

THE RELATIVE EFFECTS OF FISH AND COPEPOD PREDATION ON THE
DENSITY AND SIZE STRUCTURE OF A ZOOPLANKTON COMMUNITY

© Fred Raess

A Thesis
in
The Department
of
Biological Sciences

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

December, 1981

© Fred Raess, 1981

ABSTRACT

THE RELATIVE EFFECTS OF FISH AND COPEPOD PREDATION ON THE DENSITY AND SIZE STRUCTURE OF A ZOOPLANKTON COMMUNITY

Fred Raess

In situ experiments were performed in a shallow, turbid reservoir using 212 liter polyethylene cages. By varying the densities of yellow perch and cyclopid copepods in the cages, the effects of each type of predator on the zooplankton community were determined.

Perch predation reduced the densities of large surface dwelling zooplankton but did not adversely affect bottom dwelling species. Cyclopid predation did not limit prey populations.

Selection by perch of large individuals within a prey species was not generally observed but the presence of fish altered the depth distribution of the size classes of three prey species. Cyclopid predation affected the size distribution of four zooplankton species.

The presence of perch resulted in Daphnia galeata populations with shorter helmets and longer spines than the non-fish populations. Predation by cyclopoids had no effect on Daphnia morphology.

Releasing the zooplankton community from fish predation decreased the diversity of the community by allowing the larger, surface-dwelling cladocerans to increase in relative abundance.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisor, Dr. Ed Maly, for his encouragement, assistance, and suggestions throughout this study. The work was supported by NSERC grant A9883 and a Concordia Teaching Fellowship.

I am grateful to all my committee members for their suggestions and criticisms which aided the writing of this thesis.

Special thanks go to François Chabot for his invaluable assistance in the field. J. Tilton and H. Miller were particularly helpful in the preparation of the final manuscript.

Last, but not least, my thanks to Kim Gilbride for her moral support throughout.

TABLE OF CONTENTS

	<u>Page</u>
Title Page	
Abstract	
Acknowledgements	
List of Tables and Figures	
Introduction.....	1
Literature Review.....	5
Vertebrate Predation	5
Invertebrate Predation	11
Cyclomorosis and Polymorphism	16
Material and Methods.....	21
Study Area	21
Experimental Procedure	23
Procedure with Samples	27
Results.....	29
Discussion.....	48
Conclusions.....	57
Appendix.....	59
Table A1. Characteristics of study area	59
Table A2. Effects of fish predation on helmet & spine length in <u>D. galeata</u>	60
Table A3. Effects of fish predation on height and antennule length in <u>B. coregoni</u>	61
Literature cited.....	62

LIST OF TABLES AND FIGURES

		PAGE
Table 1.	Mean predation rates of some copepods	14
Table 2.	Characteristics of the zooplankton species of Lac Choinière	26
Table 3.	Density of zooplankton on Day 0 and Day 10 of experiment	37
Table 4.	Density of zooplankton on Day 17 of experiment	38
Table 5.	Mean length of zooplankton on Day 10 of experiment	39
Table 6.	Correlation between PCD and prey density	40
Table 7.	Significance of size selective predation by cyclopoid copepods	40
Table 8.	Effect of perch predation on relative abundances of zooplankton and community diversity	41

Fig. 1	Map of Lac Choinière	22
Fig. 2	Size frequency distributions of <u>B. coregoni</u> under high and low cyclopoid predation	42
Fig. 3	Size frequency distribution of <u>C. reticulata</u> under high and low cyclopoid predation	42
Fig. 4	Size frequency distribution of <u>D. galeata</u> under high and low cyclopoid predation	43
Fig. 5	Size frequency distribution of <u>D. leuchtenbergianum</u> under high and low cyclopoid predation	43
Fig. 6	Size frequency distribution of <u>D. minutus</u> under high and low cyclopoid predation	44
Fig. 7	PCD versus % preferred prey/cage of <u>B. coregoni</u> and <u>C. reticulata</u>	45
Fig. 8	PCD versus % preferred prey/cage of <u>D. leuchtenbergianum</u> and <u>D. minutus</u>	45
Fig. 9	Effects of perch predation on helmet length in <u>D. galeata</u>	46
Fig. 10	Effects of perch predation on spine length in <u>D. galeata</u>	46
Fig. 11	Effects of perch predation on carapace height in <u>B. coregoni</u>	47
Fig. 12	Effects of perch predation on antennule length in <u>B. coregoni</u>	47

INTRODUCTION

The role of predation in shaping the species composition and size structure of zooplankton communities has been intensively studied over the last twenty years. The two main groups of predators in these communities are small, tactile-feeding invertebrates such as copepods and large, visually feeding vertebrates such as fish.

The crustacean planktivores (eg. copepods, Leptodora, Polyphemus) and the aquatic larvae of some insects (eg. Chaoborus) are known to prey preferentially on smaller zooplankton species and small individuals within a species. (Dodson 1975, Brandl and Fernando 1978, Confer and Applegate 1979, Jamieson 1980).

Recent evidence indicates that invertebrate predation may confer an adaptive advantage on the development of spines, helmets, horns and other protuberances of the carapace in some cladoceran species; notably prey species of the genera Daphnia and Bosmina (Kerfoot 1975, O'Brien and Vinyard 1978, Grant and Bayly 1981, Krueger and Dodson 1981).

Predation by visually feeding predators such as fish, on the other hand, has been found to fall most heavily on larger zooplankton species and on large individuals within a species (Wells 1970, Kerfoot 1975a, Stenson 1976, Jacobs 1978). Feeding rates of fish are extremely high, being 3 orders of magnitude higher than that of invertebrate predators. In clear water, feeding rates of over 500 zooplankters eaten per hour per fish are not uncommon, (eg. Werner and Hall 1974, Janssen 1980, Gardner 1981). These feeding rates will be lower in highly turbid bodies of water where the fishes' reactive distance, or maximum distance at which the predator can see a prey item of a given size, is decreased (Vinyard and O'Brien 1976). Although turbidity decreases feeding rates it has no effect on the fishes' usual selection for larger zooplankters (Gardner 1981).

In an aquatic system where planktivorous fish are present, pressure from these predators would fall most heavily on large cladocerans and copepods. Since large copepods are among the most voracious invertebrate predators (see Table 1), the presence of fish would result in the smaller cyclopoid copepods becoming the dominant invertebrate predator (it is assumed that large, relati-

vely transparent predators such as Chaoborus larvae, which could avoid predation by fish are not present). With slower feeding small cyclopoids supplying all the invertebrate predation pressure, predation by fish should control zooplankton community structure and size to a far greater extent.

If we further suppose that the lake is also highly turbid, it would be expected that zooplankton species which prefer the lower regions of the water column where light penetration is low would suffer less piscine predation than species which inhabit the upper waters where fish feeding would be most intense.

In situ enclosure experiments were performed in Lac Choinière, a eutrophic, turbid reservoir in the Eastern Townships of Québec which supports populations of both planktivorous perch and predatory cyclopoid copepods (Cyclops vernalis and Mesocyclops edax). The experiments were designed to provide evidence to answer the following questions.

When a zooplankton community is exposed to both vertebrate and invertebrate predation simultaneously, what is the relative importance of each in determining prey species densities?

How do the two types of predation affect the size distribution of the zooplankton community, with respect to both individuals within a species and species within the community?

What are the relative effects of perch and cyclopoid predation on development of variable morphological features in two cladocerans, Daphnia galeata and Bosmina coregoni.

Is relatively high turbidity in a lake sufficient to allow the maintenance of a population(s) of large zooplankters in the presence of fish.

What is the overall response, if any, of the zooplankton community to predation by these two contrasting types of planktivores?

LITERATURE REVIEW

VERTEBRATE PREDATION

Since the mid 1960's, it has been widely known that visually feeding planktivorous fish have a significant impact on the species composition and size structure of zooplankton communities. Many species of fish are either obligate or facultative planktivores and virtually every species consumes zooplankton at some point in their life cycle. These include many cyprinids: Notropis atherinoids (Siefert 1972), N. volucellus, Hybognathus nuchalis, Notemigonus crysoleucas, Pimephales notatus, Fundulus diaphanus, and Etheostoma nigrum (Gascon and Leggett 1977); centrarchids: Lepomis gibbosus (Confer and Blades 1975), and L. macrochirus (O'Brien et al 1976); perch: Perca flavescens (Wong and Ward 1972, Noble 1975) and P. fluviatilis (Stenson 1976); salmonoids: Salmo gairdneri (Gailbraith 1967), Salvelinus namaycush (O'Brien et al 1980); and coregonids: Alosa pseudoharengus (Wells 1970), Osmerus mordax (Siefert

1972), and Dorosoma cepedianum (Drenner and McComas 1980).

These planktivores can be extremely voracious. Janssen (1980) reports that a single 25 cm ciscoe (Coregonus artedii) can consume over 1300 Daphnia in 15 minutes. Gut content analysis of fingerling yellow perch (Perca flavescens) show that up to 400 zooplankters may be found in a single stomach (Siefert 1972, Noble 1975).

Fish predation appears to be size selective with larger prey species being preferred over small species for post-larval predators. A large increase in the alewife population in Lake Michigan in the early 1960's resulted in a sharp decline in density of the larger zooplankters (Daphnia galeata, D. retrocurva, Epischura lacustris, Diaptomus sicilis, and Mesocyclops edax) and an increase in the smaller genera such as Bosmina, Ceriodaphnia and Cyclops (Wells 1970). After a subsequent crash in the alewife population in 1967, the zooplankton community began to shift back towards the larger species. Kerfoot (1975a) found that the three-spined stickleback (Gasterosteus aculeatus) preferred

copepods and large cladocerans over a small cladoceran (Bosmina longirostris) and copepod nauplii.

Planktivorous fish will also select the larger individuals within a species or several closely related species. Stenson (1976) found that Bosmina coregoni was eaten by perch in larger numbers than the smaller B. longirostris, even when the smaller species was more abundant in the lake. The minnow Phoxinus laevis preferred Daphnia hyalina to the smaller D. cucullata (Jacobs 1978). The three-spined stickleback (Gasterosteus aculeatus) has been reported to select the larger individuals of Bosmina longirostris (Kerfoot 1975a).

These patterns of selection of large species and large individuals within a species are valid only for post-larval fish. For example, the fry of perch, white sucker, bluegill, emerald shiner, and rainbow smelt ate mainly small nauplii larvae while the predator was less than one centimeter in length and switched to the larger prey, Bosmina coregoni when a length of 1.5 cm was attained (Siefert 1972). Wong and Ward (1972) have shown that perch less than 2 cm in length could not ingest Daphnia pulex of a length of 1.3 mm or more. This limitation was attributed to the relationship between the predators' mouth gape width and the maximum

body depth of Daphnia that could be handled; resulting in the perch selecting smaller than average sized Daphnia for the first three weeks of the fishes' life in the lake following hatching.

There are several variable prey characteristics which may increase any given prey species' success at evading piscine predators. For example, increased transparency is thought to aid zooplankton in escaping detection by fish. Extremely large zooplankton (greater than 2 cm length) such as Leptodora kindtii and Chaoborus larvae are transparent except for the head area. The carapace in cladocerans is transparent which reduces the volume of the body seen by a visual predator. Similar sized copepods (which are completely opaque) are therefore more susceptible as a fish food item. Among the cladocerans it has been proposed that the diameter of the highly pigmented compound eye is a strong factor influencing the ability to escape detection by fish (Zaret 1972, Zaret and Kerfoot 1975, Kerfoot 1980). A large eyespot would make a zooplankter more conspicuous to a fish.

Escape ability, or maximum velocity attainable by a zooplankter also plays a role in the diet of planktivorous fish. Calanoid copepods have the greatest maxi-

9.

imum velocity while large cladocerans and cyclopoids are intermediate with small cladocerans being the slowest (Lehman 1977, Kerfoot 1978, Kerfoot et al 1980). The most common method of zooplankton ingestion by fish is the rapid expansion of the buccal cavity causing a vacuum or siphon effect (O'Brien 1979). Studies using an artificial siphon have shown that the fastest zooplankters are best able to avoid the simulated fish while slow swimmers are easily captured (Drenner and McComas 1980).

The mechanism by which planktivorous fish feed has been well studied (eg. O'Brien et al 1976, Confer and Blades 1975, O'Brien et al 1980, Janssen 1980, and see O'Brien 1979 for a good review) and factors which can decrease feeding rates have been uncovered. As was mentioned in the Introduction, low light intensities and high turbidity decrease the fishes' reactive distance, or the maximum distance at which the predator can see a prey item of any given size (Vinyard and O'Brien 1976). Although high turbidity reduces the feeding rate of fish, it does not alter the predators selection for large prey items. In darkness however, alewives (Alosa pseudoharengus) and ciscoes (Coregonus artedii) have

been shown to feed at reduced rates in a non-size selective manner while choosing larger zooplankton when feeding in light (Janssen 1980). This suggests that light is an important factor in determining the feeding behavior of planktivorous fish.

