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LA THÈSE A ÉTÉ
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COPEPOD PREDATION AND PREY DEFENSE

by

CHONG KIM WONG

A Thesis

presented to the School of Graduate Studies and Research of the
University of Ottawa in partial fulfillment of the requirements
for the degree of Master of Science in Biology.

Ottawa, Ontario, 1980.



UNIVERSITÉ D'OTTAWA
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ABSTRACT

I. Within the freshwater zooplankton community, Epischura lacustris, a calanoid copepod, preys upon a variety of cladocerans and copepods, including Bosmina longirostris, Ceriodaphnia reticulata, and Diaptomus minutus. Epischura rarely kills Bosmina >0.40 mm in length. Below this threshold there is no size selection, because predation rates are affected mainly by the encounter rate and the ingestion probability. When Epischura is presented with Bosmina and Ceriodaphnia of similar size, it eats more Bosmina. When Diaptomus of various developmental stages are offered, predation on copepodites is more intense than on adults and nauplii. Epischura exhibits no threshold feeding behaviour and continues to search for prey even at low food concentrations. Because of this sustained activity and the lack of energy reserves, Epischura lacks tolerance to starvation. Epischura shows no true behavioural preference or switching and its diet includes all the prey that it can detect, capture, and ingest successfully. Bosmina and Ceriodaphnia do not have the evasive ability of Diaptomus to escape capture and must rely on their carapace and shape to thwart ingestion.

II. In Pinks Lake, Quebec, individuals of the cladoceran Bosmina longirostris undergo a 5-30% increase in mucral spine length during the summer at a time when adults of the predaceous copepod Epischura lacustris appear. Predation experiments demonstrated that Bosmina with enlarged mucral spines were less susceptible by factors of 3-15 to Epischura predation than similar-sized prey without this adaptation. Although it is not clear what proximal factor (or factors) induce cyclomorphosis in Bosmina, it appears that the change is an adaptation for reducing mortality due to copepod predation.

III. Copepods sense other animals by mechanoreception and rely on their speed to escape predation. Diaptomus and Cyclops are able to detect the hydromechanical signals created by a small moving sphere of size comparable to those of most crustacean zooplankters (~1 mm). The escape probability and escape distance are affected by the size, location, and direction of movement of the sphere. Additionally, the detection ability is not reduced by ambient turbulence. While the herbivorous Diaptomus escapes from all signals, the predaceous Cyclops escape only from large signals and recognizes small signals as prey.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	iv
ABSTRACT	v
Chapter	page
I. GENERAL INTRODUCTION,	1
II. PREDATORY FEEDING BEHAVIOUR OF <u>EPISCHURA LACUSTRIS</u> (COPEPODA, CALANOIDA) AND PREY DEFENSES	4
Introduction	4
Materials and Methods	7
Experimental Animals	7
Predation Experiments	7
Starvation Experiments	8
Omnivorous Feeding	9
Behavioural Observations	9
Results and Discussion	11
Standard Predation Experiments	11
Bosmina	14
Bosmina and Ceriodaphnia	23
Diaptomus	28
Starvation Experiments	32
Omnivorous Feeding	34
III. CYCLOMORPHOSIS IN <u>BOSMINA</u> AND COPEPOD PREDATION	39
Introduction	39
Materials and Methods	41
Results and Discussion	45
IV. THE RESPONSES OF COPEPODS TO HYDROMECHANICAL STIMULI	55
Introduction	55
Materials and Methods	58
Results and Discussion	61
Avoiding Predators	61
Predator-Prey Interactions	72
V. CONCLUDING DISCUSSION	75
BIBLIOGRAPHY	79

LIST OF TABLES

Table	page
1. Predation rate by <u>Epischura</u> when <u>Bosmina</u> > 0.40 mm and <u>Bosmina</u> < 0.25 mm were offered.	16
2. Predation rate by <u>Epischura</u> when <u>Bosmina</u> 0.28-0.35 mm and <u>Bosmina</u> < 0.25 mm were offered.	18
3. Predation rate by <u>Epischura</u> when <u>Bosmina</u> 0.28-0.35 mm and <u>Bosmina</u> < 0.25 mm were offered.	19
4. Ingestion probabilities for <u>Bosmina</u> of various size classes after being grasped by <u>Epischura</u>	20
5. Predation rate by <u>Epischura</u> on various developmental stages of <u>Diaptomus</u>	29
6. Predation rate by <u>Epischura</u> when <u>Diaptomus</u> copepodite I-III and adults were offered at a 1:1 ratio	31
7. Survival of <u>Epischura</u> exposed to starvation and algae	33
8. Average mucral spine length/body length (x) for <u>Bosmina</u>	44
9. Predation rates of <u>Epischura</u> on <u>Bosmina</u>	52

LIST OF FIGURES

Figure	page
1. Predation rates of <u>Epischura</u> on <u>Bosmina</u> as a function of prey density.	12
2. Predation rates of male and female <u>Epischura</u> on <u>Bosmina</u>	13
3. Size selection by <u>Epischura</u> on <u>Bosmina</u> at different prey densities.	15
4. Lateral and ventral views of (A) <u>Ceriodaphnia</u> and (B) <u>Bosmina</u> showing the differences in body shape.	24
5. Logarithm of the forage ratio for <u>Bosmina</u> by <u>Epischura</u>	25
6. Logarithm of the forage ratio for <u>Bosmina</u> by <u>Epischura</u> trained to <u>Bosmina</u> or <u>Ceriodaphnia</u>	26
7. Predation rate of <u>Epischura</u> on <u>Bosmina</u> in the presence of <u>Ankistrodesmus</u>	35
8. Predation rate of trained <u>Epischura</u> on <u>Bosmina</u> in the presence of <u>Ankistrodesmus</u>	36
9. Morphological changes in <u>Bosmina</u> from laboratory cultures, (A), and Pinks Lake, June 1979, (B).	42
10. Seasonal change in mucral spine length of <u>Bosmina</u> from Pinks Lake.	46
11. Concentrations of <u>Epischura</u> , <u>Bosmina</u> , <u>Daphnia</u> and <u>Diaphanosoma</u> in Pinks Lake.	51
12. Handling time (time from capture until discard of dead <u>Bosmina</u> by <u>Epischura</u>) by <u>Epischura</u> on <u>Bosmina</u>	53
13. Sketch of the experimental set-up for studying the escape responses of copepods.	59
14. Escape probabilities of <u>Diaptomus</u> from a moving sphere.	62
15. Escape probabilities of <u>Cyclops</u> from a moving sphere.	63

16. Effect of sphere size on the escape probability of (A) Diaptomus and (B) Cyclops. 65
17. Effect of the location and direction of movement of the sphere on the escape probabilities of Diaptomus. 66
18. Effect of the location and direction of movement of the sphere on the escape probabilities of Cyclops. 67
19. Comparing escape probability of Diaptomus and Cyclops 69
20. Effect of turbulence on the escape probabilities of Diaptomus. 71

Chapter I

GENERAL INTRODUCTION

In a food chain, plants which capture radiant energy and take up chemical nutrients are the primary producers. The plants are ingested by herbivores, which are ingested by carnivores, which are in turn ingested by other carnivores. Thus, any of these species are subject to two very important selective pressures: to obtain food and to avoid being preyed upon. Many of the most striking structural, behavioural, and life history adaptations in animals are concerned with predation. The sharp teeth of a shark, the speed and alertness of an antelope, the communal hunting behaviour of lions, wild dogs and wolves, and the synchronous emergence of many insects are but a few of the numerous obvious examples.

While most predators feed on many different kinds of prey with different defense adaptations, most prey animals are subject to the predation pressure from a number of predatory species, each with a different hunting strategy. Zooplankton have to cope with two main types of predators: fish and other zooplankters. Fish, because of their visual bias, tend to select larger and more conspicuous prey (Confer and Blades 1975, O'Brien et al. 1979). In contrast,

zooplankton planktivores feed mostly on small prey due to an upper size limit imposed by their mouthparts (Kerfoot 1978). Therefore, the selective pressures imposed by these two types of predators tend to push the zooplankton in one of two opposite directions; one makes the species larger and the other makes it smaller. As a consequence, zooplankton communities may consist of large or small species, depending on which type of planktivore is predominant.

The variety of ways by which zooplankters defend themselves against fish predation have already been reviewed by O'Brien (1979a). My research concentrates on the predator-prey interactions among zooplankters. It is hoped that a careful study of zooplankton predator-prey interactions will allow more insight into the intricacies of the co-evolution between hunting strategies and prey defense mechanisms.

Throughout this study the hypothetical approach of Gerritsen and Strickler (1977) of breaking up predation into a series of four events: encounter, attack, capture, and ingestion is followed. In this study, encounter is defined as an event when a prey is within the sensory range of the predator so that it will be recognized. It is easy to see that any prey animal can reduce the impact of predation by evolving defense mechanisms that help it in any one of these events. For instance, many small animals avoid encountering the predators with crypsis (Kerfoot 1977a, 1978, Zaret and

Strickler 1976). Other large and easily detected prey may disguise themselves as distasteful or inedible objects (Kerfoot 1980). When attacked, fast swimmers are able to avoid capture by evasive tactics, whereas slow-moving prey may evolve morphological defenses, such as spines and tough armour, to minimize the ingestion probabilities.

Chapter 2 investigates the relationships between predator hunting strategies and prey defense tactics. The interactions between Epischura, a large copepod planktivore, and a variety of different types of prey species with different defense strategies are examined. Dodson (1974b) suggested that cyclomorphosis is an adaptation against invertebrate predation. Chapter 3 documents the morphological responses of Bosmina to predation pressure by Epischura. Zooplankters use mechanical perception to detect other animals, but the responses of copepods to hydromechanical stimuli have not been studied quantitatively. Chapter 4 studies the responses of copepods to such hydromechanical stimuli.

Chapter II

PREDATORY FEEDING BEHAVIOUR OF EPISCHURA LACUSTRIS (COPEPODA, CALANOIDA) AND PREY DEFENSES

2.1 INTRODUCTION

Recent studies have shown that selective removal of large zooplankton species by visually feeding planktivorous fish shifts the composition of zooplankton communities in lakes by favouring the survival of small species (Brooks and Dodson 1965, Galbraith 1967, Hrbacek 1962, Stenson 1973, 1976). According to O'Brien (1979a), large zooplankters may minimize the predation rate by avoiding encounter with the planktivorous fish employing strategies such as transparency, vertical migration, and submersed vegetation shelter, or by evolving rapid evasive tactics. When predation pressure by planktivorous fish is minimal or absent, the zooplankton community is often dominated by large species (Brooks 1968, O'Brien 1975). Brooks and Dodson (1965) thought that large species, because of their greater efficiency in obtaining and utilizing food resources, competitively eliminate smaller forms. An alternative hypothesis (Dodson 1974a) is that large zooplankton planktivores, such as many predaceous copepods, become abundant in the absence of fish predation, and their selective feeding on smaller prey places small zooplankton at a distinct disadvantage.

