaptomus copepodites minimized predation by the former on the latter. At times the Diaptomus population there would have been in a precarious position with respect to extinction without it. Knowledge of the factors causing mortality in early naupliar stages is probably extremely important to the understanding of the persistence of Diaptomus species (Gehrs and Roberston, 1975), but study of the adults should also increase our understanding of the mechanisms promoting their survival.

Other causes of distribution.

The predator-prey and cannibalistic relationships in Hill Pond which have been discussed to this point cannot account completely for the vertical distributions of zooplankters there. These mechanisms can account for the relative proximity of most of the categories of zooplankton to the bottom of Hill Pond during the day. However, they cannot account for the decrease in the number of zooplankton categories towards the surface during the same period.

Notonectids, which were abundant near the surface of Hill Pond (but

rarely taken in sub-surface samples), and which readily ate late instar Chaoborus in small aquaria in the laboratory (Melville, unpublished data), might have prevented the latter from coming closer to the surface during the day. There did not appear to be any predators nor competitors which could have prevented the filter feeders from occupying a stratum nearer the surface.

The partial mortality of prey groups which occurred in vertical long-cage control treatments in this study might provide some insight into this problem. The prey categories at least were comprised of negatively buoyant zooplankters (zooplankters without morphological positive buoyancy adaptations). If they behaved as they probably did when they were free in Hill Pond, they would have maintained themselves up in the water column of vertical cages thus expending more energy than they would have in horizontal cages. In the latter cages they would not sink very far, hence would not have to expend so much energy maintaining their position in the water column. However, the zooplankters in the vertical cages, being negatively buoyant, could not have maintained a position immediately below the surface. Eventually, some would not have been able to hold a position at all; these would have been the zooplankters that died. The position one might expect the others to have been able to maintain would have been further down the water column, the exact position depending on (amongst other things) the mass of the animals. As one might expect of the zooplankton of Hill Pond, nauplii seemed to concentrate nearest the surface, copepodites of Diaptomus and immature Daphnia were found primarily at mid-depth, and mature Daphnia were found nearest the bottom. The alteration of this order at night (e.g. modes of adult Diaptomus abundance at the surface and bottom) might partially have been the result

of the great reduction of light intensity hence the loss of the environmental cue by which the animals oriented themselves during the day. This proposal has obvious implications with respect to diurnal vertical migration, but they won't be discussed here.

If the partial mortality of prey groups in vertical long-cage control treatments was an artifact of enclosure, the reason is not obvious. The large mesh size (maximum diameter 300 μ), and the fact that each enclosure was made entirely of it suggest that the flow of water containing food particles and O_2 was not seriously hampered. Even if no food was available fewer animals than the number that died would probably have starved to death over the duration (3 days) of each set of replicates. Threlkeld (1976) found from experiments and a review of the literature that most zooplankters of a size similar to those I used as prey survived longer than 3 days if starved. Dagg (1977) found that mortality did not occur in females of the copepods Centropages typicus and Acartia tonsa until 3 days had passed when the copepods were starved. He considered both to be species which depended on constant food availability.

It is doubtful whether confinement itself caused the mortality discussed above. Sampling data and laboratory observations suggest that the strongest tendency in the animals appeared to be that of vertical movement; if this was the case one might expect that mortality would have been greatest in horizontal control treatments. The opposite occurred i.e. mortality was greatest in vertical control treatments. Almost no mortality occurred in the horizontal control treatments.

Limits to the importance of vertical separation.

There are biological limits to the importance of vertical separation.

some of which have already been mentioned. In a similar vein, there is the problem of the coexistence of late instar Chaoborus and salamanders, which both concentrated at the bottom in Hill Pond during the day.

I suspect they coexisted mainly because they were both ambush predators. According to the model of Gerritsen and Strickler (1977), an ambush predator is best able to take fast moving prey since,

"Very slow animals have a low probability of encountering ambush predators..."