INVERTEBRATE PREDATION

Omnivorous and carnivorous crustacean zooplankton can significantly affect a zooplankton community. The order Copepoda contains most of the predacious zooplankton species, many of which are widely distributed (eg. Cyclops vernalis, Cyclops bicuspidatus, Mesocyclops edax). There are several cladocerans which are predacious such as Leptodora kindtii (Cummins et al 1969) and Polyphemus pediculus (Monakov 1972). The aquatic larvae of the dipteran genus Chaoborus are important predators when abundant (Fedorenko 1975, Swift and Fedorenko 1975). Since the latter two orders of invertebrate predators are usually less abundant, I will limit the following discussion to the Copepoda.

Both calanoid and cyclopoid copepods, upon hatching from eggs, undergo six naupliar larvae instars followed by six copepodid instars, the last of which is reproductive. Only the last two or three copepodid instars of predacious species have the capacity for carnivory (Fryer 1957, Jamieson 1980). One species, Cyclops viridis is known to mature and reproduce on a diet consisting solely of algae suggesting that some species, at

least, are not obligate carnivores in their later instars (Smyly 1970). When late instar copepods were fed zooplankton however, they matured more quickly, produced more and larger broods, and had a longer life span. This seems to be due to energetic considerations. Monakov (1972) reports that the assimilation efficiency for algal food is low (0.3 to 0.4%) compared to that of crustacean food (30 to 40%) in a study of omnivorous copepods.

Predatory copepods tend to prey selectively on smaller species and smaller individuals within a species. This behavior pattern is followed by many copepod species including: Mesocyclops edax (Brandl and Fernando 1978, Williamson 1980), M. leuckarti (Gophen 1977, Jamieson 1980), Cyclops vernalis (Brandl and Fernando 1974, Li and Li 1979), C. vicinus (Brandl and Fernando 1975b), Macrocyclus albidus (Confer and Applegate 1979), Megacyclus sp. (O'Brien et al 1979), Heterocope septentrionalis (Dodson 1975), Epischura nevadensis (Kerfoot 1977), and E. lacustris (Confer and Applegate 1979). Table 1 indicates the tendencies of higher predation rates on zooplankton as prey size decreases, and higher predation rates as predator size increases.

Several factors are known to modify predation rates by cyclopoids. Low ambient temperature will decrease the rate at which Mesocyclops leuckarti preys on Ceriodaphnia reticulata (Gophen 1977) and C. dubia (Jamieson 1980).

Increases in prey density can also increase predation rates by cyclopoids. This has been observed for Macrocyclus albidus feeding on Daphnia pulex and Diaptomus pallidus (Confer and Applegate 1979) and Mesocyclops leuckarti feeding on a variety of five types of cladocerans and copepods (Jamieson 1980).

Recent evidence indicates that specific features adopted by some prey species may increase the chances of successfully avoiding predation by cyclopoids. Li and Li (1979) found that Cyclops vernalis preferred Diaphanosoma leuchtenbergianum and Diaptomus franciscanus to the smaller prey Bosmina longirostris and Chydorus sp. They noted that Cyclops could not easily bite through the carapaces of the small cladocerans while the carapaces of Diaphanosoma and Diaptomus were eaten entirely. Similarly, the relatively thick carapace of Bosmina longirostris protects it from the predatory Mesocyclops edax (Williamson 1980).

The explanation for the predators' preference for relatively thick carapaced large prey may lie in food

Table 1. Mean predation rates by some copepods. (prey per predator per day).

Predator size	Prey size	Prey type	Predation rate	Sources*
small (<1.5 mm)	small	Nauplii	2.5	4,7,9
		Copepodids	0.8	3,4,5,9
	large	Small Cladocerans	1.3	2,3,4,8,9,12
		Large Cladocerans	0.5	4,6,8
medium (1.5-2.5 mm)	small	Copepodids	1.4	6,10
	large	Small Cladocerans	1.2	6,10
		Large Cladocerans	0.3	6
large (>2.5 mm)	small	Nauplii	7.2	7
		Copepodids	6.5	1
	large	Small Cladocerans	4.6	7,11
		Large Cladocerans	1.9	11

*1. Anderson (1970) 2. Brandl and Fernando (1974) 3. Brandl and Fernando (1975a)
 4. Brandl and Fernando (1978) 5. Confer (1971) 6. Confer and Applegate (1979)
 7. Dodson (1975) 8. Gophen (1977) 9. Jamieson (1980) 10. Kerfoot (1977) 11.
 O'Brien et al (1979) 12. Williamson (1980)

chain efficiencies. Using radiotracer experiments, Brandl and Fernando (1975a) found that while 80% of a Ceriodaphnia reticulata ingested by Mesocyclops edax was assimilated, only about 30% of the whole biomass of a living Ceriodaphnia was assimilated. In other words, about 50% of the caloric content of the prey was lost to the predator between capture and ingestion of the prey. This was apparently due to loss of prey tissue into the surrounding water during dismemberment by the predator. When offered nauplii, which can be eaten more or less whole, the predator assimilated over 80% of the caloric content of the prey, reducing loss of nutrients to the surrounding water by reducing handling time of the prey. Increased handling time leads to higher "leakage" of nutrients from an injured prey (eg. from hemolymph fluid).

CYCLOMORPHOSIS AND POLYMORPHISM

The term cyclomorphosis describes the frequently observed phenomenon of cyclical or seasonal change in morphology of individuals of an asexually reproducing population. This change in morphology usually consists of the development of long spines, helmets, or other protuberances during the warm summer months while the cooler spring and autumn weather finds these appurtenances reduced or absent. Cyclomorphosis has been observed in a wide variety of limnetic organisms including dinoflagellates, rotifers, and cladocerans. While my discussion will be limited to the Cladocera, an excellent review of the earlier literature on the subject for all these groups may be found in Hutchinson (1967).

There is a similar, yet distinct, phenomenon which has received much attention in the last decade. This is intraspecific polymorphism. This occurs when two or more clones or subpopulations of a species have different fitnesses such that one genotype is abundant at certain times while another is dominant at some other times. This situation has been described as "clonal replacement cycles" by Kerfoot and Peterson (1980).

Another aspect of intraspecific polymorphism is two genetically and morphologically distinct clones whose differing fitnesses to some biological factor determine their often distinct geographical distribution.

In the cladocerans, cyclomorphosis is most widely manifested in the genera Daphnia and Bosmina. The posterior spine and especially the anterior lamellate head shield or helmet in Daphnia are the cyclomorphotic structures which have attracted attention in the past. The helmets of some species can reach huge proportions and approach the length of the carapace. D. retrocurva in North America (eg. Brooks 1946) and D. carinata in Asia and Australia (eg. O'Brien and Vinyard 1978) are two such species.

In Bosmina, the mean seasonal lengths of the antennules and the mucrones vary. The species best known is B. longirostris (eg. Kerfoot 1975b).

The physical factors affecting helmet growth in Daphnia are well studied (Brooks 1946, Jacobs 1962, 1980, Hazelwood 1966, Hebert 1978a). High temperature, light, turbulence, and adequate food supply all promote large helmets on Daphnia under experimental conditions.

Factors affecting spine growth have received little attention.

The adaptive significance of large helmets, spines, antennules, and other variable structures was not well understood until recently. Many studies of the last five years (eg. Kerfoot 1975a, O'Brien and Vinyard 1978, Krueger and Dodson 1981, Grant and Bayly 1981, O'Brien et al 1980) have concluded that invertebrate predation is a strong selective force favoring the production of exaggerated helmets in Daphnia and long antennules and mucrones in Bosmina. O'Brien and Vinyard (1978) found that the notonectid predator Anisops ate about three times more small helmeted morphs of Daphnia carinata than large helmeted morphs. A later study on six different morphs of the Daphnia species showed that the mere presence of the predator Anisops, even when the predator and prey were separated in the experimental chamber by a mesh partition, was a more important factor in determining helmet length than temperature, turbulence, or oxygen (Grant and Bayly 1981).

Similarly, Daphnia pulex may produce a small toothed protuberance on the posteriodorsal area of the head when reared with the larvae of Chaoborus (Krueger and

Dodson 1981). This structure formed on Daphnia even when the predator and prey were separated by a sieve partition or when Daphnia was reared with an extract made from macerated Chaoborus. The last two references cited suggest that, in some cases at least, helmet growth in Daphnia may be promoted by a water soluble chemical agent excreted by the predator.

Other studies also indicate that cyclomorphosis may decrease predation by copepods. The helmeted form of Daphnia longiremis was better able to avoid predation by the calanoid copepod Heterocope septentrionalis than the small headed morph (O'Brien et al 1980). Another calanoid, Epischura nevadensis, preferred preying on Bosmina longirostris with short antennules and mucrones (Kerfoot 1975a).

Evidence has accumulated indicating that cases of what was previously thought to be cyclomorphosis are actually an example of intraspecific polymorphism. Work involving electrophoretic techniques has suggested that the long and short featured morphs of Bosmina longirostris are two genetically distinct sub-populations, carrying different alleles at the phosphoglucosomerase locus. (Manning et al 1978, Kerfoot and

Peterson 1980). The Australian species of Daphnia carinata was thought to be very plastic in regard to the morphology of the helmet (ie. cyclomorphic).

Electrophoretic experiments by Hebert (1977) indicate that this "species" is made up of as many as nine reproductively isolated species. Work by Jacobs (1961) has also suggested that cyclomorphosis in Daphnia galeata may actually be an example of clonal replacement cycles.

The ecological significance of cyclomorphosis and polymorphism is now being worked out in some detail, yet many uncertainties will remain until further work is done. There is no clear correlation between head size in Daphnia and density of invertebrate predators, and some unhelmeted Daphnia species in the northern latitudes are often found coexisting with large predacious copepods (Hebert 1978b).

MATERIALS AND METHODS

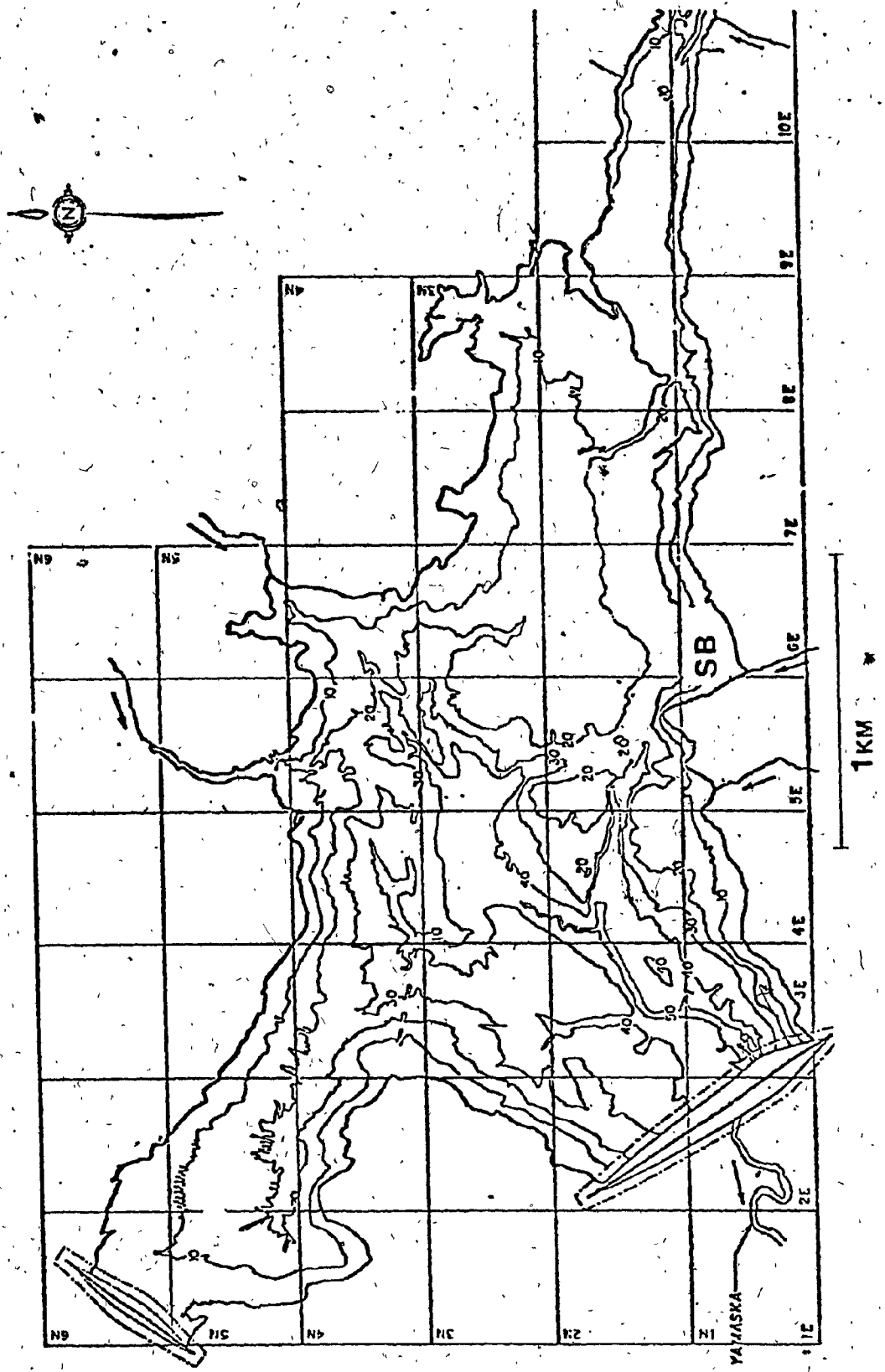
STUDY AREA

This study was carried out in Lac Choinière, a turbid, eutrophic, man-made reservoir in the Quebec Eastern Townships located approximately 100 kilometers east of Montreal, Quebec (approx. 45°24'N, 72°33'W). The reservoir was formed in 1976 following the construction of dams across the course of the North Yamaska river. (see Fig. 1)

A large proportion of the drainage basin of the lake is composed of agricultural land which contributes to the water's eutrophic state. Its high summer turbidity (up to 35 Jackson Turbidity Units) is caused primarily by large populations of the blue-green algae Aphanizomenon ovalisporum and Anacystis sp.