Many authors have observed that zooplankton predators prefer small zooplankters to large ones (Anderson 1970, Brandl and Fernando 1975, 1978, Confer 1971, Confer and Blades 1975, Kerfoot 1977a, McQueen 1969, O'Brien et al. 1979, Smyly 1970). Unfortunately, very few of the data were obtained by giving the predator more than one prey type at a time and thus the differential mechanisms of the selection are often unclear. The present study considers the following questions: 1) What determines the selection pattern when a predator is offered two prey species that are similar in size? 2) Does switching occur in the predatory behaviour of zooplankters? 3) What is the relationship between prey size and prey vulnerability? 4) How is predation intensity distributed with respect to developmental stages in species whose growth includes changes in shape and swimming speed as well as in size? To study these questions, the interactions between Epischura lacustris, a predaceous calanoid copepod, and several zooplankton prey species (Bosmina longirostris, Ceriodaphnia reticulata, and Diaptomus minutus) were investigated. Epischura is a common copepod in the lakes of northeastern North America (Main 1962) and is often the dominant predator of the zooplankton in the summer and fall (Kerfoot 1977a). Some aspects of the predatory behaviour of Epischura have been described by Kerfoot (1977a, 1978) and Strickler and Twombly (1975).

Switching is defined as the ability of a predator to take a disproportionately large number of the most abundant prey species (Murdoch 1969). Natural selection favours predators that can, as a result of learning or physiological changes, switch quickly to an alternate food when one food type becomes scarce. Learning, in the form of increasing the efficiency in finding or handling one particular prey with time, would result in an increased encounter rate and/or attack and capture probabilities. Earlier studies on switching and the effect of previous diet on the feeding behaviour of copepods have been concerned mainly with filter-feeding marine species (Barnett 1974, Conover 1966, Donaghay 1978, Lonsdale et al. 1979, Mullin 1979). Here, switching and the role of previous diet on prey selection by Epischura on two cladoceran prey (Bosmina and Ceriodaphnia) is investigated. Predator switching influences the outcome of competition between prey species (Murdoch 1969). Thus it is important to determine whether switching is a normal feature of copepod predation. Moreover, since Epischura adults are omnivorous (Friedman 1977, Main 1962), the effect of the presence of algae on the predation rate of Epischura is also studied.

2.2 MATERIALS AND METHODS

2.2.1 Experimental Animals

Epischura lacustris and Diaptomus minutus were collected once a week from Pinks Lake, Gatineau Park, Quebec. With the exception of one experiment where animals collected from Pinks Lake were exposed immediately to Epischura for direct observations of attacks, all Bosmina longirostris were obtained from laboratory cultures raised from specimens collected from Pinks Lake one year prior to the beginning of the experiments. Ceriodaphnia reticulata, which do not occur in Pinks Lake, were originally collected from Heney Lake, Quebec, six weeks before they were used. Preliminary tests indicated that Epischura could not tolerate starvation, therefore, Epischura were maintained in a 40-liter aquarium at 20°C with the following zooplankton prey species from Pinks Lake: Bosmina, Daphnia, Diaphanosoma, and Diaptomus.

2.2.2 Predation Experiments

All predation experiments were done in 600 ml plastic tissue culture bottles containing filtered lake water from Pinks lake. Bottles were positioned horizontally in the dark at 20°C. Adult Epischura were transferred from the aquarium to small beakers 15-30 min before the experiments began. Prey of different sizes and developmental stages were selected with a stereomicroscope. Diaptomus adults and

copepodites were immobilized with ether to facilitate handling and staging. A single Epischura was added to the bottle after the prey were introduced (except in two experiments with Diaptomus when 2 Epischura were used). All experiments with cladoceran prey lasted for 4-5 hrs while the duration of experiments involving Diaptomus ranged from 10-20 hrs (exact time recorded). At the end of each experiment the water was filtered through a piece of plankton netting and the prey were counted under the stereomicroscope. Recovery of prey from controls was always 100%. Since Epischura ingests Bosmina without seriously damaging the carapace, the bodies of attacked Bosmina are easily distinguishable from molts which contain no soft tissues. The body length of each live and killed Bosmina was measured at the end of the experiment. For Ceriodaphnia and Diaptomus, a missing individual was scored as being preyed upon by the predator.

2.2.3 Starvation Experiments

The tolerance of adult Epischura to starvation was studied by keeping the animals individually in 50 mm-diameter Petri dishes filled with 0.45 μ m Millipore filtered lakewater. To determine if adult Epischura can survive on algal food alone, some animals were exposed to Ankistrodesmus. For the control, one group of Epischura was given both Ankistrodesmus and Bosmina. Algal concentration and prey

density were not determined. The animals were examined after 12, 24, and 48 hrs. The control experiments were terminated after 24 hrs. Individuals without heart beats were considered dead.

2.2.4 Omnivorous Feeding

In order to determine whether the presence of phytoplankton affects the predation rate of Epischura, Bosmina were offered to the predator with various concentrations of laboratory cultured Ankistrodesmus spp. (Woods Hole HBL medium, Wayne Nichols 1973). Algae were centrifuged and resuspended in filtered lake water before being used. Algal concentrations were determined by counting at least 500 cells in a haemocytometer. The experiments were carried out in bottles wrapped in black plastic and fixed on a plankton wheel (1.5 rev./min). To study the training effects of previous diet, Epischura were kept in Ankistrodesmus suspension for 24 hrs before Bosmina were introduced to the bottle. Since algal concentrations may change, those referred to represent the concentrations at the beginning of the training period.

2.2.5 Behavioural Observations

Direct observations of Epischura attacking prey were made with a stereomicroscope. An adult Epischura, starved for about 20 hrs, was transferred into 20 ml of filtered

lake water in a 50 mm-diameter Petri dish containing 20-40 prey of various species. Epischura usually recovered from the handling procedure within 2-3 min and began to attack prey. An attack was scored if the predator had grasped the prey with its mouthparts. All attacked Bosmina, whether alive or ingested, were removed immediately, fixed in 10% formalin, and measured.

Zooplankton swimming and sinking speeds were determined by observing animals in a 50 mm-diameter Petri dish or in a 90x40x15 mm tank each fitted with a grid of 1-mm squares. The time required to traverse 10 squares was recorded with a stop watch.

2.3 RESULTS AND DISCUSSION

2.3.1. Standard Predation Experiments

Predation rates of Epischura on various densities of Bosmina are presented in Fig. 1. Predation rate increased with prey density and leveled off at high prey densities. Marine herbivorous copepods minimize energy losses by reducing filtering rate at food concentrations below certain threshold levels (Fernandez 1979, Frost 1975, Lam and Frost 1976). Because my results indicate that Epischura does not exhibit such threshold feeding behaviour, the expected consequence is that Epischura lacks tolerance to starvation. Another feature of the results presented in Fig. 1 is the wide variations in the number of prey killed per predator at each prey density. Since adult female Epischura are visibly larger than males, differences in feeding rate between males and females could have been the cause of the variabilities. (Fig. 2) shows that females fed at higher rates than males, but again the predation rates were highly variable. Due to the difficulties involved in obtaining enough healthy animals, both males and females were used in all the other experiments. Since the sex ratio of adult Epischura in Pinks Lake was close to 1:1 throughout the summer season, the feeding rates reported in all the following experiments probably represent the averages of males and females.

Figure 1: Predation rates of Epischura on Bosmina as a function of prey density. Vertical lines represent 95% confidence limits of 5 replicates.

No. of Prey per Predator per Day

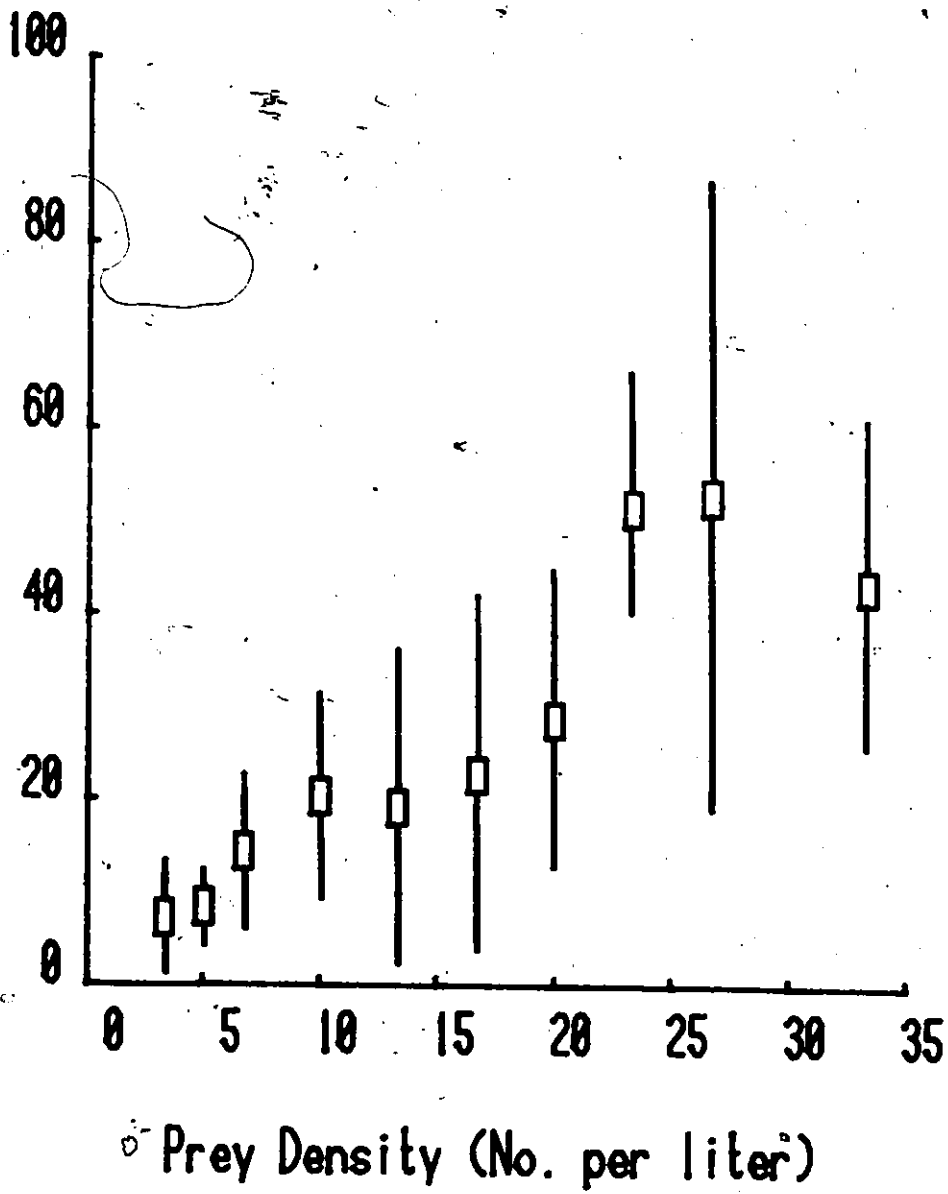
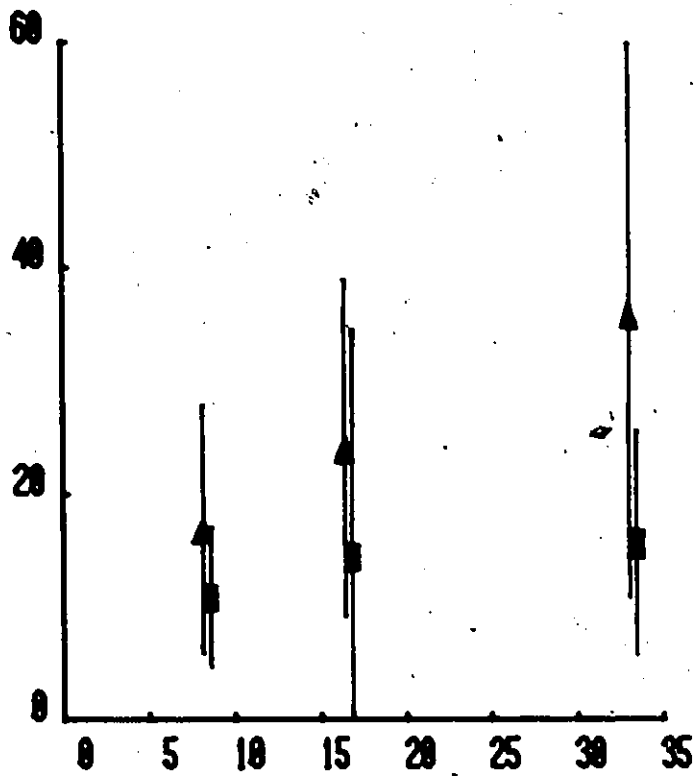


Figure 2: Predation rates of male and female Epischura on Bosmina. Vertical lines represent 95% confidence limits of 5 replicates.