(Gerritsen and Strickler, 1977)

Since an ambush predator itself moves very slowly (or infrequently) it will have a low probability of meeting its ambush predator. Thus Chaoborus had a low probability of meeting a salamander and visa versa. That Chaoborus could comprise a significant portion of the diet of salamanders over several months (e.g. Dodson, 1970) was probably a function of the relatively high abundance of Chaoborus.

The mode of predation of the planktivore, in relation to the size or diluteness of the system, will also determine the size and abundance of zooplankton present, including invertebrate predators. In Hogan's Pond Newfoundland, a larger system than Hill Pond, the deep subalpine ponds of Dodson (1970) and other systems the predatory copepod Epischura nordenskioldi and the stickleback Gasterosteus aculeatus (probably a facultative predator on zooplankton) coexist (Davis, 1976). Yet in the lakes of Brooks and Dodson (1965), many of which were comparable in size to Hogan's Pond, the obligate predator Alosa eliminated Epischura. In extremely large lakes, such as Lake Michigan (Wells, 1970), large invertebrate predators such as Leptodora kindtii are not necessarily eliminated by Alosa, just reduced in abundance.

The relationship between vertebrate and invertebrate predators may

be one of mutual benefit; providing that the intensity of vertebrate predation is not so excessive that it eliminates the invertebrate predators. The presence of vertebrate predators would only benefit the invertebrate predators if net equilibrium production of the invertebrate population, in the presence of the vertebrates, exceeded that attained by the invertebrates if the vertebrates were absent. The latter suggestion is similar to the suggestion made by Dodson (1970).

At the other extreme one must consider the most shallow systems (e.g. less than 1.0m deep) which seem generally to have only invertebrate predators (e.g. Dodson 1975) although some have vertebrate predators (e.g. Sprules, 1972). Here temporal separation between predators and prey doubtedly increases in importance, relative to vertical separation (e.g. Maly, 1976). However, significant vertical separation could occur even in some of the systems. Melville (unpublished data) found that the density of fourth instar Chaoborus americanus in a prairie Saskatchewan slough less than 0.9m deep was much greater at the bottom (3.17 l.^{-1}) than nearer the surface (1.11 l.^{-1}) during the day. It may be that vertical separation need not be considered for small zooplankters only in the most extreme of shallow systems.

CONCLUSIONS

- 1) Pelagic zooplankton groups and their main predators may often have significantly different vertical distributions in relatively shallow bodies of water. In such systems, pelagic zooplankton groups may be much less abundant if they do not have such vertical distributions when their predators are relatively abundant.
- 2) If a pelagic zooplankton group in a shallow system does not have a vertical distribution which is significantly different from those of its main predators the species to which the group belongs might even be eliminated from the system. Significant separation may be particularly important at times when the potential prey species is present at low to moderate densities and its predators are relatively abundant, and may also be particularly important (but not restricted) to mature females carrying clutch.
- 3) Most investigators of Chaoborus predation in relatively shallow systems have not adequately considered the vertical distributions and migrations of predators and prey, and have overestimated encounter probabilities. Investigators of predation by other zooplankters (copepods) in such systems have at times considered the above but have not presented their data, therefore it is not possible to evaluate their studies.
- 4) Investigators generally appear to have overestimated the impact of zooplankton predation on other zooplankton in nature. This resulted from the use of feeding rates which were too high. Some of them, particularly for relatively shallow chaoborid systems, were high because differences between the vertical distributions of Chaoborus and prey, hence differences in encounter probabilities, were not considered.

Many of the copepod predators for which predation rates were determined might have been eating prey in nature other than those considered in the studies. The reason: predation rates were very low at prey densities similar to those found in nature, even if the predators and prey appeared to have similar distributions. Other factors must have caused a significant proportion of the mortality to prey if population estimates of the latter in some of the copepod predator studies were accurate.