The crustacean zooplankton community of the lake is made up of Diaphanosoma leuchtenbergianum, Daphnia galeata mendotae, Daphnia retrocurva, Ceriodaphnia reticulata, Bosmina coregoni, Leydigia quadrangularis, Diaptomus minutus, Cyclops vernalis, and Mesocyclops

Fig. 1. Diagram of Lac Choiniere. Depth contours in feet. SB is site of 1980 experiments. Modified from Bourassa and Belanger (1978).



edax. Small seasonal populations of Epischura lacustris, Bosmina longirostris, and Leptodora kindtii were also detected. Characteristics of the dominant zooplankton species are listed in Table 2.

The more abundant fish species in the lake include yellow perch (Perca flavescens), pumpkinseed (Lepomis gibbosus), pickerel (Esox niger), and an unidentified cyprinid.

Some physical and chemical aspects of the lake were recorded and are given in Table A1 of the Appendix. Oxygen readings were taken in 1979 with a YSI portable oxygen meter while the 1980 results come from a modified Winkler oxygen test (Hach Chemical Co.). A weak metalimnion was present during August of 1979 and 1980 at about 5 meters depth.

EXPERIMENTAL PROCEDURE

Experiments were performed in 212 liter cylindrical polyethylene cages which were 30 cm in diameter and 300 cm in length. Nine 20 cm. sq. nylon screens (98um mesh size) were installed in spiral fashion along

the length of the cage to aid in exchange of water from the cage and the lake while being of sufficiently fine mesh to prevent the entrance or escape from the cages of the zooplankton species under investigation. Naupliar larvae may have been an exception however.

The cages were suspended, using styrofoam and plastic floats, in a bay on the south side of the lake (see Fig. 1). They were then inspected by a SCUBA diver to ensure that no support ropes had become tangled and that the cages were hanging vertically in the water. Immediately before introducing the experimental populations, all cages were emptied by lifting the bottom of the cage to the surface, drained of water, and then allowed to refill by lowering the bottom of the cage into the lake while taking care to ensure that the top of the cage remained above water level. Thus water entering the cage did so via the mesh windows and was free of crustacean zooplankton.

Twelve such cages were divided into three groups of four replicates each. The three groups were treated as follows. Group 1 zooplankton was collected from the lake the day preceding the initiation of the experiment. The dominant zooplankers, at the time being

B. coregoni and D. galeata, were isolated under a Wild dissecting microscope (20X) and transferred to a 250 ml Erlenmeyer flask containing 200 ml of 48 um filtered lake water. Approximately 75 B. coregoni and 25 D. galeata were collected for each of four flasks. The contents of these flasks were introduced into the Group 1 cages at the beginning of the experiment.

For Group 2 cages, four vertical tows of three meters each with a 15 cm diameter conical plankton net (124 um mesh) were taken. The volume sampled this way is approximately 212 liters, which is the volume of the cage. The contents of these four tows were introduced into one of the Group 2 cages. Other Group 2 cages were treated identically.

Zooplankton were added to Group 3 cages in the same manner as in Group 2. Then, four yellow perch (Perca flavescens) between 5 and 6 cm standard length were added to each cage.

All 12 cages were covered with a sheet of polyethylene during the experimental period. The initiation of the experiment was considered Day 0 (August 29, 1980) with samples being taken after 10 days (hereafter Day 10) and 17 days (Day 17).

Table 2. Characteristics of zooplankton present during experiment. Abbrev. is abbreviation used in tables and figures. See text for SFR (size at first reproduction). Preferred depth is depth of relative concentration of species during day in non-fish cages. All lengths in μm .

Species	Abbrev.	Size at birth	SFR	Maximum size	Preferred depth
<u>Daphnia galeata</u>	D. gal	470	890	1470	surface
<u>Diaphanosoma leuchtenbergianum</u>	D. leu	408	756	1300	bottom
<u>Ceriodaphnia reticulata</u>	C. ret	256	528	810	surface
<u>Bosmina coregoni</u>	B. cor	290	435	630	surface
<u>Leydigia quadrangularis</u>	L. qua	200	300	405	bottom
<u>Mesocyclops edax</u>	M. eda	320*	710**	1160	bottom
<u>Cyclops vernalis</u>	C. ver	300*	700**	870	bottom
<u>Diaptomus minutus</u>	D. min	300*	783**	870	No Preference

* Copepodid I

** Females only

Samples were taken with a two liter Schindler-Patalas trap and preserved in a formaldehyde-sucrose solution. The reservoir and all cages were sampled at 0.5, 1.5, and 2.5 meters depth with three replicate samples taken per depth per cage. In all, 117 samples were taken on each sampling day.

PROCEDURE WITH SAMPLES

Counting of zooplankters was done under a Wild dissecting microscope at 20X magnification. All samples were examined in their entirety and all individuals of a species counted with the following exception. If a particular species was present at a density of much greater than 100 per liter then only one half of the sample was counted for that particular species. All zooplankton were identified to species according to Edmondson (1959).

D. galeata and B. coregoni were measured under a compound microscope at 100X magnification to the nearest 15 um. For D. galeata, measurements taken were core body length (hereafter CBL): the distance from the center of the compound eye to the posterior edge of the

carapace, helmet length: the distance from the center of the eye to the anterior end of the head shield, and spine length: distance from the posterior edge of the carapace to the distal end of the caudal spine. Measurements for B. coregoni were body length: total body length, height: distance from dorsal edge of carapace to anterioventral process of carapace, and antennule length: distance from proximal edge to distal edge of antennule.

All other species were measured to the nearest 29 μ m at 31.25X magnification. Cladoceran lengths were total body lengths and copepod lengths were metasomal lengths (distance from anterior end of body to the metasomal wings).

The size at first reproduction (hereafter SFR) was calculated for each species as the size at the tenth percentile of the size frequency distribution of gravid females as given by Culver (1980).

RESULTS

The method employed to initiate the experiment was not 100% effective since copepods and cladocerans other than Daphnia and Bosmina were found in the Group 1 cages on Day 10. The most probable reasons for this problem were either that the zooplankters could pass through the mesh windows of the cage relatively easily or that the technique used to empty the cages initially was insufficient to completely remove all the zooplankton.

A pilot experiment, performed to test the ability of the cages to exclude zooplankton from the reservoir, indicated that the cages were over 90% effective in excluding larger cladocerans such as Daphnia, Bosmina, and Diaphanosoma but only about 65% effective in excluding smaller organisms such as Leydigia and naupliar larvae. The effectiveness of the cages in regard to copepods was probably high also, but the situation would be confused with the maturation of the naupliar larvae (ie. immature copepods) which infiltrated the cages.

The presence of most of the larger zooplankton other than Daphnia and Bosmina in the Group 1 cages can therefore be attributed to drawbacks in the method of emptying the cages at the initiation of the experiment.

Creases which formed in the plastic while the cages were being emptied would have held small quantities of water containing zooplankton. This seems the most probable source of the unwanted larger zooplankton which were probably present at the beginning of the experiment in low numbers only.

The loss of one Group 1 cage and one Group 2 cage was experienced between Day 10 and Day 17.

Predation by fish significantly reduced all populations of prey species after 10 days with the non-fish cages supporting much higher zooplankton densities than either the fish cages or the reservoir on that date.

(Table 3). After 17 days however, only the numbers of D. galeata, C. reticulata, M. edax, D. minutus and C. vernalis were significantly lower in the cages containing piscine predators. (Table 4). No difference was observed for any other prey with the exception of L. quadrangularis which was significantly more abundant.

The statistical test used was the 2-tailed Student's t-test for independent means (Sokal and Rohlf 1969).

Similar statistical tests were done comparing mean lengths of a given prey species between fish and non-fish cages on Day 10 (Table 5). When comparing cages as a whole only the cyclopoid copepods seemed to have their mean lengths affected by the presence of fish with C. vernalis being shorter and M. edax being longer.

When the fish and non-fish cages are compared at the individual depths sampled however, an interesting phenomenon is revealed. The mean lengths of B. coregoni, C. reticulata, and D. minutus were significantly smaller at 0.5 meters in the fish cages compared with the non-fish cages while being significantly larger than the populations in the non-fish cages in the deeper regions of the cage (Table 5). The presence of fish seems to alter the vertical distribution of different size classes of these three prey species.

Although cyclopoid copepods were present in the Group 1 cages, by combining Group 1 and Group 2 cages the range of cyclopoid densities among these eight cages was sufficiently large to allow an examination of the effects of these predators on their zooplankton prey. A one-way analysis of variance on the mean cyclopoid densities showed a significant difference among the cages ($F=13.0$ $dF=7,56$ $p<.001$). The mean density of cyclopoids ranged from 2.7 to 14.2 per liter in the eight cages.

When considering the effects of cyclopoid predation, one must keep in mind that only the older instars of the animals are predacious. The density of planktivorous cyclopoids was therefore considered to be the density of cyclopoids the length of an adult male or

larger (ie. M. edax larger than 480 um and C. vernalis larger than 405 um). This variable shall be termed the predacious copepod density (PCD).

To determine if cyclopoid predation was an important factor regulating zooplankton densities, Pearson correlation coefficients were calculated between cyclopoid density and prey density in the eight non-fish cages on Day 10. No significant negative correlations were found between prey density and PCD for any prey species (Table 6) indicating these invertebrate predators had little effect in controlling prey population densities.

Size selective predation by copepods was estimated by constructing size frequency distributions of the potential prey species comparing cages with high and low PCDs (Figs. 2 to 6). Any instar or size class of a prey species which was much less abundant in the high PCD cage than in the low PCD cage was considered to be the preferred size class of prey for the cyclopoids. This method of analysis indicated that four prey species, namely B. coregoni, C. reticulata, D. leuchtenbergianum, and D. minutus exhibited the effects of size selective predation by cyclopoids. In

each case, the preferred size of prey was not the smallest individuals but those of an intermediate size (Figs. 2 to 6).

To provide further evidence that the above prey species suffered size selective predation, the percentage of prey individuals in the preferred size class was plotted against the PCD found in each of four non-fish cages which were examined in detail. As the dependent variable here was a proportion (% prey in preferred size class), the arcsine transformation was used to normalize the data (Sokal and Rohlf 1969). This method of analysis revealed that the percentage of the preferred size class found in any particular cage, for all four prey species involved, was inversely proportional to the PCD of that cage (Figs. 7 and 8). This relationship supports the theory that size selective predation by cyclopoid copepods can affect the size distribution of its zooplankton prey. This alteration of prey size frequency distribution seems more pronounced for the cladoceran prey than for the calanoid prey since the slope of the regression lines for the former are roughly twice as steep as that of the latter type of prey (Table 7). To test the significance of the correlations between %

preferred prey and PCD a student t-test was performed on each correlation coefficient. Due to the small sample size associated with each coefficient an overall significance test for combined probabilities was used to increase the degrees of freedom thereby yielding a more powerful test. (Sokal and Rohlf 1969). Table 7 indicates the probabilities of the students t that each correlation coefficient is zero and the chi-square probability for the combined tests. The correlations are significant at the 0.5% level.

With the measurement of over 1500 D. galeata, instars of this species could be determined from size frequency distributions. Helmet and spine length were plotted against instar number and t-tests were performed between similar instars under the different experimental conditions (ie. fish versus non-fish cages, low PCD versus high PCD cages). Although the number of B. coregoni measured was similar to that of D. galeata, individual instars could not be determined. Therefore, body length in B. coregoni was divided into 50 um size classes and mean carapace height and mean antennule length was plotted against body size class. Student t-tests were then performed in a manner similar to that used for D. galeata.

By comparing the lengths of these variable structures in Bosmina and Daphnia in the highest and lowest PCD cages examined, it was found that cyclopoids did not affect the morphology of either cladoceran.

It was found however, that Daphnia in the fish cages exhibited significantly shorter helmets and significantly longer spines than individuals in the non-fish cages (Figs. 9 and 10, Table A2 in Appendix). The morphology of B. coregoni individuals in the fish cages however, was virtually identical to that of the individuals in the non-fish cages (Figs. 11 and 12, Table A3 in Appendix).

To detect any changes in community structure resulting from differences in predation pressure between experimental groups, the following quantities were calculated. The relative abundance of each species on Day 0 and Day 17 (fish and non-fish communities done separately on second date), the Shannon-Weaver diversity index (H') which measures how evenly distributed the relative proportions of the different species present are, and the Equitability index (J) which measures how close the diversity of the particular community comes to its theoretical maximum (see Pielou 1975).