Prey per Predator, per Day



■ male Epischura

▲ female Epischura

Prey Density (No. per liter)

2.3.2 Bosmina

Bosmina, picked randomly from the cultures to obtain a range of size were offered to Epischura at densities ranging from 4 to 20 individuals per bottle. A Wilcoxon matched-pair signed-ranks test ($P=0.03$) showed that the mean size of the alive Bosmina was larger than the mean size of the killed Bosmina (Fig.3A). However, Bosmina over 0.40 mm were never killed, and the smallest Bosmina were killed in only 6 of the 14 experiments. When the result were analysed again, excluding all Bosmina over 0.40 mm (Fig.3B), the difference between the mean sizes of the alive and the killed Bosmina was not significant (Wilcoxon matched-pairs signed-ranks test, $P=0.18$). When 5 Bosmina <0.25 mm were offered to Epischura together with 5 Bosmina >0.40 mm, the predation rate on the smaller Bosmina was higher than that on the larger ones (Table 1).

Epischura rarely killed Bosmina >0.40 mm and those few that were killed were never completely consumed. There seems to be an upper limit of prey size which may be determined by the mouthpart morphology of the predator. Kerfoot (1977a) reported that Epischura reduced the populations of Bosmina (0.2-0.3 mm) and Ceriodaphnia (0.3-0.4 mm) but not that of Daphnia (>0.4 mm). Epischura uses the swimming legs to form part of the floor of the feeding chamber, it cannot grasp securely a Bosmina which is longer than the distance between its first swimming legs and its first antennae (Ker-

Figure 3: Size selection by Epischura on Bosmina at different prey densities. Dead animals referred to those killed by Epischura. A) Bosmina of all sizes are included, B) Bosmina > 0.40 mm are excluded because they were never killed by Epischura.

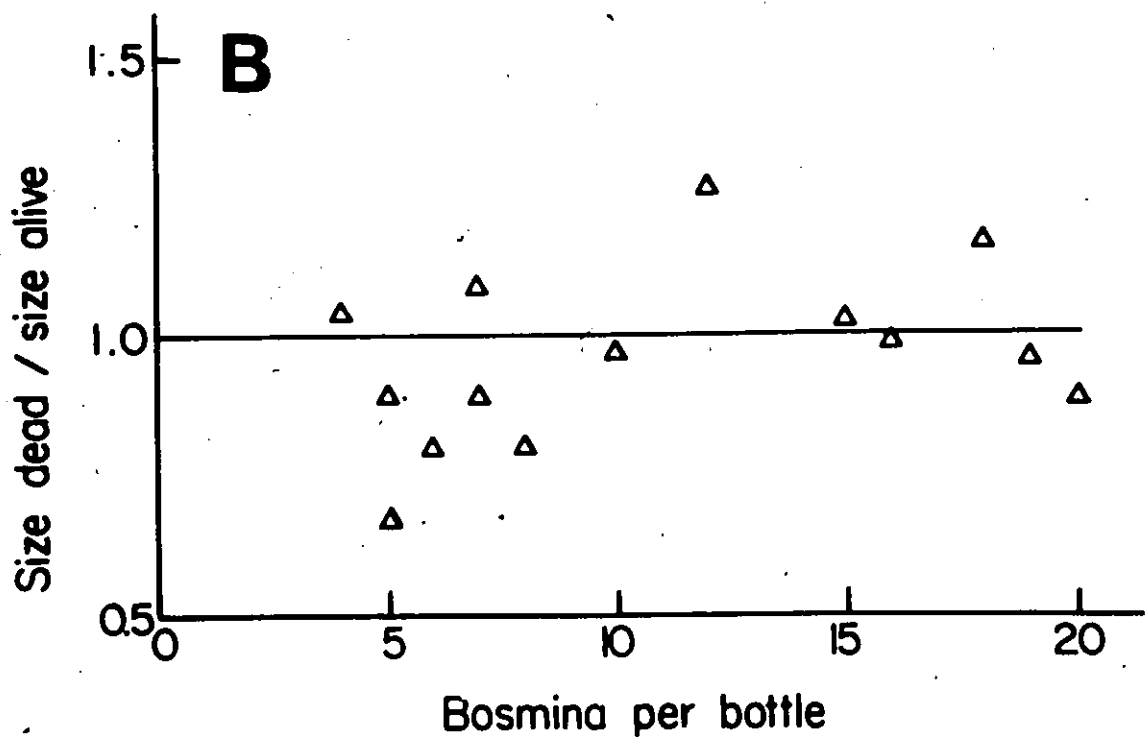
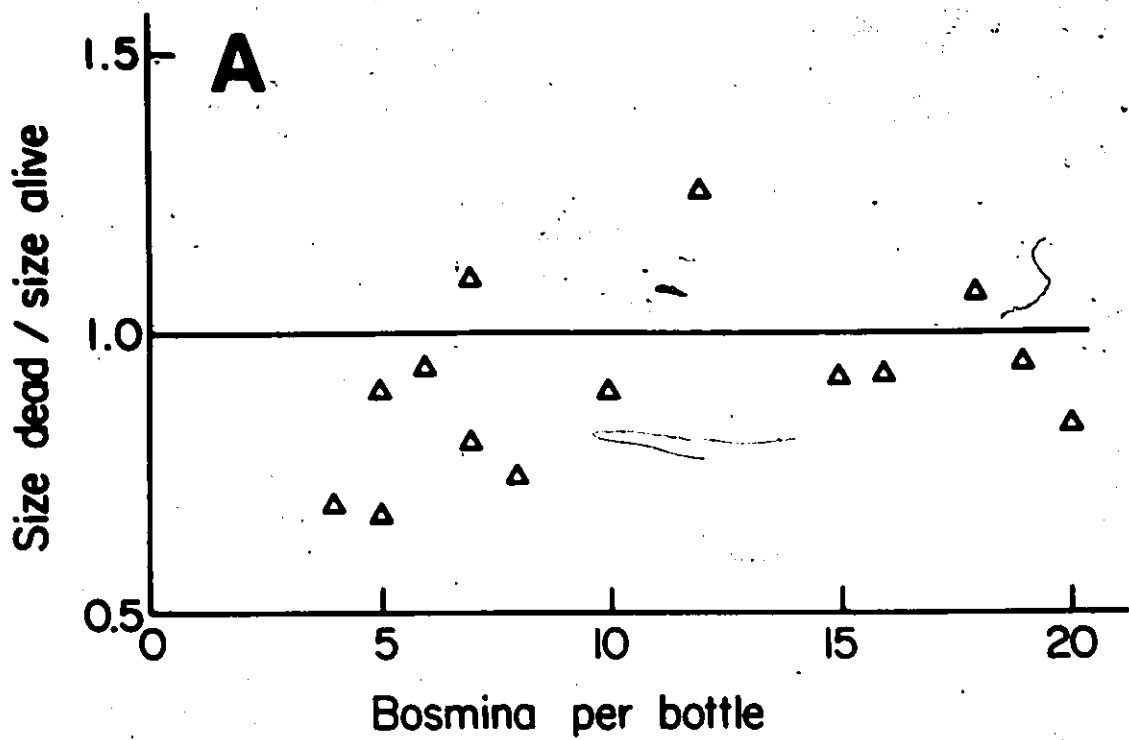


TABLE 1

Predation rate by Epischura when Bosmina > 0.40 mm and Bosmina < 0.25 mm were offered.

Prey/bottle	Replicates	Total prey killed	Ratio				Chi-square*		
			Expected		Observed				
L	S		L	S	L	S			
5	5	4	12		6	6	1	11	8.33

L = > 0.40 mm

S = < 0.25 mm

* Chi-square 0.05 for 1 df=3.84

foot 1978). In Epischura lacustris the length of the feeding chamber averages 0.43 mm (n=10) for male and 0.47 mm (n=10) for females. Therefore a Bosmina >0.40 mm and with the addition of a mucral spine (average length 0.02-0.04 mm) would be difficult for Epischura to manipulate.

To study size selection when Epischura is offered prey that are of manageable sizes, Bosmina <0.25 mm and those of 0.28-0.35 mm were offered in a 1:1 ratio. The pattern of size selection was studied at prey densities of 4, 10, and 20 Bosmina per bottle. The results, given in Table 2, show that Epischura did not select Bosmina on the basis of size at any of the prey densities studied. To determine whether Epischura shows selection when the proportion of one size class in the prey population increases, Bosmina of the same two size classes were offered in ratios of 1:3 and 3:1 with prey density kept at 20 prey per bottle. Epischura killed the two size classes according to the ratios at which they were offered (Table 3); therefore, Epischura did not show size selection even when small Bosmina represented a greater proportion of the population.

Bosmina of various sizes avoid an attacking Epischura by sinking passively (Kerfoot 1977a, 1978). Direct observations of Epischura attacking Bosmina reveal that the predator will attack prey of any size, but the smaller the Bosmina, the greater the probability of ingestion after being grasped by the copepod (Table 4). Since Bosmina <0.25

TABLE 2

Predation rate by Epischura when Bosmina 0.28-0.35 mm and Bosmina < 0.25 mm were offered.

Prey/bottle	Replicates	Total prey killed	Ratio				Chi-square*	
			Expected		Observed			
I	S		I	S	I	S		
2	2	9	23	11.5	11.5	12	11	0.04
5	5	9	21	10.5	10.5	13	8	1.19
10	10	8	39	19.5	19.5	24	15	2.08

I = 0.28-0.35 mm

S = < 0.25 mm

* Chi-square 0.05 for 1 df=3.84

TABLE 3

Predation rate by Epischura when Bosmina 0.28-0.35 mm and Bosmina < 0.25 mm were offered.