5) Differences between age (size) groups of both predator and prey species should be considered in at least the preliminary portions of predation assessment studies.

6) The energetic costs of maintaining a position in the water column may be such that negatively buoyant zooplankters must maintain a position somewhat below the surface, the exact position depending on (amongst other things) the mass of the animals. These energetic costs may be so great as to be excessive to the weaker individuals causing their deaths prematurely. Therein may lie the adaptive value of diurnal vertical migration i.e. to spend as little time as possible near the surface when food may be less available.

7) The co-existence of late instar Chaoborus and salamanders demonstrates that there are biological limits to the importance of vertical separation. They probably co-exist mainly because they are both ambush predators. There may also be physical limits to the above i.e. vertical separation may not need to be considered for small zooplankters in the most extreme of shallow systems.

REFERENCES

- Ali Khan, F.E.A. and D. Kennedy. 1971. Survey of aquatic fauna in intensive agriculture and water pollution project, A. MacKenzie (Ed.). (unpublished manuscript).
- Allan, J.D. 1973. Competition and the relative abundances of two cladocerans. *Ecology* 54: 484-498.
- Anderson, S.R. 1967. Diaptomid copepods from two mountain ponds in Alberta. *Can. J. Zool.* 45: 1043-1047.
- _____. 1970. Predator relationships and predation rates for crustacean zooplankters from some lakes in western Canada. *Can. J. Zool.* 48: 1229-1240.
- Attar, E. and E.J. Maly. 1979. (Title?, submitted).
- Begg, G.W. 1976. The relationship between the diurnal movements of some of the zooplankton and the sardine Limnothrissa miodon in Lake Kariba, Rhodesia. *Limnol. Oceanogr.* 21: 529-239.
- Bishop, S.C. 1967. Handbook of salamanders. Cornell.
- Brooks, J.L. 1965. Predation and relative helmet size in cyclomorphic Daphnia. *Proc. Nat. Acad. Sci.* 33:119-126.
- _____. 1966. Cyclomorphosis, turbulence and overwintering in Daphnia. *Verh. Int. Ver. Limnol.* 16: 1653-1659.
- _____. 1968. The effects of prey size selection by lake planktivores. *Syst. Zool.* 17: 272-291.
- _____, and S. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150: 28-35.
- Carter, J.C.H. 1969. Life cycles of Limnocalanus macrurus and Senecella calanoids, and seasonal abundance and vertical distributions of various planktonic copepods, in Parry Sound, Georgian Bay. *J. Fish. Res. Bd. Can.* 26: 2543-2560.
- _____, and J.K. Kwik. 1977. Instar succession, vertical distribution, and interspecific competition among four species of Chaoborus. *J. Fish. Res. Bd. Can.* 34: 113-118.
- Confer, J.L. 1971. Intra-zooplankton predation by Mesocyclops edax at natural prey densities. *Limnol. Oceanogr.* 16: 663-666.
- _____, and P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. *Limnol. Oceanogr.* 29: 571-579.