Fish predation had a significant effect on the zooplankton community by decreasing the relative abundance of both D. galeata and C. reticulata, allowing species such as B. coregoni, D. leuchtenbergianum, and L. quadrangularis to become more abundant (Table 8). The lower community diversity in the non-fish cages, due to the dominance of D. galeata, indicates that the presence of perch can increase the diversity of zooplankton communities by feeding selectively on dominant species.

Table 3. Densities + standard error per 2 liter sample of zooplankton in experimental cages and resevoir initially and on Day 10. Sample size in parentheses. Significance of t values: *(p<.05) **(p<.01). See text for details.

Species	Depth	Initial	Resevoir	No Fish	Fish	α
D. gal	0.5M		8.7±3.5 (3)	104.2±23.1 (24)	18.1±5.5 (12)	*
	1.5M		9.0±3.0 (3)	68.1±17.8 (24)	19.6±5.1 (12)	
	2.5M		9.0±2.6 (3)	23.4±5.9 (24)	7.8±1.6 (12)	
	Total	1.8±0.4	8.8±1.6 (9)	64.0±10.6 (72)	15.2±2.6 (36)	**
B. cor	0.5M		96.6±9.4	527.1±105.6	73.4±12.1	**
	1.5M		52.4±14.8	544.8±142.2	110.2±30.2	*
	2.5M		22.6±5.6	278.2±76.6	36.2±2.7	*
	Total	18.8±2.3	57.2±12.0	419.3±71.4	62.5±5.9	**
C. ret	0.5M		9.4±1.4	40.1±10.1	14.3±3.5	
	1.5M		12.0±0.6	46.8±7.1	21.8±4.6	*
	2.5M		28.6±5.2	20.5±3.0	7.5±1.6	**
	Total	0.9±0.5	16.6±3.4	35.4±4.6	14.3±2.2	**
D. leu	0.5M		7.4±3.2	10.9±2.4	3.7±1.1	*
	1.5M		8.0±1.8	25.9±6.2	8.4±2.4	
	2.5M		11.0±2.4	21.1±3.0	10.5±2.1	*
	Total	3.2±0.7	8.8±1.4	19.0±2.5	7.5±1.2	**
M. eda	0.5M		4.0±1.0	4.5±0.9	1.1±0.3	*
	1.5M		3.0±1.0	3.3±0.6	2.3±0.7	
	2.5M		3.4±1.8	5.7±1.0	3.1±0.4	
	Total	1.0±0.5	3.4±0.6	4.5±0.5	2.1±0.5	**
C. ver	0.5M		10.8±1.2	8.1±1.0	2.8±0.8	**
	1.5M		6.4±1.0	9.5±1.4	5.3±1.4	
	2.5M		4.6±0.7	10.6±1.3	5.7±1.4	*
	Total	4.6±0.8	7.0±0.6	9.4±0.7	4.6±0.7	**
D. min	0.5M		9.0±2.6	12.4±1.4	6.8±1.5	*
	1.5M		6.4±1.8	9.3±1.1	8.1±1.3	
	2.5M		1.6±0.6	10.4±1.3	7.6±2.0	
	Total	2.8±0.4	5.6±1.4	10.7±0.7	7.3±0.9	**
L. qua	0.5M		7.7±2.0	6.0±0.6	6.8±1.9	
	1.5M		5.0±2.5	10.8±1.6	6.4±1.8	*
	2.5M		4.0±0.6	11.4±1.7	3.7±0.7	**
	Total	6.4±1.0	6.0±1.1	9.4±0.8	5.6±0.9	**

Table 4. Densities \pm standard error per 2 liter sample of zooplankton in experimental cages and resevoir on Day 17 (as in Table 3).

Species	Resevoir	No Fish	Fish	α
D. gal	0.3 \pm 0.3	36.8 \pm 15.8 (9)	4.4 \pm 1.2 (9)	
	0.7 \pm 0.7	90.9 \pm 17.9 (9)	6.0 \pm 1.1 (9)	*
	1.3 \pm 0.9	25.6 \pm 5.9 (9)	6.8 \pm 2.5 (9)	**
	0.8 \pm 0.4	51.7 \pm 12.6 (27)	5.7 \pm 1.0 (27)	**
B. cor	18.0 \pm 4.2	13.2 \pm 2.8	14.2 \pm 2.3	
	26.3 \pm 5.0	26.1 \pm 6.8	23.4 \pm 7.5	
	15.0 \pm 0.0	7.2 \pm 1/4	12.7 \pm 4.0	
	19.8 \pm 2.5	15.5 \pm 2.8	16.8 \pm 3.0	
C. ret	1.3 \pm 0.3	12.1 \pm 3.7	2.7 \pm 0.3	*
	2.0 \pm 0.6	27.3 \pm 8.8	6.7 \pm 1.6	*
	1.3 \pm 0.3	8.3 \pm 1.7	4.3 \pm 1.6	
	1.4 \pm 0.2	15.9 \pm 3.5	4.5 \pm 0.8	**
D. leu	4.0 \pm 0.6	2.4 \pm 1.1	1.2 \pm 0.4	
	4.0 \pm 0.6	5.7 \pm 1.5	1.4 \pm 0.5	*
	4.3 \pm 0.7	7.1 \pm 1.9	6.9 \pm 3.1	
	4.1 \pm 0.3	5.1 \pm 0.9	3.2 \pm 1.1	
M. eda	0.3 \pm 0.3	0.3 \pm 0.2	0.1 \pm 0.1	
	0.3 \pm 0.3	1.1 \pm 0.5	0.1 \pm 0.1	
	0.0 \pm 0.0	1.2 \pm 0.5	0.2 \pm 0.1	
	0.2 \pm 0.1	0.9 \pm 0.2	0.1 \pm 0.1	**
C. ver	3.3 \pm 0.7	1.2 \pm 0.4	2.7 \pm 0.3	*
	2.7 \pm 0.9	4.1 \pm 1.0	2.2 \pm 0.5	
	2.7 \pm 0.3	4.7 \pm 0.7	2.1 \pm 0.6	*
	2.9 \pm 0.4	4.1 \pm 0.5	2.3 \pm 0.3	**
D. min	4.0 \pm 0.6	7.0 \pm 1.6	2.3 \pm 0.4	*
	3.0 \pm 0.6	4.0 \pm 0.5	2.9 \pm 0.8	
	2.0 \pm 0.6	6.3 \pm 1.0	2.9 \pm 1.2	*
	3.0 \pm 0.4	5.8 \pm 0.7	2.7 \pm 0.5	**
L. qua	0.7 \pm 0.3	0.4 \pm 0.2	4.6 \pm 0.9	**
	0.7 \pm 0.3	1.6 \pm 0.4	4.4 \pm 0.8	*
	1.0 \pm 0.6	1.7 \pm 0.3	4.3 \pm 0.8	
	0.8 \pm 0.2	1.2 \pm 0.2	4.4 \pm 0.6	**

Table 5. Mean length of zooplankton (μm) \pm standard error in experimental cages. Significance of t value: *($p < .05$) **($p < .01$). See text for details.

Species	Depth	No Fish	Fish	α
D. gal	0.5M	812 \pm 11 (493)	753 \pm 15 (186)	**
	1.5M	793 \pm 10 (478)	817 \pm 14 (209)	
	2.5M	801 \pm 13 (312)	817 \pm 18 (98)	
	Total	802 \pm 7 (1283)	793 \pm 9 (493)	
B. cor	0.5M	383 \pm 3 (323)	365 \pm 3 (352)	**
	1.5M	374 \pm 3 (397)	385 \pm 3 (433)	**
	2.5M	376 \pm 3 (409)	375 \pm 3 (307)	
	Total	377 \pm 2 (1129)	376 \pm 2 (1092)	
C. ret	0.5M	431 \pm 11 (155)	384 \pm 19 (143)	*
	1.5M	453 \pm 8 (262)	497 \pm 9 (195)	**
	2.5M	442 \pm 9 (196)	506 \pm 12 (89)	**
	Total	444 \pm 5 (613)	461 \pm 8 (427)	
D. leu	0.5M	703 \pm 17 (93)	708 \pm 25 (45)	
	1.5M	743 \pm 11 (239)	717 \pm 21 (79)	
	2.5M	713 \pm 13 (206)	709 \pm 16 (123)	
	Total	724 \pm 7 (538)	711 \pm 11 (247)	
M. eda	0.5M	402 \pm 9 (52)	435 \pm 23 (11)	
	1.5M	427 \pm 15 (54)	442 \pm 20 (31)	
	2.5M	420 \pm 11 (99)	468 \pm 25 (48)	*
	Total	417 \pm 7 (205)	455 \pm 15 (90)	**
C. ver	0.5M	402 \pm 6 (86)	349 \pm 9 (73)	**
	1.5M	409 \pm 5 (153)	380 \pm 9 (90)	**
	2.5M	411 \pm 6 (170)	411 \pm 11 (90)	
	Total	409 \pm 3 (409)	382 \pm 6 (246)	**
D. min	0.5M	525 \pm 17 (82)	456 \pm 17 (79)	**
	1.5M	483 \pm 13 (127)	488 \pm 17 (75)	
	2.5M	474 \pm 12 (144)	549 \pm 20 (98)	**
	Total	489 \pm 8 (353)	502 \pm 11 (252)	

Table 6. Pearson correlation coefficients of PCD and zooplankton density. N=8 for all r. α = significance of r. See text for details.

Species	r	α
D. gal	-0.038	0.90
B. cor	0.366	0.40
C. ret	0.901	0.001
D. leu	0.914	0.001
L. qua	0.413	0.40
Nauplii	0.672	0.10
D. min	0.917	0.001

Table 7. Preferred size class of prey and regression analysis of relationship between percentage preferred prey and PCD. α = probability of r (N=4) and χ^2 = chi square value for combined probabilities.

Species	Preferred Size	b	r	α	
D. gal	No preference	-	-	-	
B. cor	400-500	-1.31	-.91	.10	$\chi^2=23.47$ dF=8 p<.001
C. ret	550-625	-1.23	-.82	.20	
D. leu	450-650	-1.23	-.76	.40	
D. min	500-600	-0.69	-.99	.001	

Table 8. Effects of perch predation on relative abundances of zooplankton species. α = significance of t (arcsine transformation) *p .01 **p .001. H' = Shannon-Weaver Diversity Index. J = Equitability Index. N = sample size.

Species	Day 0	Day 15		α
		No Fish	Fish	
D. gal	0.091	0.500	0.132	**
B. cor	0.427	0.150	0.390	**
C. ret	0.018	0.154	0.104	**
D. leu	0.072	0.049	0.074	*
L. qua	0.145	0.012	0.102	**
Nauplii	0.059	0.044	0.033	-
M. eda	0.023	0.009	0.002	-
C. ver	0.100	0.040	0.053	-
D. min	0.064	0.056	0.063	-
N	385	2792	1163	
H'	1.78	1.59	1.75	
J	0.81	0.72	0.80	

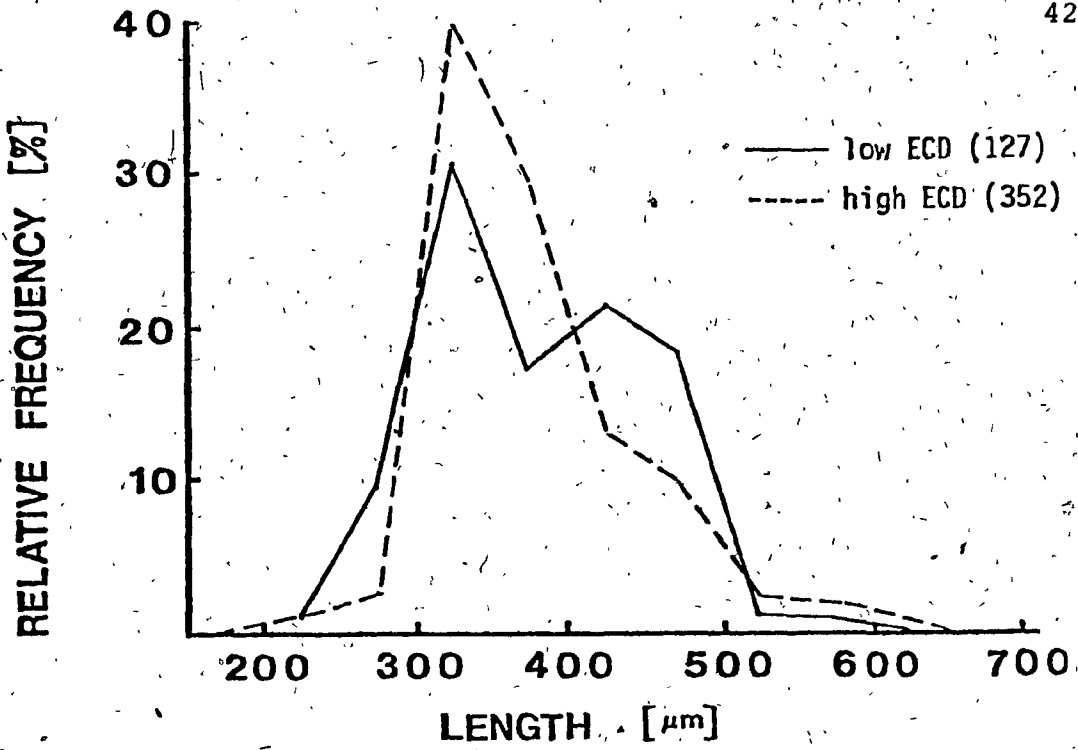


Figure 2. Size frequency distribution of B. coregoni in high and low ECD cages. Sample size in parentheses.