Prey/bottle	Replicates	Total prey killed	Ratio				Chi-square*
			Expected		Observed		
I	S		I	S	I	S	
5	15	6	14.25	42.75	15	42	0.05
15	5	5	21.75	7.25	22	7	0.01

I = 0.28-0.35 mm

S = < 0.25 mm

* Chi-square 0.05 for 1 df=3.84

TABLE 4

Ingestion probabilities for Bosmina of various size classes
after being grasped by Epischura

<u>Bosmina</u> size (mm)		No. attack observed	% ingested (100-% escape)
<0.25	L	21	66.6
	F	18	33.4
0.26-0.30	L	8	12.5
	F	23	8.7
0.31-0.35	L	7	0.0
	F	7	0.0

L = Bosmina from laboratory culture

F = Bosmina collected from Pinks Lake on June 25, 1979

mm and Bosmina of 0.28-0.35 mm were preyed upon at the same rate (Table 2, 3), the larger Bosmina must have encountered the predator at a higher rate than their smaller counterparts. Both large and small Bosmina swim at about 1.5 mm/s, therefore, swimming speed does not explain the different encounter probabilities. Epischura detects prey primarily through mechanical disturbances in the water (Strickler and Trowbly 1975). Assuming the amount of disturbance caused by a swimming Bosmina increases with the size of the animal, then the larger the Bosmina, the greater the distance from which it is detected by Epischura. Hence, large Bosmina have low ingestion probability, but this advantage is counteracted by a higher encounter rate. This point is supported by the results of the following experiments. When Bosmina collected from Pinks Lake during the summer months were exposed to Epischura, in every size class far fewer were ingested than than the laboratory raised Bosmina (Table 4). The only visible difference between the two groups of Bosmina was the length of the mucral spine (Fig.9, Table 8). Small Bosmina with long mucral spines achieve an increase in relative size and, therefore, a decrease in ingestion probability while still keeping a low encounter rate. These results, like those of Kerfoot (1975a, 1977a), demonstrate the importance of mucral spines for defense in Bosmina.

Previous work (Anderson 1970, Brandl and Fernando 1975, Confer 1971) has related the importance of size to se-

lective predation among zooplankters. Other recent studies (Gerritsen 1978, Kerfoot 1978, Li and Li 1979) have suggested that factors such as shape, carapace thickness, and swimming behaviour may also influence the selective processes. However, when prey that are similar in these characteristics are used, it is generally assumed that predation rate would decrease with increasing prey sizes. The results presented here show that Epischura cannot handle Bosmina >0.40 mm effectively, but when offered Bosmina <0.40 mm, there is no size selection. This suggests that even for a species whose shape and swimming behaviour do not change much with growth, predation rate still may not decrease with increasing size. Therefore, Bosmina must reach at least 0.4 mm to use size as an effective defense. During the months from June through September when Epischura occurs in Pinks Lake, less than 5% of the Bosmina are over 0.40 mm. Since Bosmina survives in the lake even during the months when Epischura is most abundant, and the brood size in Bosmina increases with the body size (Kerfoot 1974), it is possible that reproduction by those Bosmina that have refuge in size is enough to stabilize or even increase the population density (i.e. the net reproductive rate of the population ≥ 1).

2.3.3 Bosmina and Ceriodaphnia

To examine prey selection and switching, Epischura was offered two prey species of similar size (0.28-0.35mm) but differing morphology (Fig. 4). Adult Bosmina and first instar Ceriodaphnia were presented in different ratios with the total prey density kept at 20 prey per bottle. The preference for a given prey is demonstrated by using the logarithm of Jacob's (1974) modified version of the forage ratio

$$Q = r(1-p)/p(1-r)$$

where r is the fraction in the diet and p is the fraction in the environment. A value for $\log Q > 0$ indicates positive selection and for $\log Q < 0$ indicates negative selection. The fact that Epischura preferred Bosmina to Ceriodaphnia is shown by $\log Q$ for Bosmina > 0 at all prey ratios (Fig.5). To study the effect of previous diet the experiments were repeated using Epischura that had been exposed to either Bosmina or Ceriodaphnia for a 24-hr training period at a prey density of 10 prey per bottle. Only predators that had killed at least one prey during the training period were used. The results indicate that previous diet did not alter the predators' preference for Bosmina (Fig.6). A regression

Figure 4: Lateral and ventral views of (A) Ceriodaphnia and
(B) Bosmina showing the differences in body shape.

A₁



B₁



A



0.1mm

B

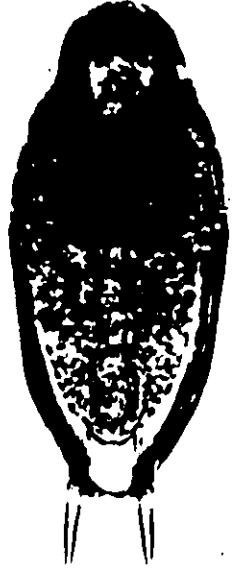


Figure 5: Logarithm of the forage ratio for Bosmina by Epischura as a function of the percentage of Bosmina offered. Ceriodaphnia was the alternative prey (Regression: $y=0.278+0.003x$, $r=0.202$, $P>0.25$)

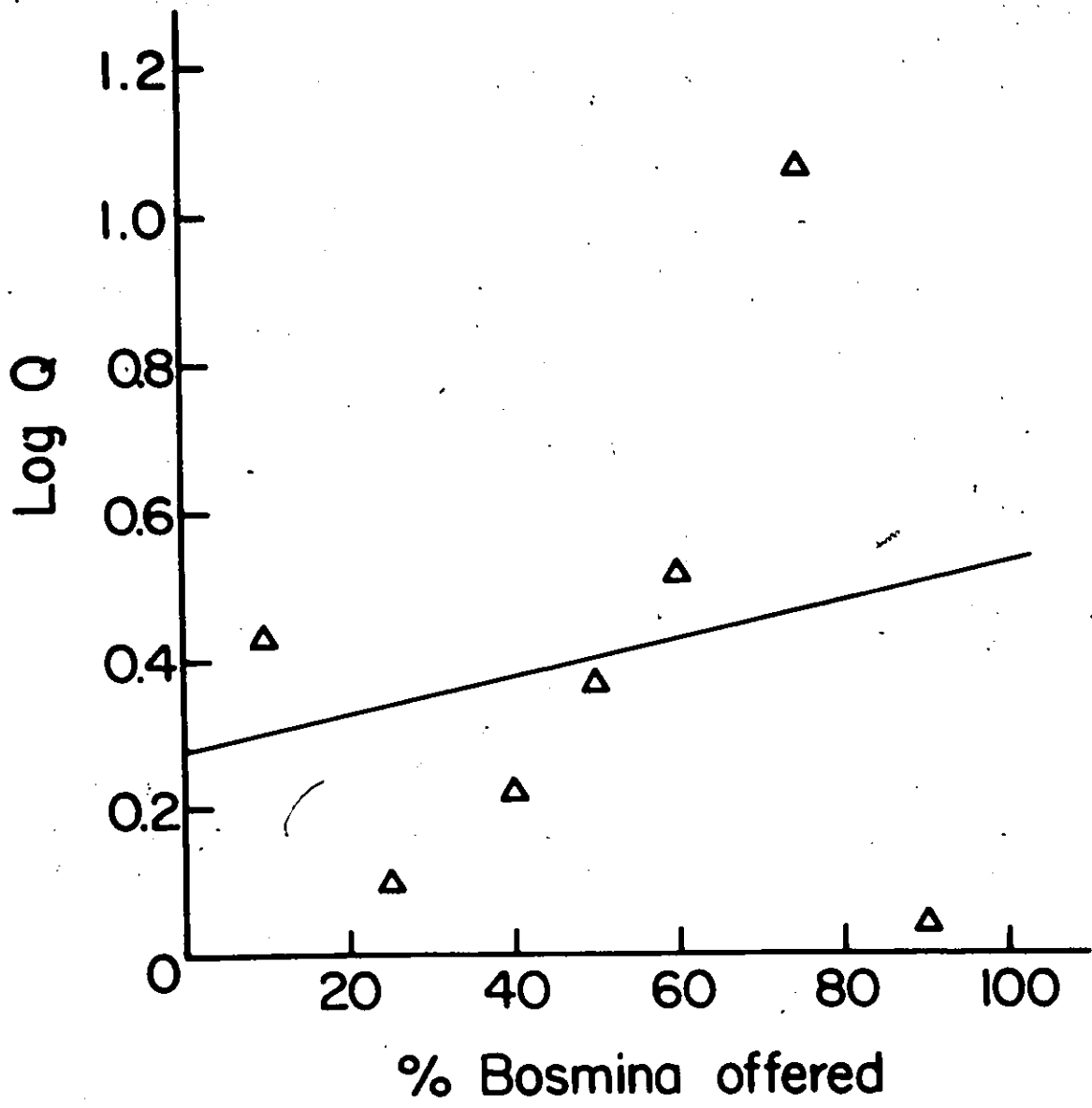
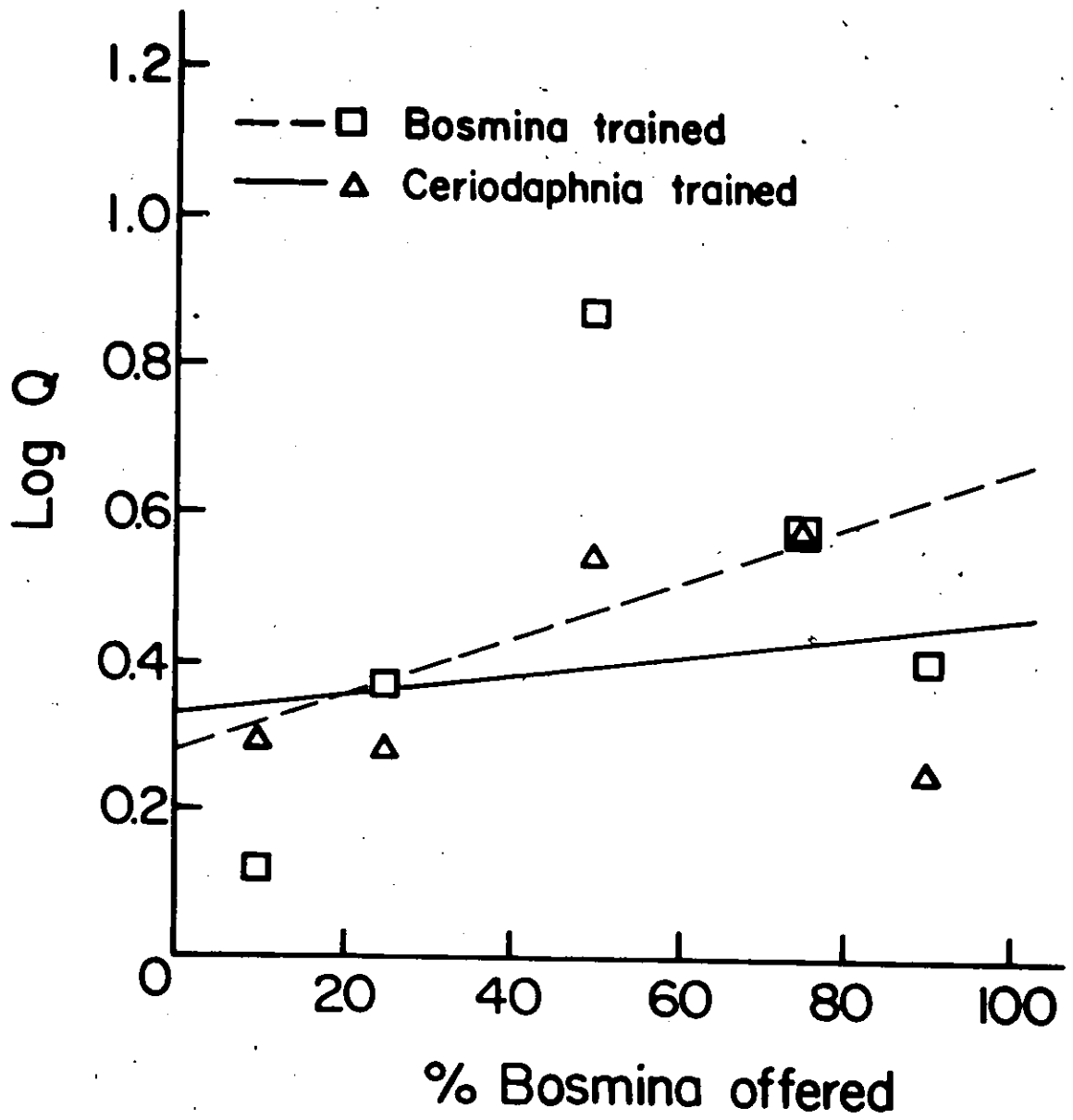