- _____ and J.M. Cooley. 1977. Copepod instar survival and predation by zooplankton. J. Fish. Res. Bd. Can. 34: 703-706.
- Cox, G.W. 1976. Laboratory manual of general ecology. Brown, Dubuque, Iowa.
- Dagg, M. 1976. Some effects of patchy food environments on copepods. Limnol. Oceanogr. 22: 99-107.
- Davis, C.C. 1976. Simultaneous quantitative comparison of planktic Crustacea in two Newfoundland boreal lakes. Int. Revue ges. Hydrobiol. 61: 807-823.
- Dodson, S.I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15: 131-137.
- _____ 1974a. Zooplankton competition and predation; an experimental test of the size efficiency hypothesis. Ecology 55: 605-613.
- _____ 1974b. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721-729.
- _____ 1975. Predation rates of zooplankton in arctic ponds. Limnol. Oceanogr. 20: 426-433.
- Dumont, H.J. 1972. A competition-based approach of the reverse vertical migration in zooplankton and its implications chiefly based on a study of the interactions of the rotifer Asplanchna priodonta (Gosse) with several Crustacea Entomostraca. Int. Revue ges. Hydrobiol. 57: 1-38.
- Edmondson, W.T. (Ed.) 1959. Freshwater biology. Wiley, New York.
- Fedorenko, A.J. 1975a. Instar and species-specific diets in two species of Chaoborus. Limnol. Oceanogr. 20: 238-249.
- _____ 1975b. Feeding characteristics and predation impact of Chaoborus (Diptera, Chaoboridae) larvae in a small lake. Limnol. Oceanogr. 20: 250-258.
- _____ and M.C. Swift. 1972. Comparative biology of Chaoborus americanus and Chaoborus trivittatus in Eunice Lake, British Columbia. Limnol. Oceanogr. 17: 721-730.
- Fordyce, C. 1900. The Cladocera of Nebraska. Trans. Am. Microsc. Soc. 22: 119-174.
- Fox, L.R. 1975. Cannibalism in natural populations. Ann. Rev. Ecol. Syst. 6: 87-106.

- Fryer, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. *J. Animal Ecol.* 26: 263-286.
- Gailbraith, M.G. 1967. Size-selective predation on Daphnia by rainbow trout and yellow perch. *Trans. Amer. Fish. Soc.* 96: 1-10.
- Gehrs, C.W. and A. Robertson. 1975. Use of life tables in analyzing the dynamics of copepod populations. *Ecology* 56: 665-672.
- Gerritsen, J. and J.R. Strickler:1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Bd. Can.* 34: 73-82.
- Gilbert, J.J. and C.E. Williamson. 1978. Predator-prey behavior and its effect on rotifer survival in associations of Mesocyclops edax, Asplanchna girodi, Polyarthra vulgaris, and Keratella cochlearis. *Oecologia* 37: 13-22.
- Green, J. 1967. The distribution and variation of Daphnia lumholzi (Crustacea: Cladocera) in relation to fish predation in Lake Albert, East Africa. *J. Zool.* 151: 181-197.
- Hall, D.J. 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata mendotae. *Ecology* 45: 94-112.
- _____, W.E. Cooper and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15: 839-982.
- _____, S.T. Threlkeld, C.W. Burns and P.H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.* 7: 177-208.
- Hammer, U.T. and W.M. Sawchyn. 1968. Seasonal succession and congeneric associations of Diaptomus spp. (Copepoda) in some Saskatchewan ponds. *Limnol. Oceanogr.* 13: 476-484.
- Hart, R.C. and B.R. Allanson. 1976. The distribution and diel vertical migration of Pseudodiaptomus hessei (Mrazek) (Calanoida:Copepoda) in a subtropical lake in southern Africa. *Freshwat. Biol.* 6: 183-198.
- Hutchinson, G.E. 1967. A treatise on limnology, vol.2. Wiley, New York.
- Jacobs, J. 1965. Significance of morphology and physiology of Daphnia for its survival in predator-prey experiments. *Naturwissenschaften* 52: 141-142.
- _____. 1966. Predation and rate of evolution in cyclomorphic Daphnia. *Verh. Int. Ver. Limnol.* 16: 1645-1652.