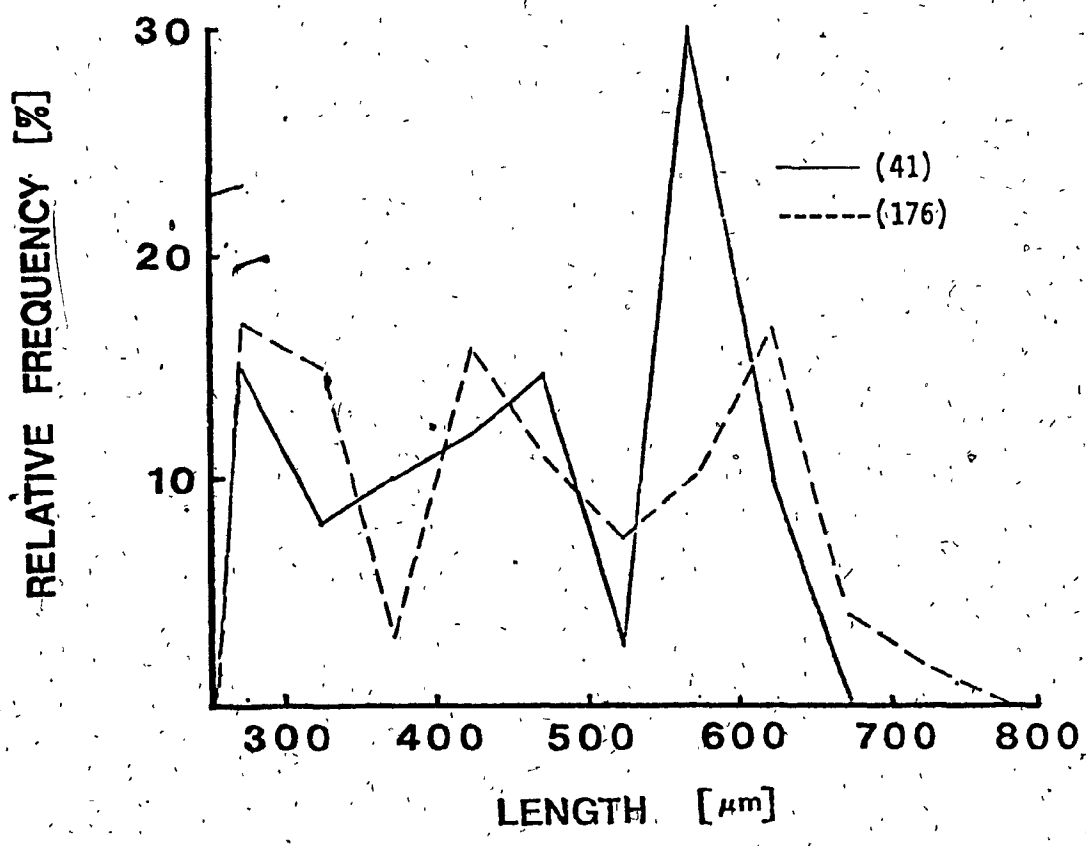


Figure 3. Size frequency distribution of C. reticulata. Legend as in Figure 2.

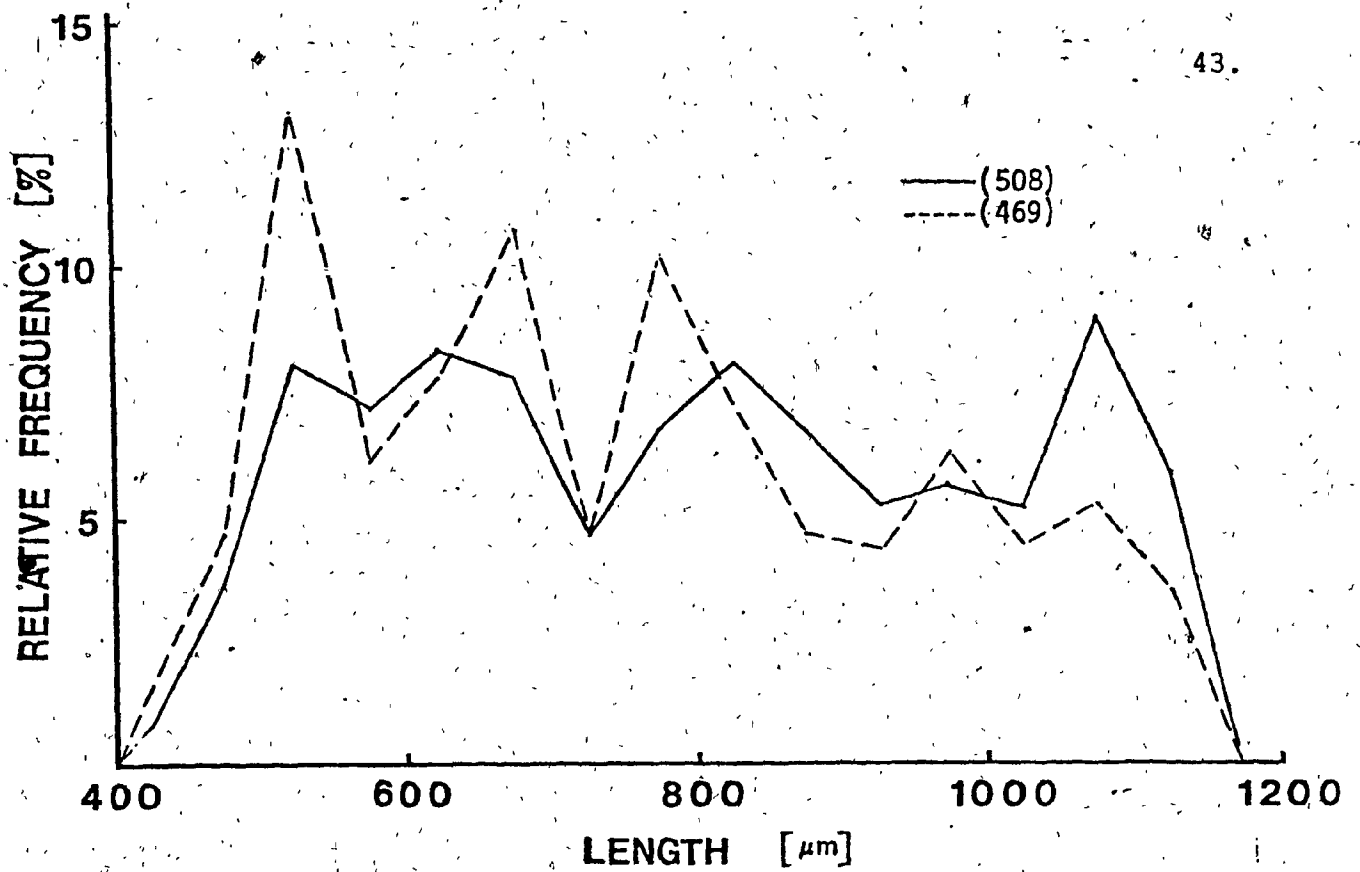


Figure 4. Size frequency distribution of *D. galeata* in high and low ECD cages. Legend as in Figure 2.

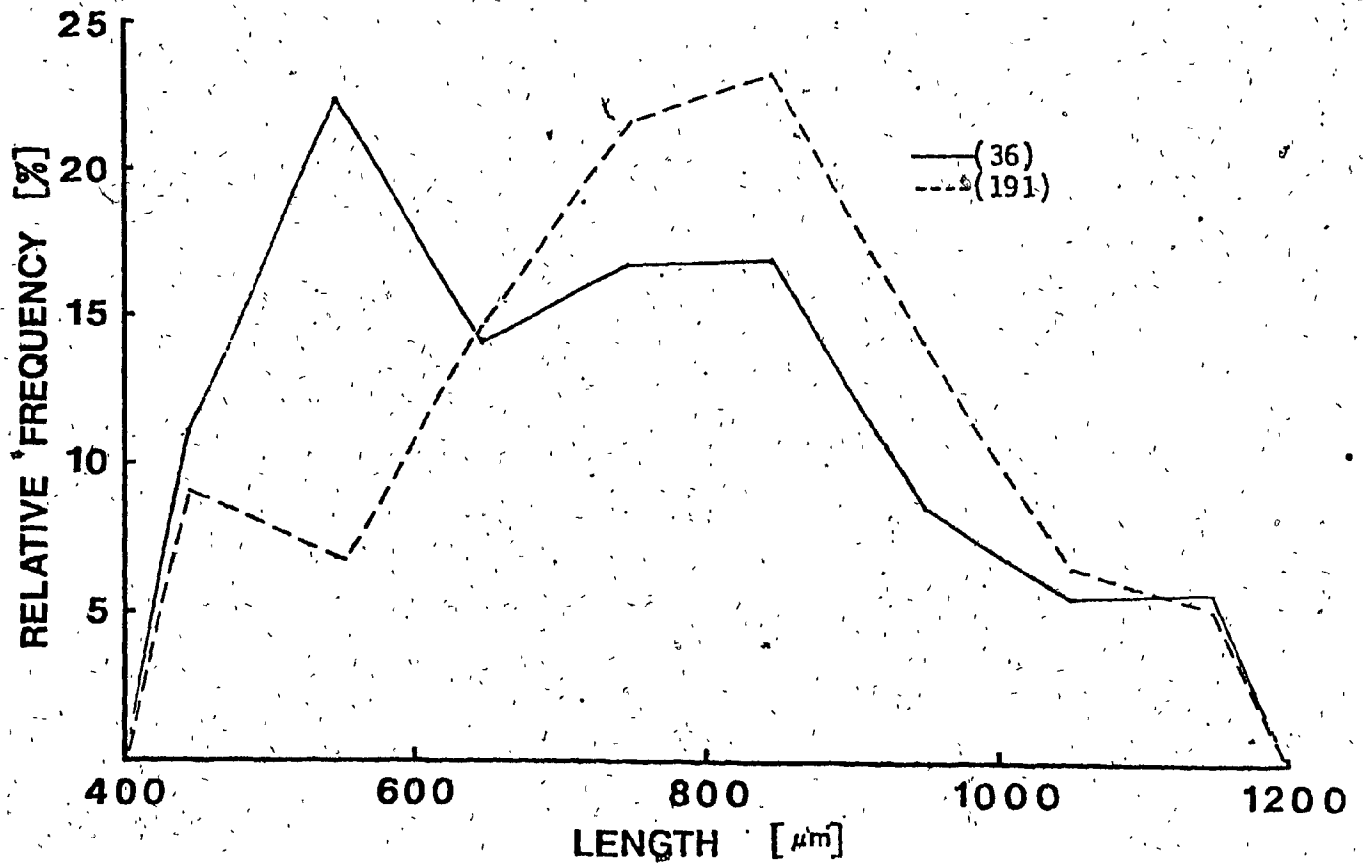


Figure 5. Size frequency distribution of *D. leuchtenbergianum* in high and low ECD cages. Legend as in Figure 2.

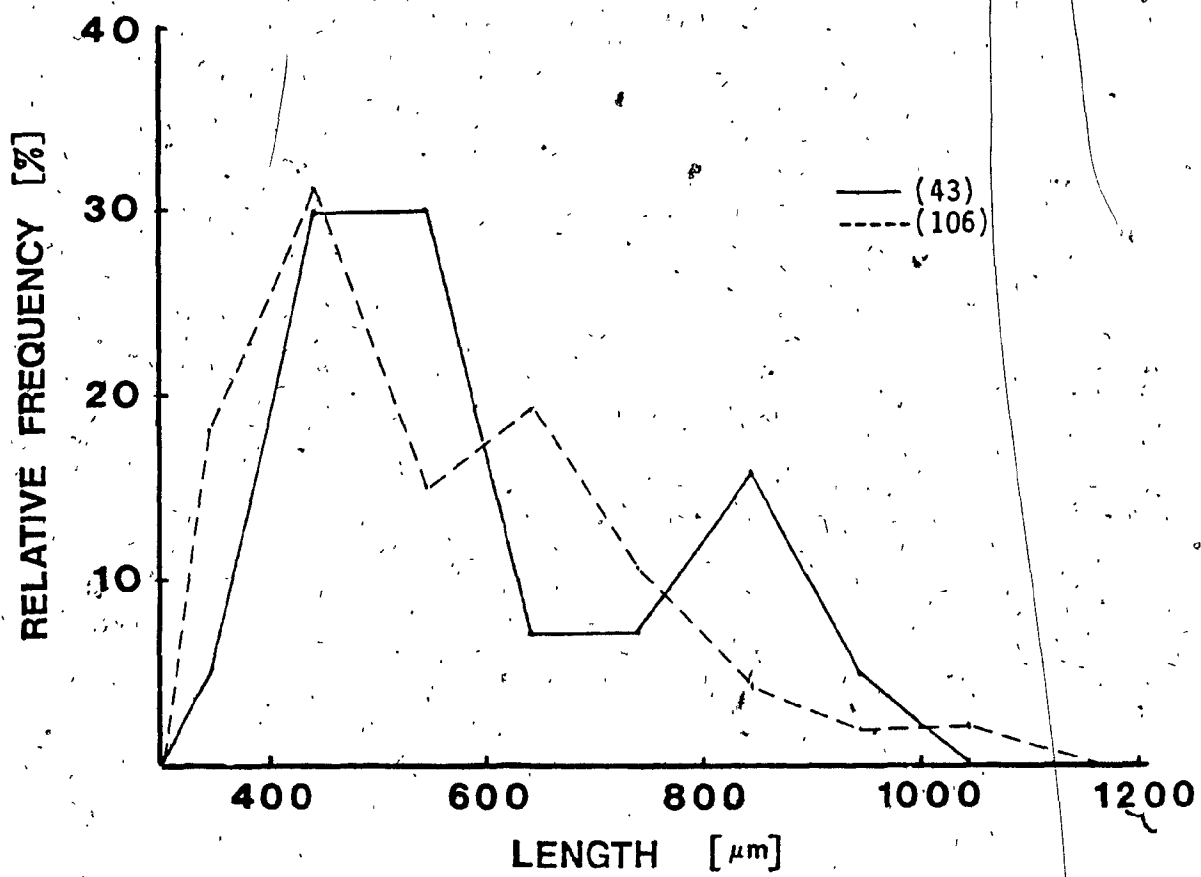


Figure 6. Size frequency distribution of *D. minutus* in high and low ECD cages: Legend as in Figure 2.