Figure 6: Logarithm of the forage ratio for Bosmina by Epischura trained to Bosmina or Ceriodaphnia as a function of the percentage of Bosmina offered. Ceriodaphnia was the alternative prey (Bosmina trained-regression: $y=0.283+0.004x$, $r=0.443$, $P>0.20$; Ceriodaphnia trained-regression: $y=0.333+0.001x$, $r=0.273$, $P>0.25$)



analysis was performed on each of the 3 sets of data on Figures 5 and 6. An analysis of covariance shows that the 3 regression lines are statistically identical ($F=0.070$, $F[2,11]=3.98$ for $P=0.05$). Furthermore, since the slopes of the 3 regression lines do not differ from zero (t-test), Epischura did not show any switching.

Ceriodaphnia hangs motionless in the water for a long period between swimming bouts. This swimming behaviour gives it a mean speed of 1.5-2.5 mm/s, which is higher than that for the slow but continuously swimming Bosmina (1.5 mm/s). These differences in swimming behaviour mean that Ceriodaphnia has a higher encounter rate with Epischura than Bosmina (Zaret 1979). Since Bosmina is preyed upon at a higher rate than Ceriodaphnia, encounter probability is not the main factor that determines prey selection here. Visual observations show that Ceriodaphnia can perceive an approaching predator from as far away as 3 mm, whereas Bosmina senses a predator only at close range (<1 mm). Upon sensing the disturbances created by a swimming prey, Epischura will try to contact it by making several somersault-like loops in the disturbed area. This searching behaviour is successful with Bosmina which tries to escape by sinking vertically, but becomes ineffective with Ceriodaphnia which flees by swimming away quickly along a straight path in any direction. When grasped, Bosmina is partially protected by its carapace and mucral spine. Epischura eats Bosmina by scrap-

ing out the soft tissue through the ventral slit and usually leaves the carapace intact. On the other hand, Ceriodaphnia, whose carapace is easily torn apart by Epischura, may rely on its spherical shape, which is difficult to grasp, to frustrate the predator. The ability of Ceriodaphnia to escape after being captured was not determined, but there is little doubt that Epischura eats more Bosmina which is easier to capture.

2.3.4 Diaptomus

The predation rates of Epischura on Diaptomus of various stages are shown in Table 5. At a prey density of 20 prey per bottle, copepodites seem to experience a heavier predation rate than adults and nauplii, although the differences were not significant when tested by a one-way analysis of variance based on the number of prey eaten per predator per day ($P > 0.1$). The predation rate increased by more than four times when the density of copepodite prey was doubled from 10 per bottle to 20 per bottle. Diaptomus of all developmental stages can sense the hydromechanical signals produced by a swimming animal from distances up to 4 mm and escape by a series of rapid jumps (Chapter 3). A jump by one individual Diaptomus often results in a chain effect, causing all the animals in the bottle to make evasive responses. Thus an increase in population density leads to higher swimming activity and higher encounter probability

TABLE 5

Predation rate by Epischura on various developmental stages
of Diaptomus.

	Prey/bottle	Replicates	Total prey killed	Prey/predator /day	SD
Adults	2	5	0	0.00	
	10	5	2	0.48	0.66
	20	5	4	0.97	1.57
Copepodites I-III	2	4	1	0.32	0.63
	10	5	2	0.51	1.30
	20	5	11	2.39	0.91
Nauplii	2	3	0	0.00	
	10	2	0	0.00	
	20	5	4	0.92	1.41

with the predator. When 10 adult and 10 copepodite Diaptomus were presented together, Epischura showed strong preference for copepodites (Table 6).

Diaptomus nauplii, copepodites, and adults remain motionless in the water, occasionally jumping to a new position. While nauplii have neutral bouyancy (Gerritsen 1978), adults and copepodites steadily sink at speeds of 0.2-0.5 mm/s and must jump at a higher rate to maintain their position in the strata that are best supplied with food. Adults must occasionally increase their speed in order to encounter mates. Nauplii release few signals in terms of hydromechanical disturbances and therefore have a small active space, resulting in a very low encounter rate with the predator. Adults and copepodites are detected more often, but because the capture probability for adults is lower than that for copepodites (Gerritsen 1978), it appears that evasive ability increases with age. However, once captured by Epischura, neither adult nor copepodite Diaptomus can escape.

When presented with Diaptomus of various developmental stages, Epischura preyed at a higher rate on copepodites than on adults and nauplii. For Diaptomus, the instar duration times of nauplii (1.1-11.9 days) and copepodites I-III (2.9-28.8 days) are considerably shorter than those of copepodites IV-V (27.3- 79.6. days) (Boers and Carter 1978). Both nauplii and early copepodites face intense competition for food from the more efficient later instars. Similar to

TABLE 6

Predation rate by Epischura when Diaptomus copepodite I-III
and adults were offered at a 1:1 ratio

Prey/bottle	Replicates	Total prey killed	Ratio Observed	P *
CI-III CVI			CI-III-CVI	
10 10	5	9	8 1	0.02

* Binomial test

Bosmina, Diaptomus experiences the highest predation rate when small. However, nauplii reduce their encounter rate with predators by crypsis. The short developmental time is a result of their limited energy supply (mainly lipids stored in the egg) rather than the manifestation of evolutionary pressure to reach a 'safe' size quickly as in the case of copepodites I-III and Bosmina (Kerfoot 1974).

2.3.5 Starvation Experiments

The lack of tolerance of adult Epischura to starvation is shown in Table 7. Few animals were still alive after 24 hrs without food, and all animals died after 48 hours of starvation. In the laboratory, cyclopoid copepods survived for weeks without food. These animals decrease their swimming activity when starved and have visible energy reserves in the form of oil droplets. Epischura, on the other hand, starves quickly and die because of its sustained activity and lack of lipid energy reserves. While the survival rates at 24 hours of adult Epischura exposed to algae were higher than those of starved animals, they were lower than those of the controls. Since the guts of adult Epischura were green even after a brief exposure to algae, these results suggest that the animals cannot utilize algal food efficiently.

TABLE 7

Survival of Epischura exposed to starvation and algae

Hours	Starvation		Algal food		Control	
	No. Alive Male	No. Alive Female	No. Alive Male	No. Alive Female	No. Alive Male	No. Alive Female
0	15	15	10	15	10	12
12	15	13	10	15	10	12
24	3	2	5	13	9	10

2.3.6 Omnivorous Feeding

The predation rate of Epischura on Bosmina (10 per bottle, 0.28-0.35 mm) did not change in the presence of Ankistrodesmus (Fig.7, $r=-0.02$). However, when Epischura was exposed to Ankistrodesmus for 24 hrs prior to the introduction of prey, the predation rates for those trained to high algal concentrations were lower than the rates for those trained to low algal concentrations (Fig.8, $r=0.34$, $P<0.05$).

The presence of algae does not alter the predation rate of Epischura on Bosmina. The feeding habits of early stages of Epischura have not been studied, but nauplii are undoubtedly herbivorous while adults and copepodites are omnivorous (Friedman 1977, Main 1962). Adult Epischura ingest algae but can not utilize algal food efficiently. Main (1962) found that with the exception of Pediastrum, algal foods are not sufficient to sustain growth and reproduction in Epischura. Corner et al. (1976) found that the marine copepod Calanus, when feeding as a carnivore, assimilates its food at a higher efficiency than when feeding on algal diets. Natural selection favours animals which spend time and energy efficiently. If algal foods are incomplete or lower in nutritional value than animal foods, then the presence of algae would not affect carnivorous feeding in Epischura. Lonsdale et al. (1978) suggested that small algae do not reduce the predation rate of adult estuarine Acartia tonsa on copepod nauplii because the predator prefers the

Figure 7: Predation rate of Epischura on Bosmina in the presence of Ankistrodesmus.