- Johannsen, O.A. 1970. Aquatic Diptera. Entomological reprints, Los Angeles.
- Kerfoot, W.C. 1975. The divergence of adjacent populations. Ecology 56: 1298-1313.
- _____. 1977a. Implications of copepod predation. Limnol. Oceanogr. 22: 316-125.
- _____. 1977b. Competition in cladoceran communities. The cost of evolving defenses against copepod predation. Ecology 58: 304-313.
- _____. 1978. Combat between predatory copepods and their prey: Cyclops, Epischura, and Bosmina. Limnol. Oceanogr. 23: 1089-1102.
- Lance, G.W. 1974. Ecological parameters influencing the distribution of Chaoborus species (Diptera). M. Sc. thesis, Univ. of Saskatchewan.
- LaRow, E.J. 1968. A persistent diurnal rhythm in Chaoborus larvae. I. The nature of the rhythmicity. Limnol. Oceanogr. 13: 205-256.
- _____. 1969. A persistent diurnal rhythm in Chaoborus larvae II. Ecological significance. Limnol. Oceanogr. 14: 213-218.
- _____. 1971. The effect of oxygen tension on the vertical migration of Chaoborus larvae. Limnol. Oceanogr. 16: 357-362.
- Lewis, W.M. 1977. Feeding selectivity of a tropical Chaoborus population. Freshwat. Biol. 7: 311-325.
- Maly, E.J. 1976. Resource overlap between co-occurring copepods: effects of predation and environmental fluctuation. Can. J. Zool. 54: 933-940.
- _____. 1978. Stability of the interaction between Didinium and Paramecium: effects of dispersal and predator time lag. Ecology 59: 733-74].
- McNaught, D.C. 1975. A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. Verh. Int. Ver. Limnol. 19: 724-731.
- McQueen, D.J. 1969. Reduction of zooplankton standing stocks by predaceous Cyclops bicuspidatus thomasi in Marion Lake, British Columbia. J. Fish. Res. Bd. Can. 26: 1605-1618.
- Patalas, K. 1971. Crustacean plankton communities in forty-five lakes in the experimental lakes area, northwestern Ontario. J. Fish. Res. Bd. Can. 28: 231-244.
- Pearre, S. 1973. Vertical migration and feeding in Sagitta elegans Verill. Ecology 54: 300-314.

- Pope, G.F., J.C.H. Carter and G. Power. 1973. The influence of fish on the distribution of Chaoborus spp. (Diptera) and density of larvae in the Matamek River system, Quebec. Trans. Am. Fish. Soc. 102: 707-714.
- Raymont, J.E.G. 1963. Plankton and productivity in the oceans. Pergamon, Oxford.
- Rigler, F.H. and R.R. Langford. 1967. Congeneric occurrences of species of Diaptomus in southern Ontario lakes. Can J. Zool. 45: 81-90.
- Roger, C. and R. Grandperrin. 1976. Pelagic food webs in the tropical Pacific. Limnol. Oceanogr. 21: 731-734.
- Roth, J.C. 1968. Benthic and limnetic distribution of three Chaoborus species in a southern Michigan lake. (Diptera, Chaoboridae). Limnol. Oceanogr. 13: 242-249.
- Sandercock, G.A. 1967. A study of selective mechanisms for the coexistence of Diaptomus spp. in Clarke Lake, Ontario. Limnol. Oceanogr. 12: 97-112.
- Sokal, R.R. and F.J. Rohlf. 1969. Biometry, the principles and practice of statistics in biological research. Freeman, San Francisco.
- Sprules, W.G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375-386.
- Stavn, R.H. 1971. The horizontal-vertical distribution hypothesis: langmuir circulations and Daphnia distributions. Limnol. Oceanogr. 16: 435-466.
- Swift, M.C. and A.Y. Fedorenko. 1972. Some aspects of prey capture by Chaoborus larvae. Limnol. Oceanogr. 20: 418-425.
- Teraguchi, M. and T.G. Northcote. 1968. Vertical distribution and migration of Chaoborus flavicans larvae in Corbett Lake, British Columbia. Limnol. Oceanogr. 11: 164-176.
- Threlkeld, S.T. 1976. Starvation and size structure of zooplankton communities. Freshwat. Biol. 6: 489-496.
- Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556-565.
- Wilson, J.b. and J.C. Roff. 1973. Seasonal vertical distribution and diurnal migration patterns of Lake Ontario crustacean zooplankton. Proc. 16th Conf. Great Lakes Res. 16: 190-203.