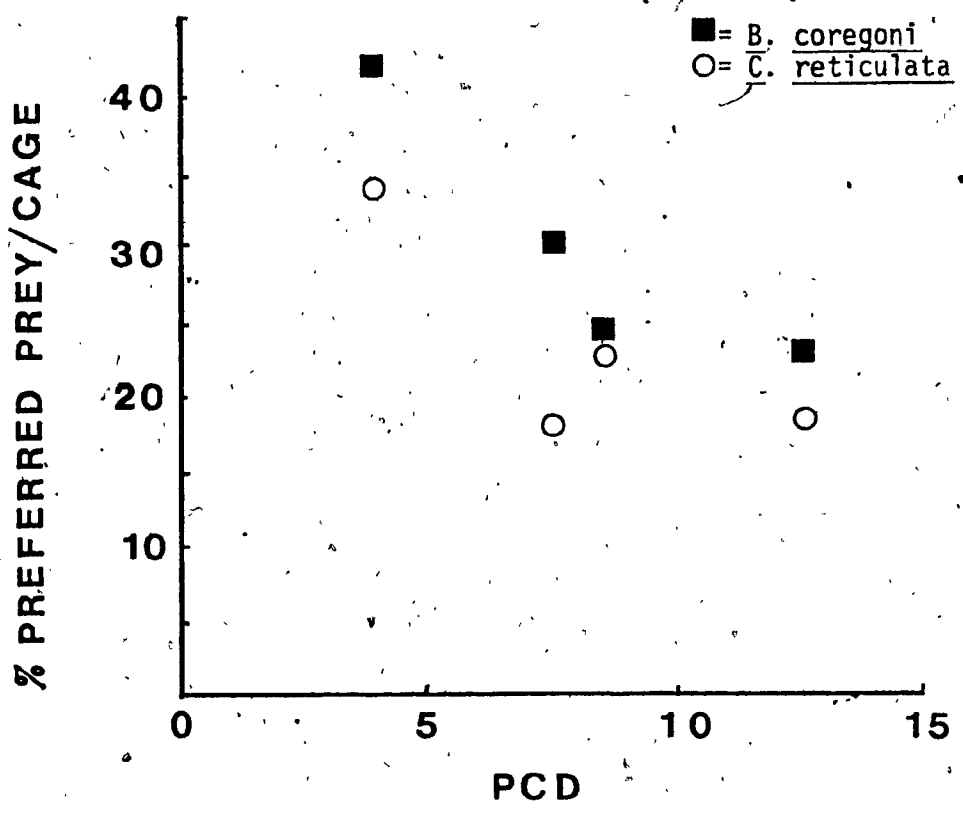


Figure 7. Effect of cyclopid predation on percentage preferred prey per cage of small zooplankton.

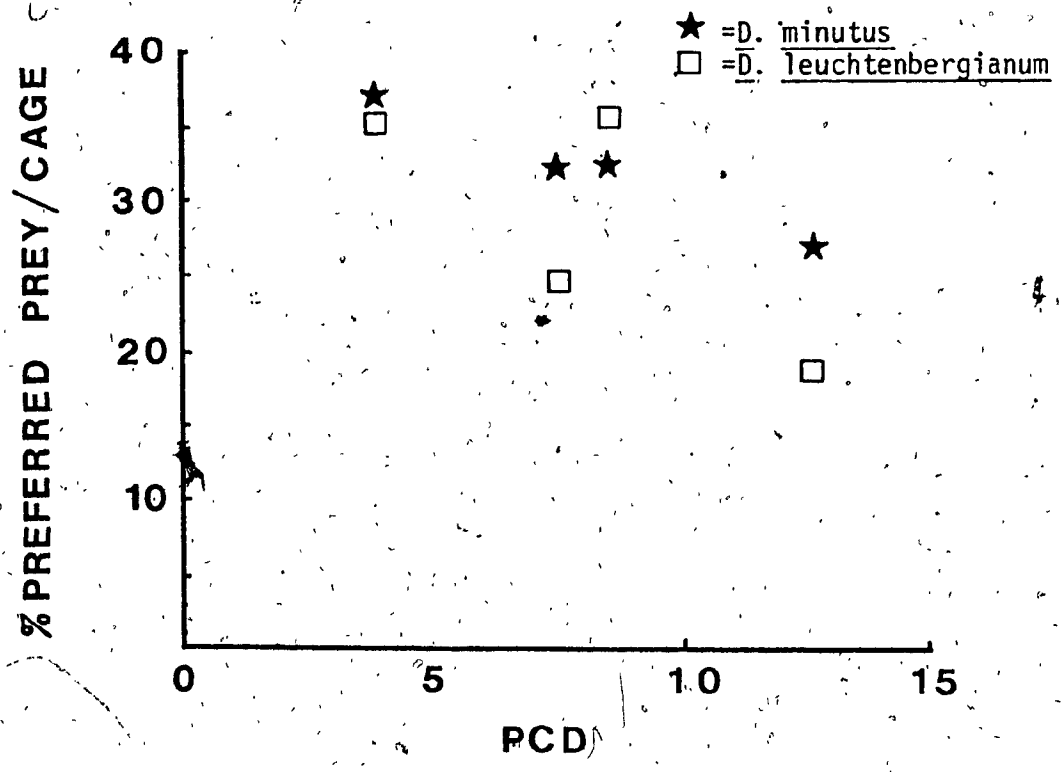


Figure 8. Effect of cyclopid predation on percentage preferred prey per cage of large zooplankton.

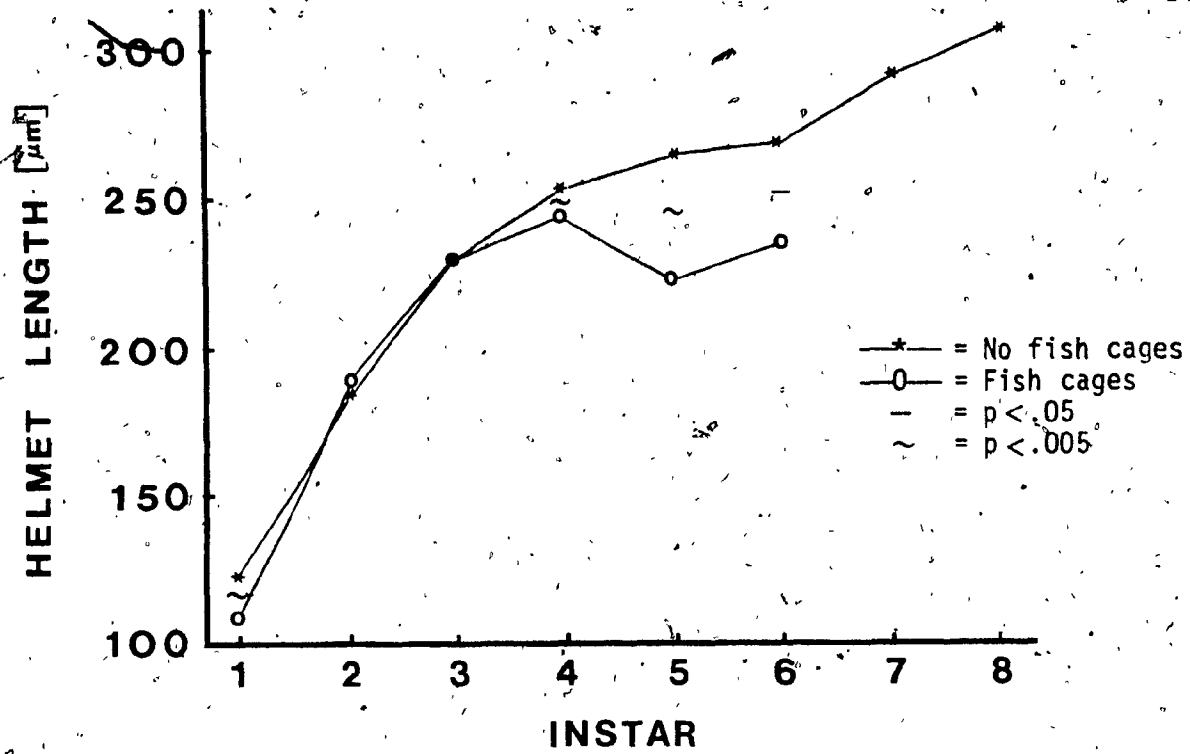


Figure 9. Effects of fish predation on helmet growth of D. galeata.
 p = significance of t (see table A2).

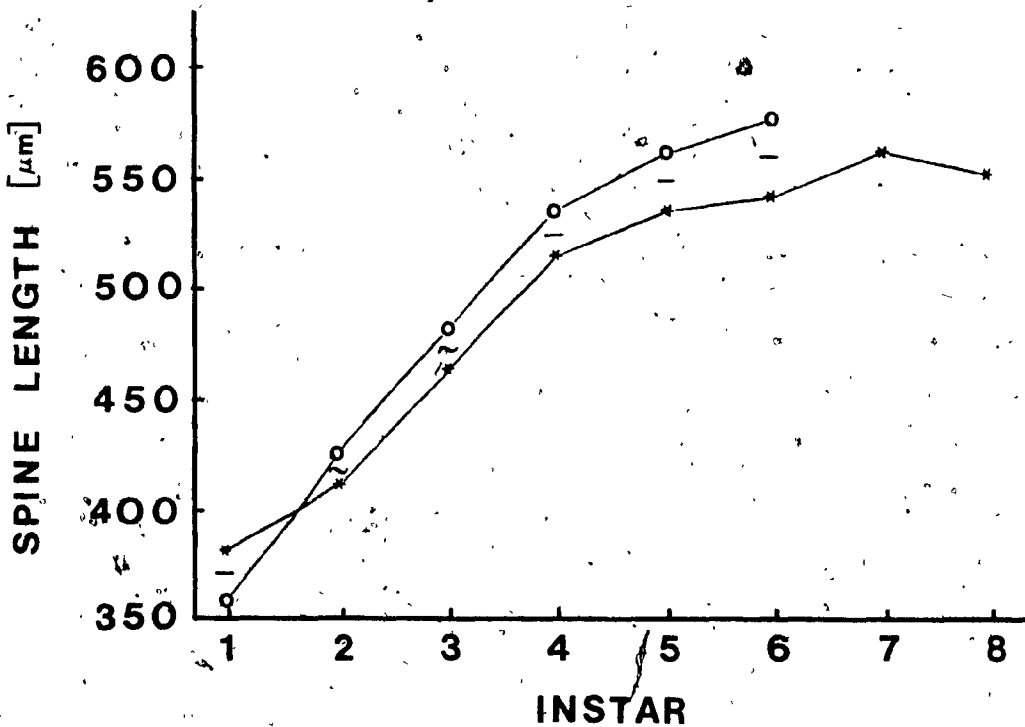


Figure 10. Effects of fish predation on spine growth of D. galeata.
 Legend as in Figure 9.