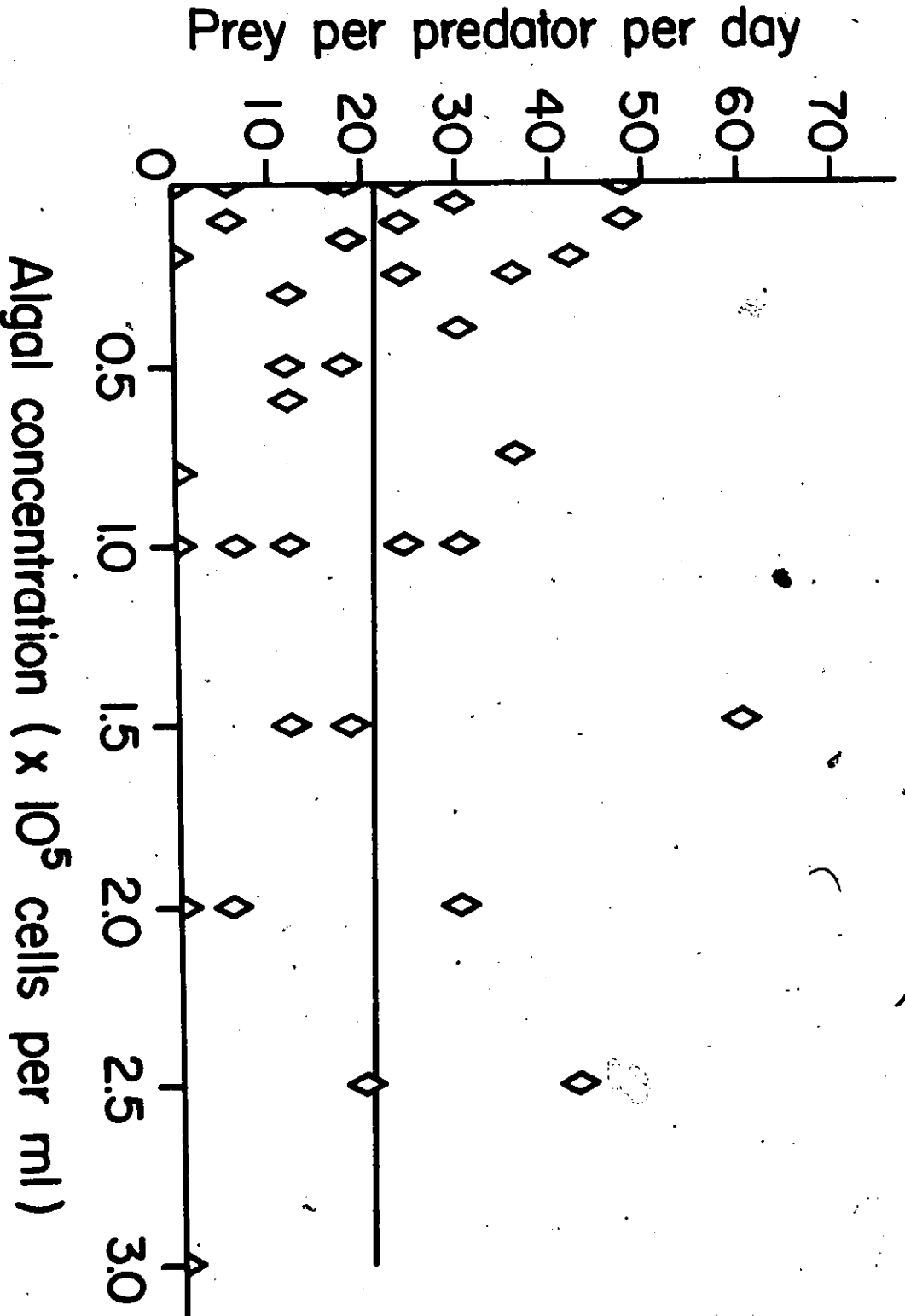
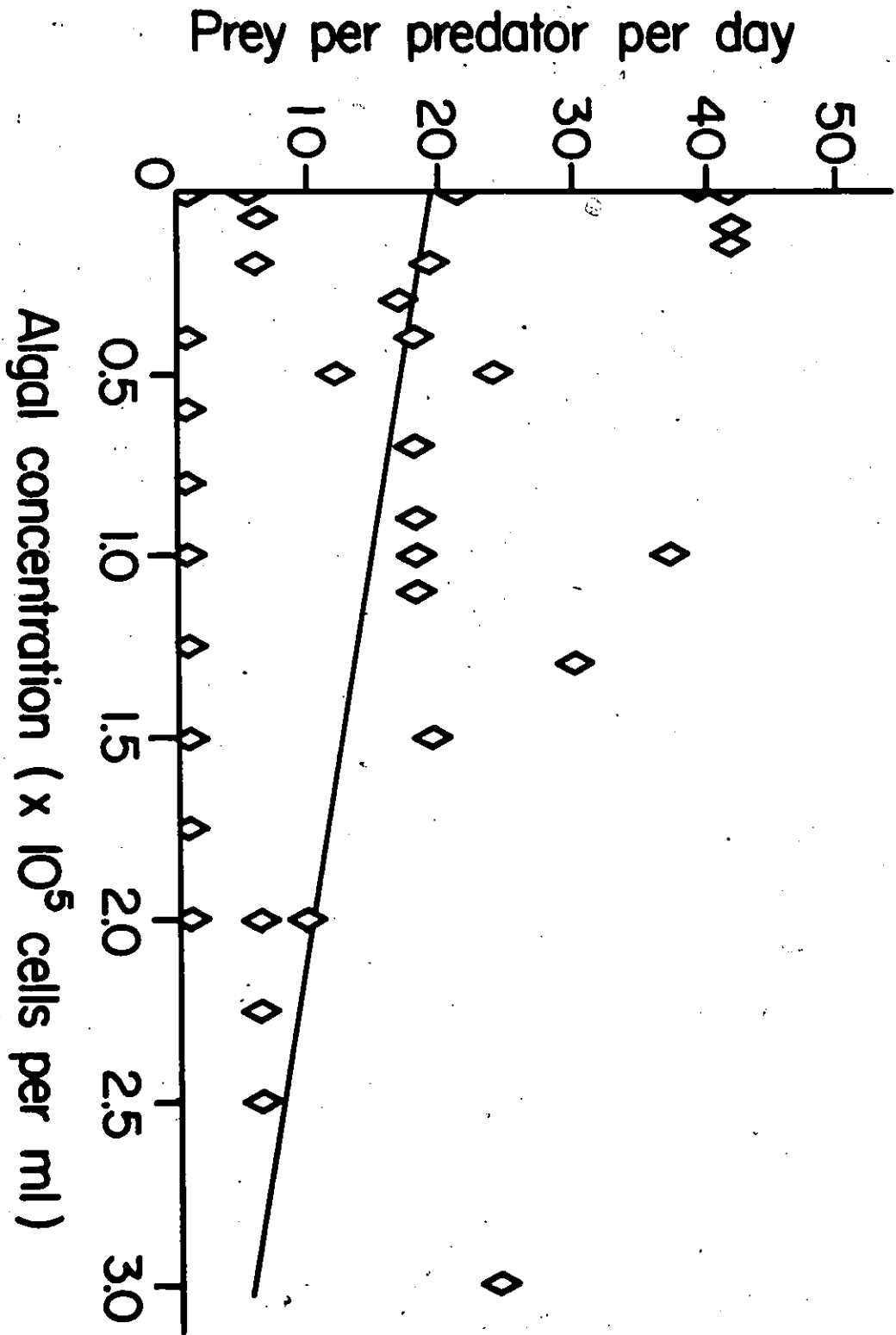


Figure 8: Predation rate of trained Epischura on Bosmina in the presence of Ankistrodesmus. Epischura trained to Ankistrodesmus at concentrations equal to the experimental concentrations.



large nauplii to the small algal cells and the feeding on small algae does not interfere with the handling of prey. Since Main (1962) found that Epischura adults feed at a higher rate on large algae than on small ones, Ankistrodesmus (3-30 μ m) may not be suitable to Epischura. Epischura that had been trained to high concentrations of algae reduces its predation rate on Bosmina. This could be the result of satiation, however, the high mortality rate of Epischura (>75% when algal concentration $>2 \times 10^5$ cells/ml) suggests that high concentration of Ankistrodesmus may have had some adverse effects on the predator.

The results presented here show that Epischura is not capable of any active choice. Selectivity reflects 1) the ability of Epischura to detect, capture, and ingest a given prey species, and 2) species differences in the effectiveness of prey defense. Epischura has low tolerance to starvation (mortality was always >50% after 24 hours without food) and has a high predation rate (e.g. 40 prey per predator per day). For a predator, the net value of a prey is its gross value minus the cost in terms of the energy required to search for and handle it. Since the handling time for prey is low (2-3 min for Bosmina and <1 min for copepodites), Epischura spends most of its time searching for prey. Searching time decreases when the number of prey types in the diet increases (MacArthur and Pianka 1966). If active selective predation is too costly in terms of time,

then Epischura may be more efficient by being a jack-of-all-trades (Kerfoot 1975a), eating whatever it can capture and handle.

Chapter III

CYCLOMORPHOSIS IN BOSMINA AND COPEPOD PREDATION

3.1 INTRODUCTION

From May to October 1979, I took a preliminary look at the zooplankton of Pinks lake, Gatineau Park, Quebec, hoping to find out what species constitute the diet of the predaceous copepod Epischura lacustris. While inspecting the zooplankton samples, I found that Bosmina longirostris from the June samples has longer mucral spines than individuals from earlier samples. Previously, Kerfoot (1977a) suggested that Epischura is an important factor in determining both the size and shape of Bosmina. Epischura which seizes Bosmina from above cannot penetrate the thick carapace and must rotate the prey before scraping out the soft parts from the ventral opening. Thus a long mucral spine would protect Bosmina by making rotation by the predator difficult. Since adults of Epischura first appear in Pink lake around the end of May, it becomes apparent that the morphological change in Bosmina may be related to Epischura predation.

In this chapter, I will describe the seasonal change in the morphology of the Bosmina populations in Pinks lake. Although it is not clear what factor (or factors) causes

this cyclomorphosis, I will present evidence to confirm that cyclomorphotic Bosmina with long mucral spines are less susceptible to Epischura predation than similar sized Bosmina with regressed spines. While my results are somewhat preliminary, together with the data of Kerfoot (1975a, 1975b, 1977a), they suggest that cyclomorphosis in Bosmina is an evolutionary adaption against predation by tactile-feeding predators (Dodson 1974b).

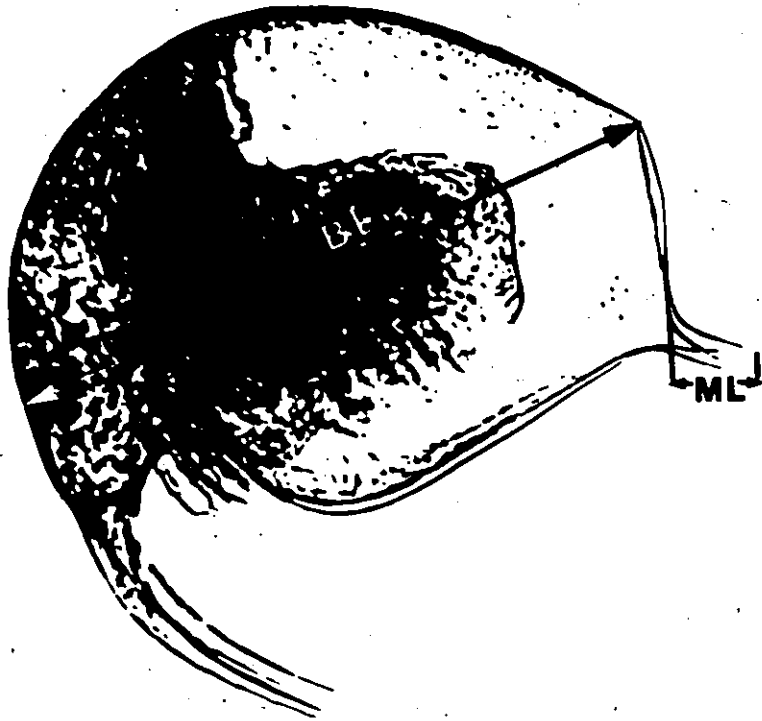
3.2 MATERIALS AND METHODS

This research was done in Pinks Lake, Gatineau Park, Quebec. The zooplankton community in Pinks Lake is comprised of Bosmina longirostris, Daphnia spp., Diaphanosoma spp., Laptodora kindtii, Epischura lacustris, Diaptomus minutus, Tropocyclops spp., and Cyclops spp.