Wilt, F.H. and N.K. Wessells (Eds.) 1967. Methods in developmental biology. Crowell, New York.

Zaret, T.M. 1969. Predation-balanced polymorphism of Ceriodaphnia cornuta Sars. Limnol. Oceanogr. 14: 301-302.

_____. 1972a. Predator-prey interaction in a tropical lacustrine ecosystem. Ecology 52: 248-257.

_____. 1972b. Predators, invisible prey, and the nature of polymorphism in the Cladocera (class Crustacea). Limnol. Oceanogr. 17: 171-184.

_____, and W.C. Kerfoot. 1975. Fish predation on Bosmina longirostris: body-size selection versus visibility selection. Ecology 56: 232-237.

Appendix 1. Some physical data for Hill Pond and Lower Lake.

I present surface temperature and dissolved O_2 data for both Hill Pond and Lower Lake in Fig.15. In Hill Pond, temperature changed dramatically throughout the season, increasing from $0^{\circ}C$ on 01 April during the spring thaw to a maximum of $28.5^{\circ}C$ on 20 July. It then decreased gradually thereafter until the pond froze in November. There was little diurnal change in the temperature of the water over the 15 and 16 August. When measured, water temperatures in Lower Lake were similar to those in Hill Pond.

Dissolved O_2 concentrations remained relatively constant for both ponds until September, when they increased with the decrease in temperature. Dissolved O_2 in Hill Pond was always much less than that in Lower Lake, probably because the excessive turbidity (see below) reduced primary productivity.

Hill Pond was extremely turbid, the result of suspended clay matter. The Secchi disc was visible from the bottom, 2m, on few sampling days. Lower Lake was less turbid; often the Secchi disc could be seen between 2 and 3m. The turbidity there was of a different nature, primarily algae and suspended organic matter.