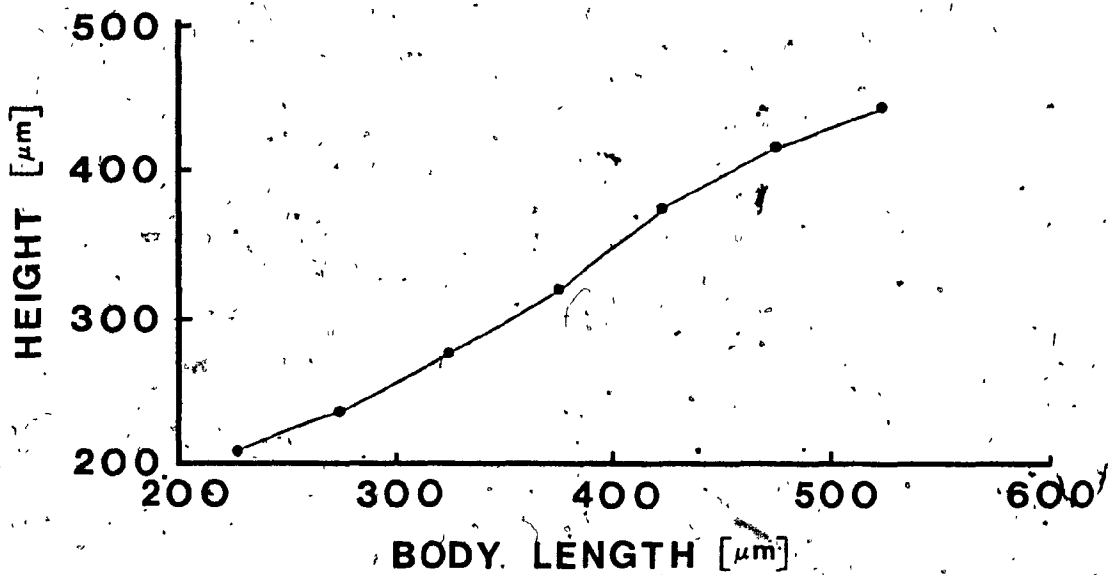


Figure 11. Relationship between body length and height of B. coregoni in non-fish cages. Values similar for fish cages. (See Table A3).

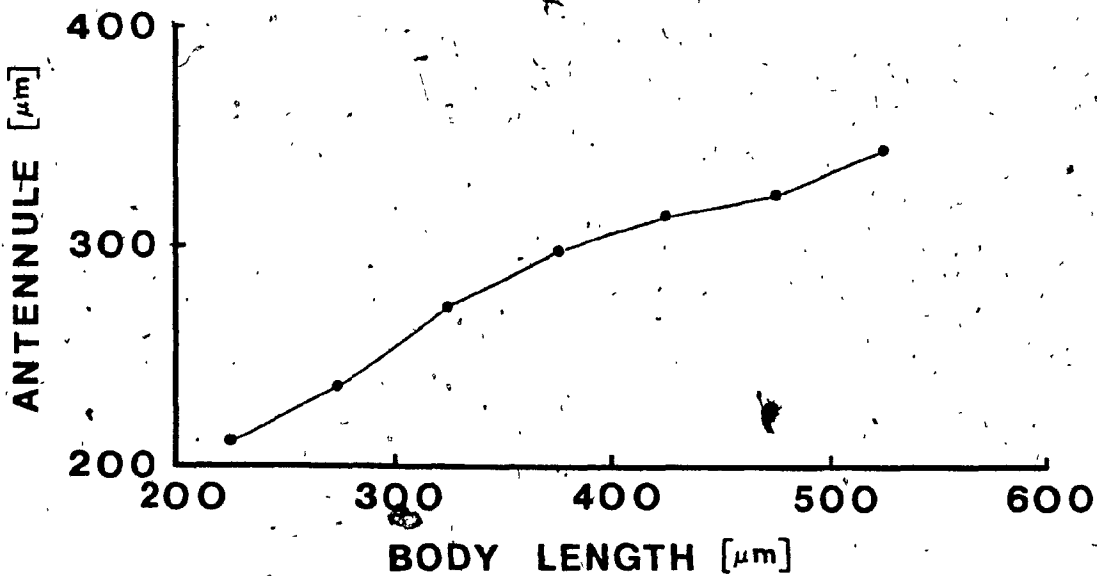


Figure 12. Relationship between body length and antennule length of B. coregoni in non-fish cages. Values similar for fish cages. (See Table A3).

DISCUSSION

Predation by cyclopoid copepods had no discernable effect on the density of its prey species under the experimental conditions (Table 6). At the initiation of the experiment, all the cladoceran species (excluding L. quadrangularis) were in a state of population increase in the lake (Table 3). The simultaneous increase in population densities of the four most abundant cladoceran species suggests that some physical factor, or perhaps food supply, became amenable to rapid reproduction for these species. If this was indeed the case, then predation by cyclopoids would certainly be obscured due to the limitation of a low predation rate (see Table 1). In addition, the cyclopoids studied, C. vernalis and M. edax, are relatively small even for invertebrate predators; thus compounding the difficulty in attempting to estimate predation rates on zooplankton. Evidence was found which suggests cyclopoids may modify the size distribution of some prey species through size selective predation (Table 7, Figs. 2 to 6). The preferred size class of zooplankton was the 500 to 600 μm class for C. reticulata, D. leuchtenbergianum,

and D. minutus while the preferred size of B. coregoni was 400 to 500 μm . No preferred size of D. galeata was apparent. A strong negative correlation exists between the PCD and the percentage of a prey population in the preferred size class for most prey species (Table 7, Figs. 7 and 8).

Cyclopoid predation seems to affect the more abundant size classes rather than the smallest size classes of the prey species (Figs. 2 to 6). Although this pattern does not concur with the findings of most previously published studies, most of these studies offered cyclopoids different sized prey in equal proportions (eg. Confer and Applegate 1979, Jamieson 1980). The size-selective feeding mechanisms of cyclopoids which are offered several sizes of prey in different proportions has not been carefully studied. High encounter probabilities with larger prey may filter copepod preference for smaller prey if the latter is sufficiently scarce due to increased energy costs of high search periods.

Another factor which may result in preferential feeding on larger prey by copepods is the relationship between handling time of a prey item by the predator and the energy value of the prey. Recently, Pastorok (1981) proposed a model for optimal feeding for the dipteran

larvae Chaoborus trivittatus. He argues that while the energy value of a food item increases as the prey size increases, the handling time for that prey item also increases. The model predicts that the optimum size of prey (maximum energy yield per unit time of handling) are mid-sized individuals. Although the feeding behavior of cyclopoid copepods is quite different from that of Chaoborus, this type of optimization of prey size-selection may play a role in the ultimate diet of the cyclopoids. It is known that the carapace integrity of the prey is important in determining the percentage of prey biomass killed which is assimilated (Brandl and Fernando 1975a). Relatively thick carapaces on prey zooplankton also increase handling time of the prey for C. vernalis (Li and Li 1979). The data collected from the cage experiments is consistent with Pastorok's optimization approach. The three cladocerans susceptible to copepod predation in the 500 - 600 um size class (Ceriodaphnia, Diaptomus, and Diaphanosoma) are relatively easily ingested by copepods. Bosmina, which has a relatively thicker carapace than the above-mentioned cladocerans, is preyed upon at a smaller size (400 to 500 um). Handling time for Bosmina is also longer than

for the other species (Li and Li 1979) while handling time and carapace thickness is even higher for Daphnia, explaining the apparent lack of size-selective predation on the latter species. The handling time to energy yield ratio may be so high for even a small Daphnia that this species is ignored by the predatory copepods in favour of more easily handled prey.

No significant difference in helmet or spine growth in Daphnia was observed between high and low PCD cages. (Figs. 9 and 10, Table A2 in Appendix). Neither did copepod predation have an effect on height or antennule growth in Bosmina coregoni (Figs. 11 and 12). Again, the relatively small size of the predators (M. edax and C. vernalis) may have been a factor. Studies which have demonstrated that the development of spines and other protuberances is an adaptive advantage in foiling the attacks of invertebrate predators have been using aquatic insects (O'Brien and Vinyard 1978, Grant and Bayly 1981, Krueger and Dobson 1981), Epischura (Kerfoot 1977), Heterocope (O'Brien et al 1979), or other large invertebrates as predators. Smaller cyclopoids, by virtue of their lower predation rates (Table 1), have

little effect on the morphology of their cyclomorphic and polymorphic prey, at least on the short term.

Predation by perch was found to be intense on all zooplankton species initially and significant on copepods, Daphnia, and Ceriodaphnia after 17 days (Table 4). On Day 17 the density of zooplankton in the fish cages was only 36% of that in the cages without fish.

Of the three prey characteristics previously mentioned (size, speed, and transparency) which could alter susceptibility to fish predation, only the highly developed swimming ability of the copepods was likely to have been limited by the experimental procedure (ie. cage diameter only 30 cm.). Prey transparency may have played a role in determining the ultimate diet of the perch. All copepods, which are highly opaque, suffered significant predation (Table 4). Diaphanosoma densities however, were unaffected by perch predation at equilibrium while Ceriodaphnia's density was reduced 72% from the non-fish cages; even though the former species is about 50% larger and presumably more visible to the fish. This suggests other factors are involved. Considering the duration of the experiment however, interpretation of differences between experimental copepod

populations should be done cautiously since the generation time of most copepods is longer than the duration of the experiment. Most of the cladocerans however, could have gone through three or four generations during the same time span.

Among the cladocerans, no overall differences in mean body length resulted from predation by perch (Table 5). Selective pressure favouring small prey size does seem to be a factor in the upper regions of the cage. The presence of planktivores significantly decreased the length of all three surface-dwelling cladocerans at 0.5M. The two smaller cladocerans, B. coregoni and C. reticulata appear to make a behavioral adaptation via the movement of larger individuals to the deeper portion of the cages (keep in mind that the mean lengths do not differ when all depths in a cage are combined). The mean length of Diaphanosoma, a bottom dwelling cladoceran, is totally unaffected by perch predation (Table 5). The turbidity of the water presumably protects these large individuals by decreasing the amount of light which penetrates to the lower reaches of the cages.

High densities of less favoured prey may cause fish to switch their feeding behaviour somewhat. For example, Bosmina was heavily preyed upon by perch between Day 0 and Day 10 but by Day 17 its densities in the non-fish and fish cages were virtually identical (Table 4). On Day 10 however, Bosmina made up nearly three quarters of the total zooplankton by numbers and was six and a half times more abundant than D. galeata, the next most common species. Since visually feeding fish are known to select the prey item that appears largest (Vinyard and O'Brien 1976, O'Brien et al 1976), a prey population at high density is not only more likely to have many individuals within the maximum reactive distance of the fish but the probability that one of its individuals will appear larger than any individual of a more scarce (and larger) species increases.

Feeding by perch also results in shorter helmets and longer spines in D. galeata (Figs. 9 and 10). In light of the present understanding of polymorphism and cyclomorphosis in Daphnia, there are two likely mechanisms by which this could occur. The fish may be feeding selectively on Daphnia with short helmets and long spines or; the presence of fish induces changes in

the growth rates of these structures. However, the design of the experiment does not lend itself to provide any information which could support either theory.

The adaptive significance of short helmets and long spines under fish predation is not clear cut. Brooks (1965) hypothesized that fish predation could favor large helmets in Daphnia, the mechanism being that more assimilated energy in helmet growth means less in carapace growth thus reducing the visual portion of the animals body. While Brooks' hypothesis was formulated to explain seasonal patterns in helmet development, patterns which are followed by D. galeata in the study lake (pers. obs.), the theory predicts that a late summer Daphnia population, released from piscine predation, would subsequently produce shorter helmets if any change in mean helmet length was to occur. The results given in Figs. 9 and 10 are contrary to Brooks' (1965) hypothesis.

Physical factors cannot be evoked to explain differences in helmet size between fish and no fish cages. Since all cages were constructed and treated identically; temperature, turbulence, and light conditions were presumably the same for both experimental groups.

Helmet growth can also be stunted by low food supply but since zooplankton densities were lower in the cages containing fish (compared to non-fish cages) it is doubtful that food was limiting helmet growth.

While recent studies have concentrated on the effects of invertebrate predation on the development of protuberances on the carapaces of cladocerans, the results reported here indicate that the role of fish predation in this phenomenon merits further investigation.

By releasing the zooplankton community from fish predation, the relative abundance of large surface-dwelling cladocerans increased while small and bottom dwelling cladocerans decreased (Table 8). Fish seem to affect this zooplankton community by removing the larger (and theoretically competitively superior) species near the surface, presumably due to the higher visibility near the air-water interface in the highly turbid reservoir. Hence the increase in relative abundance of the rarer, bottom dwelling species and increased diversity and equitability of the community (Table 8).

CONCLUSIONS

Regarding the relative effects of vertebrate and crustacean predation on zooplankton communities and the response, if any, of the community to the predator pressure, five main features were revealed in this study.

- 1) Cyclopoid predation had a negligible effect on zooplankton densities while perch predation significantly reduced populations of copepods and large surface-dwelling cladocerans.
- 2) Neither copepods nor perch had an effect on the mean size of any zooplankton prey species.
- 3) Copepods are size-selective predators but do not necessarily prey most heavily on the smallest prey available.
- 4) Cyclopoids had no effect on helmet or spine development in D. galeata while perch predation resulted in Daphnia with smaller helmets and longer spines. Neither copepods nor fish affected variable characters in Bosmina coregoni.
- 5) The larger individuals of B. coregoni, C. reticulata, and D. minutus, while preferring the surface waters in the non-fish cages, migrated to the deeper portions of the fish cages.

- 6) Perch predation, by falling more heavily on large surface-dwelling zooplankton, allowed the increase in relative abundance of the small and bottom-dwelling species thus increasing community diversity.

Table A1. Some characteristics of the Choiniere Reservoir.