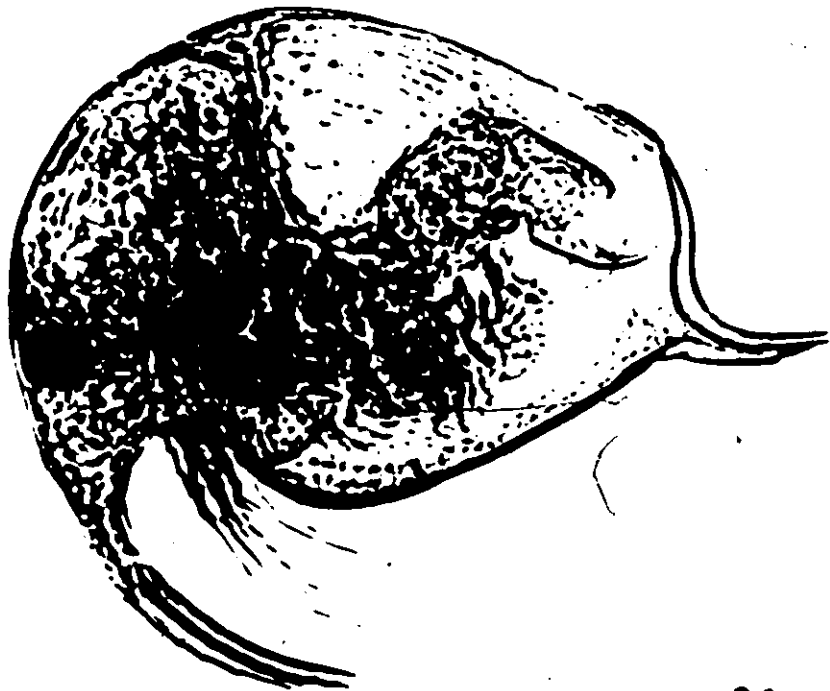
From May to October 1979, zooplankters were collected from Pink Lake once a week by horizontal tows using a plankton net with 100 μ m mesh. For estimating population densities, three stations were established and duplicate vertical tows were taken from each station approximately once a month. The two tows were combined, diluted to 500 ml or 1000 ml, and preserved in 10% formalin. The study was terminated in November when the National Capital Commission, Canada, closed the road to Pinks Lake. Bosmina from November were collected by casting a plankton net from the shore. In the laboratory, zooplankton densities were estimated by counting subsamples under a stereomicroscope. At least two 10 ml subsamples were counted for each sample. In the case of Epischura where the population densities were too low, five to ten 10 ml subsamples were analyzed. For morphological measurements, Bosmina was put on a glass slide, and measured at 320x using a light microscope with an ocular micrometer. Two morphological characters were measured: body length and mucral spine length (Fig. 9). Because of the small size of Pinks Lake, no differences in morphology bet-

Figure 9: Morphological changes in Bosmina from laboratory cultures, (A), and Pinks Lake, June 1979, (B). ML=mucral spine length, BL=body length.

A



B



0.1 mm

ween sampling stations were expected, and indeed none have been found. Subsequently, data from all stations were pooled.

The predation rates of Epischura on two types of Bosmina (Fig.9, Table 8) were determined. Bosmina with enlarged mucral spines were obtained from Pinks Lake during the month of June by horizontal tows and used within three days after arriving in the laboratory. Bosmina with regressed mucral spines were obtained from laboratory cultures raised from specimens collected from Pinks Lake about one year prior to the beginning of this experiment. While the causes for the regression in mucral spine growth is not known, a similar phenomenon has been reported by Kerfoot (1975b). Predation experiments were carried out in methods similar to those described in Chapter 1. Only Bosmina of body size from 0.28-0.35 mm were tested.

TABLE 8

Average sacral spine length/body length (\bar{x}) for Bosmina

<u>Bosmina</u> size (mm)		\bar{x} (n)	SD	P *
<0.25	L	0.158 (10)	0.037	0.000
	F	0.241 (11)	0.025	
0.26-0.30	L	0.123 (11)	0.024	0.000
	F	0.194 (21)	0.020	
0.31-0.35	L	0.100 (13)	0.025	0.000
	F	0.173 (24)	0.018	

L = Bosmina from laboratory cultureF = Bosmina collected from Pinks Lake on June 25, 1979.

* t-test

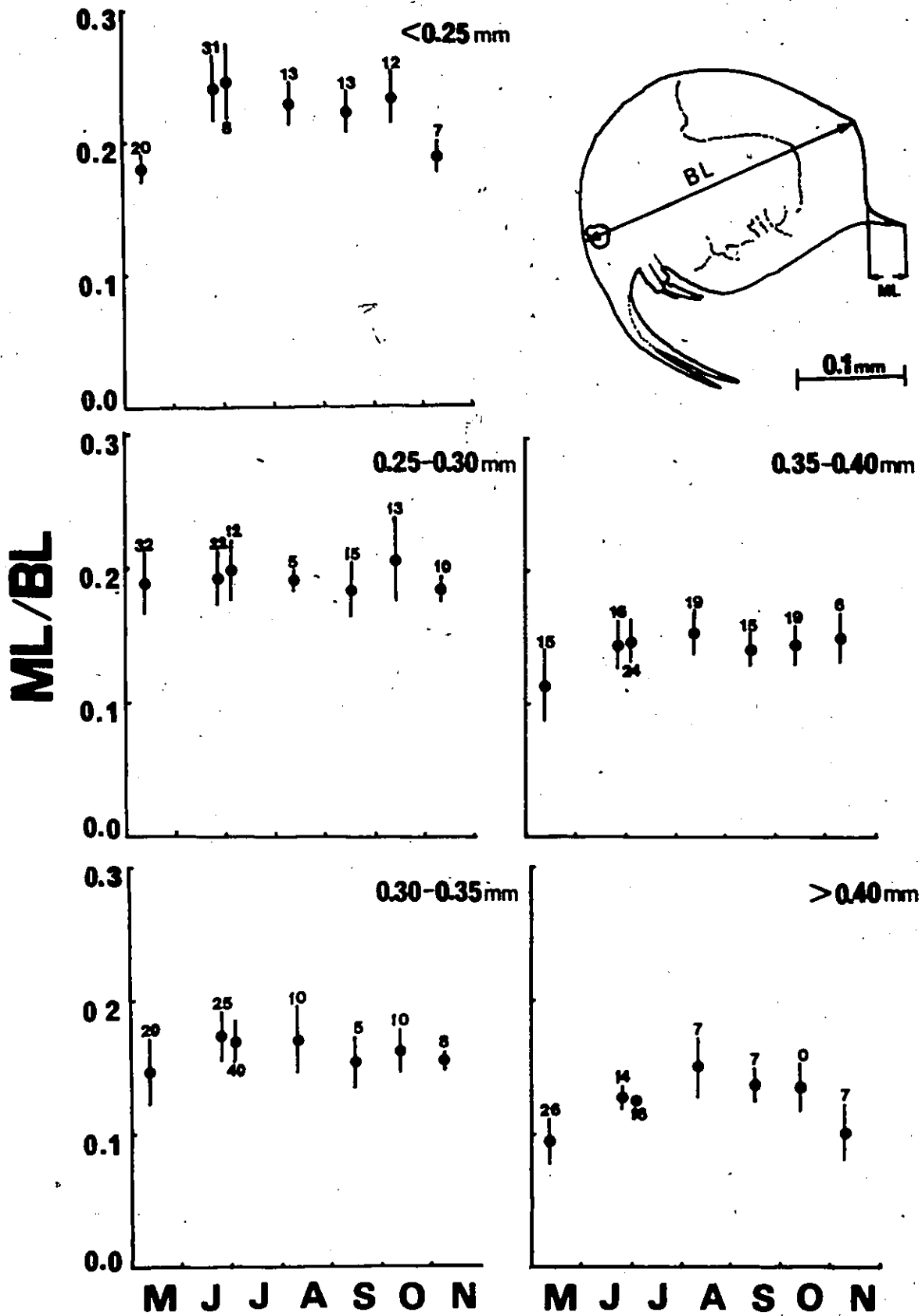
3.3 RESULTS AND DISCUSSION

The changes in the mucral spine length of Bosmina in Pinks Lake during the summer are illustrated in Fig. 10. A 2-way analysis of variance shows that the differences in mucral spine length upon body length due to both size classes and months are highly significant ($P < 0.001$). Thus small Bosmina have relatively longer mucral spines than large Bosmina. For the size classes of < 0.25 mm, $0.30-0.35$ mm, $0.35-0.40$ mm, and > 0.40 mm, Bosmina from the June 25 samples have significantly longer mucral spines than Bosmina from the May 11 samples (Tukey's tests, at $P = 0.05$). Since Epischura was rarely observed to kill Bosmina > 0.40 mm, the increase in mucral spine length in the upper size class cannot yet be explained. The mucral spine length appears to reach a maximum during the months of June, July, and August. Slight decreases were recorded after October, significant only in the < 0.25 mm size class.

Cyclomorphosis has been reported in planktonic algae, dinoflagellates, rotifers, copepods, and cladocerans (reviewed by Hutchinson 1967). However, it is among the genus Daphnia of the Cladocera, where the phenomenon is most conspicuous and has been studied extensively.

Two physical factors, temperature and turbulence, have been shown to be the proximal causes inducing cyclomorphosis (Brooks 1946, 1947, Coker and Addlestone 1938, Egloff 1968, Hazelwood 1966, Hrbacek 1959, Jacobs 1962). Since the

Figure 10: Seasonal change in mucral spine length of Bosmina from Pinks Lake. Each point showing mean, standard deviation and sample size. Size class indicated in each figure. ML=mucral spine length, BL=body length.



viscosity of water decreases in high temperature, exuberances such as helmets in Daphnia were once viewed as mechanisms to slow sinking in the summer. More recent experimental evidence, however, has not supported this buoyancy hypothesis. Hutchinson (1967) indicated that cyclomorphosis is almost always confined to species of the turbulent epilimnion where sinking speeds are far less than in the non-turbulent hypolimnion. Additionally, Jacobs (1967) found that helmeted Daphnia actually sink faster than the unhelmeted winter forms. Brooks (1965) associated cyclomorphosis with fish predation. During the summer when fish are abundant, Daphnia maintain high rates of growth by expanding the transparent helmet while keeping the visible central core of the body small. This hypothesis was later expanded by Dodson (1974b) who suggested that cyclomorphosis is influenced by both vertebrate and invertebrate predation. Various transparent protuberances are grown by some prey species to foil tactile-feeding invertebrates at the same time when fish predators are also abundant. Gilbert (1966, 1967, 1973) has shown that a protein released by the predaceous rotifer Asplanchna stimulates the growth of spines in the prey rotifer Brachionus. O'Brien et al. (1979) also demonstrated that the cyclomorphotic Daphnia with helmet is less susceptible to both fish and copepod predation.

Several recent studies have shown that predation by size-selective invertebrate planktivores influences the size

and shape of Bosmina. Kerfoot (1975a, 1977a) has found that in the pelagic regions of Lake Washington, Seattle, Washington, where fish predation is not intense, the Bosmina populations consist of the long-bodied morphs which are protected against predation by Epischura. However, because the long-bodied morphs require more energy for their adaptations, they are replaced by the more prolific short bodied morphs along the lily-pad margins where fish fry remove the copepods. O'Brien (1979b) reported that Bosmina in Alaskan arctic lakes with the large predaceous copepod Hetercope are larger and have longer protuberances and thicker carapace than Bosmina in nearby lakes without the predator. Furthermore, predation experiments demonstrated that Bosmina from a lake with Hetercope are less vulnerable to Hetercope predation than similar size Bosmina from a lake without Hetercope.

Cyclomorphosis in Bosmina has been reviewed by Hutchinson (1967). In Bosmina longirostris the changes appear to involve a decrease in the length of the antennule and mucral spine during the summer. Recently, Kerfoot (1975b) described similar cyclomorphotic changes in B. longirostris in Frains Lake, Michigan. However, his observations differ from mine in two very important aspects. While Bosmina in Frains Lake go through a decrease in antennule length and mucral spine length during the summer, cyclomorphosis in Bosmina in Pinks lake involves changes in only the mucral

spine length, with the maximal length achieved during the summer. Therefore when put together, our results clearly do not support the buoyancy hypothesis (W.C. Kerfoot, per. comm.). Moreover, it is doubtful that small changes in the length of the mucral spine (Fig.9) could have affected the buoyancy of Bosmina. The antennule length of Bosmina from Pinks Lake remains unchanged between May and November. Individuals of Bosmina from the winter populations in Pinks Lake have not been examined, but no regression in antennule growth has been observed in Bosmina from our laboratory cultures.