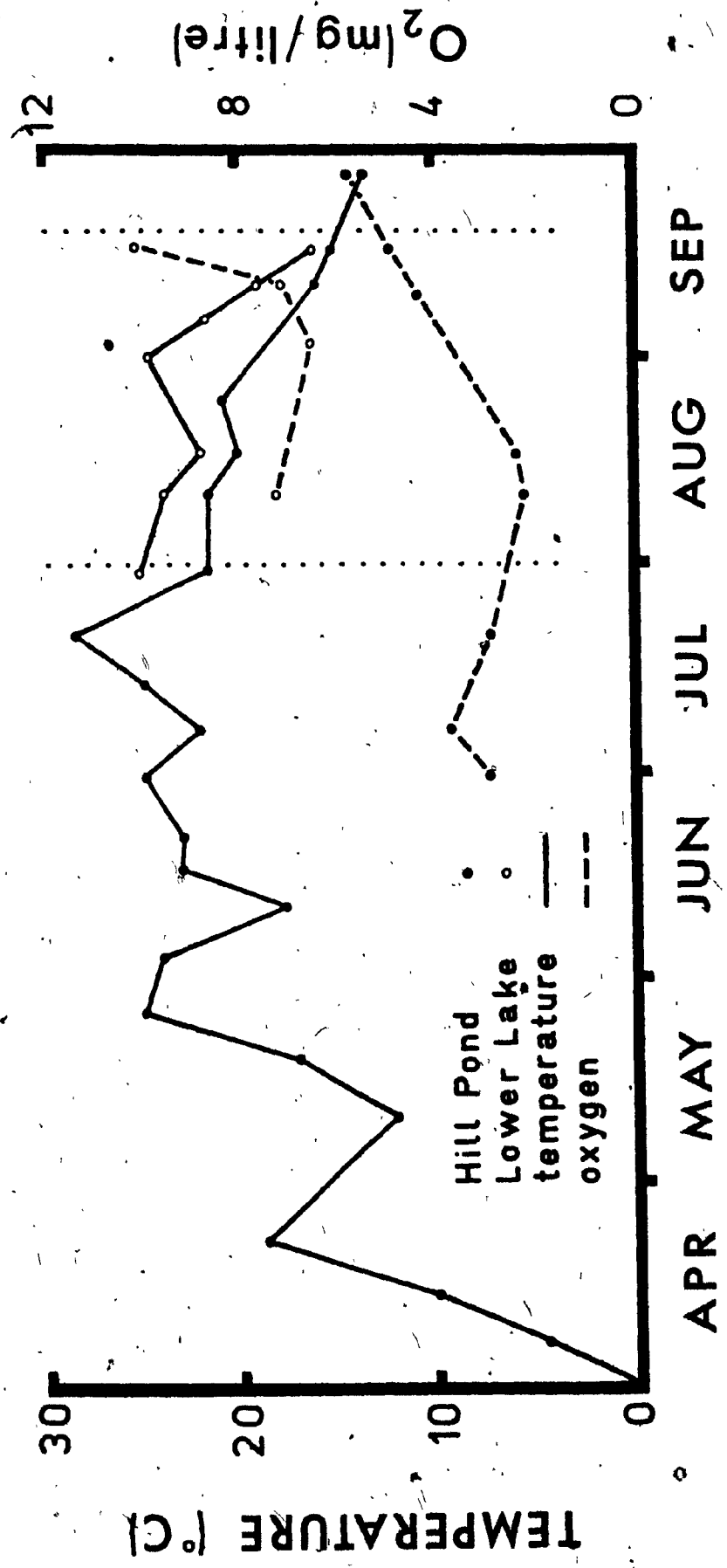


FIG. 15. Surface temperature and O₂ data for Hill Pond and Lower Lake, 1977. Vertical dotted lines represent the period when long-cage predation experiments were done.

Appendix 2. Chemistry of the waters of Hill Pond and Lower Lake.

Constituent (mg/L, except *)	Hill Pond 1977 ^a		Lower Lake 1977 ^a		1971 ^b	
	mean	range	mean	range	mean	range
NO ₃ ⁻ (+NO ₂ ⁻)	-	-	-	-	2.8	0.0 - 7.0
NO ₃ ⁻ (+ ?)	1.0 ^d	-	1.5 ^d	-	-	-
Soluable phosphate*	-	-	-	-	33.0	2.5 - 272.0
Orthophosphate	0.0	-	0.7	-	-	-
Ca	76.0	49.0- 98.0	55.0	-	33.0	19.5 - 47.0
Mg	83.0	60.0-112.0	95.0	-	17.0	13.0 - 24.0
Hardness	160.0	142.0-175.0	150.0	-	150.0	78.4 - 225.0
Alkalinity -total	150.0	110.0-200.0	141.0	-	70.0	4.9 - 185.0
ph*	7.3	6.8- 7.5	7.5	-	-	-
CO ₂	8.5	-	11.0	-	-	-

a done on 25 August, 1977

b Intensive Agriculture and Water Pollution Project, 1971.

c by Lamotte Co. water test kit.

* soluable phosphate - units not reported.

Appendix 3. The main species in the zooplankton communities in the
Arboretum ponds and Lower Lake.

Arboretum.

Hill Pond (see FIG. 1).

Diaptomus leptopus S.A. Forbes, 1882

Daphnia pulex Leydig, 1860. emend. Richard, 1896

Chaoborus americanus Johannsen, 1903

Notophthalmus viridescens viridescens Rafinesque (a salamander)

Pond (a) (see FIG. 1A)

D. leptopus

D. pulex

C. americanus

Pond (b) (see FIG. 1A)

Scapholeberis kingi Sars, 1903

D. pulex

C. americanus

Lower Lake (see FIG. 1A)

Bosmina sp.

Ceriodaphnia sp.

Perca flavescens Mitchill (yellow perch)