Surface Area		3.2 km ²
Volume		31.5x10 ⁶ m ³
Mean Depth		9.8 m
Drainage Basin Area		152 km ²
Phosphorus Input (1978)*		16,280 kg/yr
Epilimnetic Temperature	(6/7/79)	20 C
	(15/7/80)	21 C
	(17/8/79)	18 C
	(19/8/80)	21 C
	(18/9/79)	18 C
	(25/9/80)	16 C
Epilimnetic O ₂ Concentration	(6/7/79)	9.5 mg/l
	(15/7/80)	8.0 mg/l
	(17/8/79)	9.1 mg/l
	(19/8/80)	8.5 mg/l
	(18/9/79)	8.8 mg/l
	(25/9/80)	8.0 mg/l
Turbidity	(19/8/80)	35 JTU
	(25/9/80)	20 JTU

* from Provencher, Belanger and Durocher (1979).

Table A2. Comparison of Helmet and Spine patterns in Daphnia galeata between non-fish and fish cages.

Instar		Helmet		α	Spine		α
		No Fish	Fish		No Fish	Fish	
1	\bar{x}	123	108	0.001	380	355	0.01
	SD	27	23		68	38	
	N	183	58		183	58	
2	\bar{x}	184	189	0.20	409	422	0.001
	SD	31	37		31	37	
	N	248	150		248	150	
3	\bar{x}	231	231	1.0	463	480	0.001
	SD	31	50		46	50	
	N	238	157		238	157	
4	\bar{x}	254	232	0.001	514	533	0.01
	SD	31	43		50	61	
	N	245	75		245	75	
5	\bar{x}	265	224	0.001	532	561	0.05
	SD	34	45		47	62	
	N	58	17		58	17	
6	\bar{x}	269	236	0.01	540	575	0.01
	SD	38	34		35	75	
	N	74	14		74	14	
7	\bar{x}	292	-*		560	-	
	SD	37	-		33	-	
	N	44	-		44	-	
8	\bar{x}	307	-		550	-	
	SD	47	-		43	-	
	N	15	-		15	-	

* = Instar absent.

Table A3. Effect of fish predation on variable characters of *Bosmina coregoni* in experimental cages. α = significance of t.

Size class		Height		α	Antennule		α
		No Fish	Fish		No Fish	Fish	
250-300 (μm)	\bar{x}	203	201	NS*	207	201	NS
	SD	13	13		19	22	
	N	40	20		40	20	
300-350	\bar{x}	236	236	NS	237	239	NS
	SD	15	17		15	17	
	N	222	288		222	288	
350-400	\bar{x}	276	273	NS	273	262	NS
	SD	23	14		23	27	
	N	132	185		132	185	
400-450	\bar{x}	322	323	NS	297	297	NS
	SD	25	25		25	25	
	N	151	160		151	160	
450-500	\bar{x}	377	374	NS	312	310	NS
	SD	23	31		23	31	
	N	136	107		136	107	
500-550	\bar{x}	414	416	NS	323	328	NS
	SD	25	23		20	28	
	N	26	22		26	22	
550-600	\bar{x}	446	455	NS	342	370	0.02
	SD	20	38		40	23	
	N	11	3		11	3	

*= Not Significant

LITERATURE CITED

- Anderson, R.S. 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. *Can. J. Zool.* 48:1229-1240.
- Bourassa, B. and B. Belanger 1978. Reservoir Choinière - Problematique et Solution. Ministère des Richesses Naturelles, Direction Générale des Eaux.
- Brandl, Z. and C.H. Fernando 1974. Feeding of the copepod Acanthocyclops vernalis on the cladoceran Ceriodaphnia reticulata under laboratory conditions. *Can. J. Zool.* 52:99-105.
- and ----- 1975a. Investigations on the feeding of carnivorous cyclopoids. *Verh. Int. Ver. Limnol.* 19:2959-2965.
- and ----- 1975b. Food consumption and utilization in two freshwater cyclopoid copepods (Mesocyclops edax and Cyclops vicinus) *Int. Rev. Gesamten Hydrobiol.* 60:471-494.
- and ----- 1978. Prey selection by the cyclopoid copepods Mesocyclops edax and Cyclops vicinus. *Verh. Int. Ver. Limnol.* 20:2505-2510.
- Brooks, J.L. 1946. Cyclomorphosis in Daphnia. I. An analysis of D. retrocurva and D. galeata. *Ecol. Monographs* 16:409-447.
- 1965. Predation & relative helmet size in cyclomorphotic Daphnia. *Proc. Natl. Acad. Sci.* 53:119-126.
- Confer, J.E. 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.* 20:571-579.
- and G. Applegate 1979. Size selective predation by zooplankton. *Amer. Midl. Nat.* 102:378-383.

- Culver, D. 1980. Seasonal variation in the sizes at birth and at first reproduction in cladocera. pp. 358-366 in W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press New England.
- Cummins, K.W., R.R. Costa, R.E. Rowe, G.A. Moshira, R.M. Scanlon, and R.K. Zajdel 1969. Ecological energetics of a natural population of the predacious zooplankter Leptodora kindtii, Focke (Cladocera) Oikos 20: 189-223.
- Dodson, S.I. 1975. Predation rates of zooplankton in arctic ponds. Limnol. Oceanogr. 20: 426-433.
- Drenner, R.W. and S.R. McComas 1980. The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. pp. 587-593 in W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press New England.
- Edmondson, W.T. (ed.) 1959. Freshwater Biology. Wiley, New York.
- Fedorenko, A.Y. 1975. Feeding characteristics and predation impact of Chaoborus (Diptera: Chaoboridae) larvae in a small lake. Limnol. Oceanogr. 20:250-258.
- Fryer, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. Anim. Ecol. 26:263-286.
- Galbraith, M.G. 1967. Selective predation on Daphnia by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96:1-10.
- Gardner, M.B. 1981. Mechanisms of size selectivity by planktivorous fish: A test of hypotheses. Ecology 62:571-578.

Gasçon, D. and W.C. Leggett 1977. Distribution, abundance, and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphramagog. J. Fish. Res. Board Can. 34:1105-1117.

Gophen, M. 1977. Food and feeding habits of Mesocyclops leuckarti (Claus) in Lake Kinneret (Israel). Freshwater Biol. 7:513-518.

Grant, J.W.G. and I.A.E. Bayly 1981. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnol. Oceanogr. 26:201-218.

Hazelwood, D.H. 1966. Illumination and turbulence effects on relative growth in Daphnia. Limnol. Oceanogr. 12:212-216.

Hebert, P.D.N. 1977. A revision of the taxonomy of the genus Daphnia in southeastern Australia. Aust. J. Zool. 25:371-398.

----- 1978a. Cyclomorphosis in natural populations of Daphnia cephalata King. Freshwater Biol. 8:79-90.

----- 1978b. The adaptive significance of cyclomorphosis in Daphnia: more possibilities. Freshwater Biol. 8:313-320.

Hutchinson, G.E. 1967. A Treatise on Limnology II. Wiley New York.

Jacobs, J. 1961. Cyclomorphosis in Daphnia galeata mendotae Birge, a case of environmentally controlled allometry. Arch. Hydrobiol. 58:7-71.

----- 1962. Light and turbulence as co-determinants of relative growth in cyclomorphic Daphnia. Int. Rev. ges. Hydrobiol. Hydrogr. 47:146-156.

----- 1978. Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. Oecologia 35:35-54.

----- 1980. Environmental control of cladoceran cyclo-morphosis via target specific growth factors in the animal. pp. 429-437 in W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press New England.

Jamieson, C.D. 1980. The predatory feeding of copepodid stages III to adult Mesocyclops leuckarti (Claus). pp. 518-537 in W.C. Kerfoot (ed.). Evolution and Ecology of Zooplankton Communities. Univ. Press New England.

Janssen, J. 1980. Alewives (Alosa pseudoharengus) and ciscoes (Coregonus artedii) as selective and non-selective planktivores. pp. 580-586 in W.C. Kerfoot (ed.). Evolution and Ecology of Zooplankton Communities. Univ. Press New England.

Kerfoot, W.C. 1975a. The divergence of adjacent populations. Ecology 56:1298-1313.

----- 1975b. Seasonal changes in Bosmina (Crustacea, Cladocera) in Frain's Lake, Michigan: laboratory observations of phenotypic changes induced by inorganic factors. Freshwater Biol. 5:227-243.

----- 1977. Implications of copepod predation. Limnol. Oceanogr. 22:316-324.

----- 1978. Combat between predatory copepods and their prey: Cyclops, Epischura, and Bosmina. Limnol. Oceanogr. 23: 1089-1102.

----- 1980. Commentary-transparency, body size, and prey conspicuousness. pp. 609-617 in W.C. Kerfoot (ed.). Evolution and Ecology of Zooplankton Communities. Univ. Press New England.

----- D.L. Kellogg, and J.R. Strickler 1980. Visual observations of live zooplankters: evasion, escape, and chemical defenses. pp. 10-28 in W.C. Kerfoot (ed.). Evolution and Ecology of Zooplankton Communities. Univ. Press New England.

- and C. Peterson 1980. Predatory copepods and Bosmina: Replacement cycles and further influences of predation upon prey reproduction. *Ecology* 61:417-431.
- Krueger, D.A. and S.I. Dodson 1981. Embryological induction and predation ecology in Daphnia pulex. *Limnol. Oceanogr.* 26:219-223.
- Lehman, J.T. 1977. On calculating drag characteristics for decelerating zooplankton. *Limnol. Oceanogr.* 22:170-172.
- Li, J.L. and H.W. Li 1979. Species specific factors affecting predator-prey interactions of the copepod Acanthocyclops vernalis with its natural prey. *Limnol. Oceanogr.* 24: 613-626.
- Manning, B.J., W.C. Kerfoot, and E.M. Berger 1978. Phenotypes and genotypes in cladoceran populations. *Evolution* 32:365-374.
- Monakov, A.V. 1972. Review of studies on feeding of aquatic invertebrates conducted at the Institute of Biology of Inland Waters, Academy of Science, USSR. *J. Fish. Res. Board Can.* 29: 363-383.
- Noble, R.L. 1975. Growth of young yellow perch (Perca flavescens) in relation to zooplankton populations. *Trans. Am. Fish. Soc.* 104:731-741.
- O'Brien, W.J. 1979. The Predator-prey interaction of planktivorous fish and zooplankton. *Amer. Sci.* 67:572-581.
- N.A. Slade, and G.L. Vinyard 1976. Apparent size as the determinant of prey selection by bluegill sunfish (Lepomis macrochirus). *Ecology* 57: 1304-1310.
- and G.L. Vinyard 1978. Polymorphism and predation: The effect of invertebrate predation on the distribution of two varieties of Daphnia carinata in south India ponds. *Limnol. Oceanogr.* 23:452-460.

- Kettle, and H. Riessen 1979. Helmets and invisible armor: Structures reducing predation from tactile and visual planktivores. *Ecology* 60:287-294.
- D. Kettle, H. Riessen, D. Schmidt, and D. Wright 1980. Dimorphic Daphnia longiremis: Predation and competitive interactions between the two morphs. pp. 497-505 in W.C. Kerfoot (ed.). *Evolution and Ecology of Zooplankton Communities*. Univ. Press New England.
- Pastorok, R.A. 1981. Prey vulnerability and size selection by Chaoborus larvae. *Ecology* 62:1311-1324.
- Pielou, E.C. 1975. *Ecological Diversity*. John Wiley and Sons, N.Y..
- Provencher, M., B. Belanger, and H. Durocher 1979. Caractrisation de la qualité de l'eau de la riviere Yamaska-nord: rapport complémentaire. Service de la qualité des eaux: Ministère des Richesses Naturelles Québec.
- Siefert, R.E. 1972. First food of larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt. *Trans. Am. Fish. Soc.* 101:219-225.
- Smyly, W.J.P. 1970. Observations on rate of development, longevity, and fecundity of Acanthocyclops virens (Jurine) (Copepoda, Cyclopoida) in relation to type of prey. *Crustaceana* 18:21-36.
- Sokal, R.R. and F.J. Rohlf 1969. *Biometry* W.H. Freeman, San Francisco.
- Stenson, J.A.E. 1976. Significance of predator influence on composition of Bosmina spp. populations. *Limnol. Oceanogr.* 21:814-822.
- Swift, M.C. and A.Y. Fedorenko 1975. Some aspects of prey capture by Chaoborus larvae. *Limnol. Oceanogr.* 20:418-415.

Vinyard, G.L. and W.J. O'Brien 1976. Effects of light and turbidity on the reactive distance of bluegill sunfish (Lepomis macrochirus). J. Fish. Res. Board Can. 33:2845-2849.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15:556-565.

Werner, E.E. and D.J. Hall 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.

Williamson, C.E. 1980. The predatory behavior of Mesocyclops edax: Predator preferences, prey defenses, and starvation induced changes. Limnol. Oceanogr. 25:903-909.

Wong, B. and F.J. Ward 1972. Size selection of Daphnia pulicaria by yellow perch (Perca flavescens) fry in West Blue Lake, Manitoba. J. Fish. Res. Board Can. 29: 1761-1764.

Zaret, T.M. 1972. 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.