During the summer, Bosmina in Pinks Lake co-exists with three invertebrate predators, Epischura, Leptodora, and Cyclops. Leptodora appears for a short time during July and August. Thus its cycle would not explain why Bosmina undergoes increase in mucral spine length during May and June. Cyclops occurs at very low densities (<10 individuals per 100 liters) during the summer. Predation by Cyclops is known to induce size changes in Bosmina (Kerfoot 1974), whereas, major shape changes in Bosmina are often associated with Epischura (Kerfoot 1975a, 1977a).

The seasonal occurrence of individual instars of Epischura lacustris has been described by Main (1962). Adult and immature stages occur in the plankton only during the ice-free months. During the winter only resting eggs persist in the mud bottom. In Pinks Lake samples taken on May

11 contained only nauplii and copepodites I and II. The predaceous adult and late copepodite stages did not appear until the last week of May. Thus the appearance of the predaceous stages of Epischura coincides with the increase in mucral spine length in Bosmina.

Results presented in Chapter 1 have demonstrated the effectiveness of Epischura predation on Bosmina populations. Concentrations of Epischura, Bosmina, Daphnia, and Diaphanosoma in Pinks Lake are presented in Fig. 11. While the decline of Bosmina at the end of August was probably the result of competitive pressure from Daphnia, it is quite probable that the increase of Bosmina in June was suppressed by Epischura.

If the cyclomorphotic change in Bosmina is related to Epischura predation, then one would expect Bosmina with the enlarged mucral spine to be less vulnerable to Epischura than individuals without this adaptation. Results of the predation experiments are presented in Table 9. Laboratory cultured Bosmina which has a regressed mucral spine experienced higher predation rates than Pinks lake Bosmina. In addition, the result was not due to differences in handling time (Fig. 12). Since both types of Bosmina swim at about 1.5 mm/s, the observed difference in predation rates was not the result of differences in encounter probability (Gerritsen and Strickler 1977). Evidence implicating the effectiveness of the mucral spine as a defensive mechanism comes

Figure 11: Concentrations of Epischura, Bosmina, Daphnia
and Diaphanosoma in Pinks Lake.

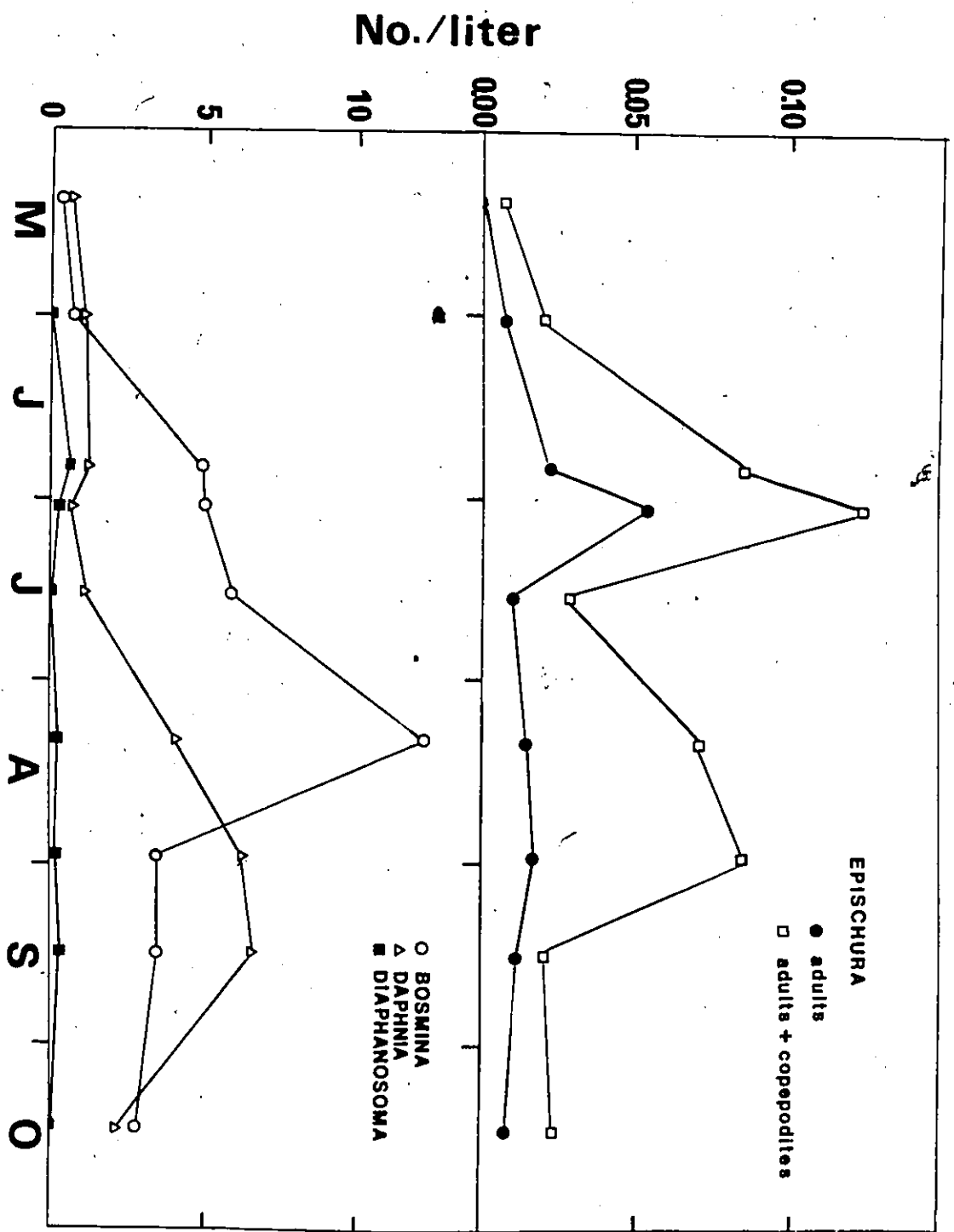


TABLE 9

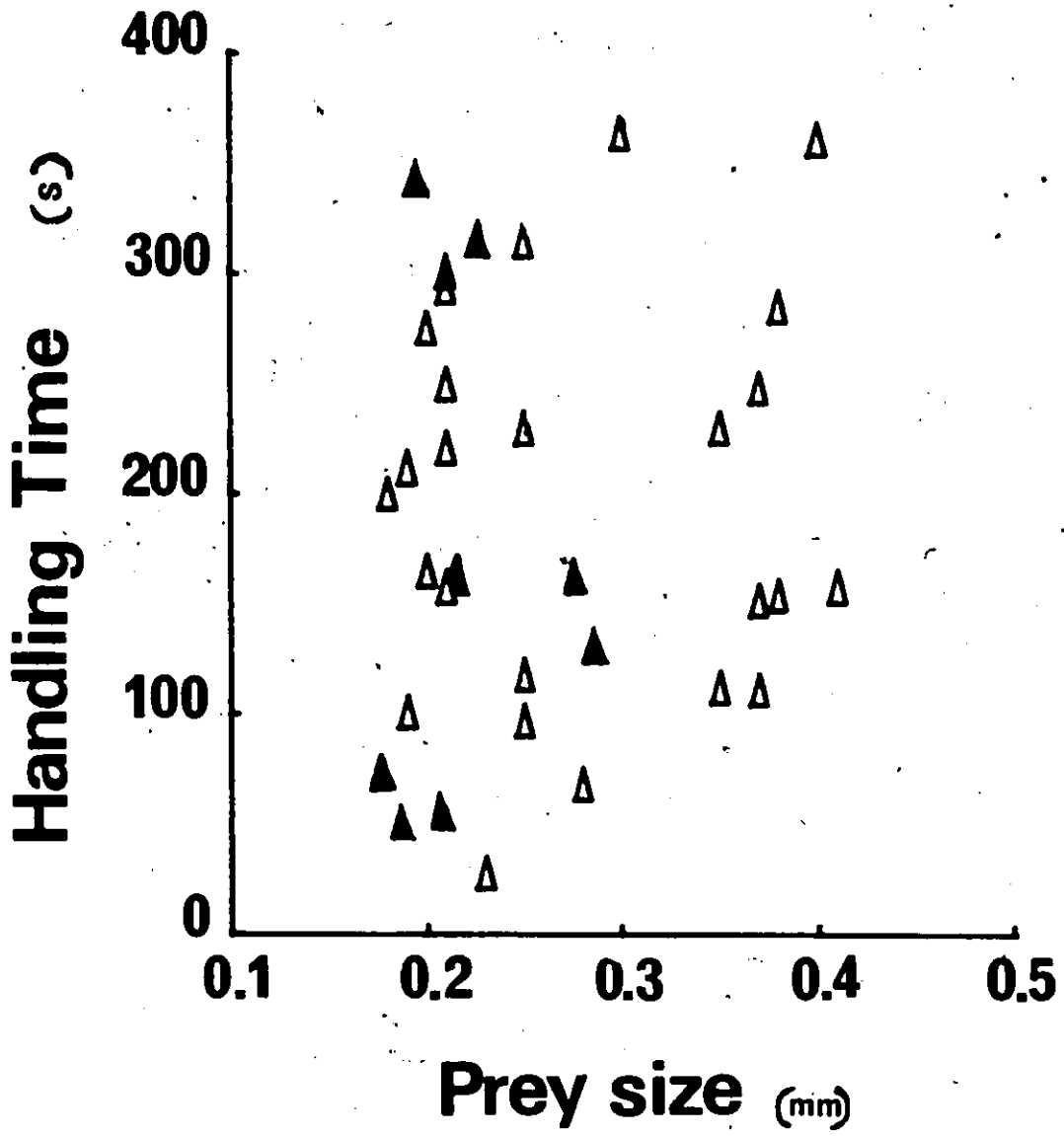
Predation rates of Epischura on Bosmina

Prey/liter	<u>Bosmina</u>	Replicates	Prey/predator /day		P *
			x	SD	
5	L	8	8.3	8.1	<0.10
	F	8	2.7	4.0	
10	L	8	19.6	12.4	<0.005
	F	8	3.4	4.0	
20	L	8	41.2	27.4	<0.005
	F	8	2.7	5.7	

L = Bosmina from laboratory culturesF = Bosmina collected from Pinks Lake on June 1979.

* t-test

Figure 12: Handling time (time from capture until discard of dead Bosmina by Epischura) by Epischura on Bosmina from Pinks Lake (closed triangles) and laboratory cultures (opened triangles).



from direct observations of Epischura attacking Bosmina (Table 4). Once seized by Epischura, the ingestion probability is always lower for the Pinks Lake Bosmina than for the laboratory cultured Bosmina. This evidence suggests that cyclomorphosis in Bosmina is an adaptation for reducing mortality due to copepod predation.

Chapter IV

THE RESPONSES OF COPEPODS TO HYDROMECHANICAL STIMULI

4.1 INTRODUCTION

Predation is an important factor in determining the species composition (Allen 1973, Dodson 1974a) and size structure (Brooks and Dodson 1965, Confer 1971, Kerfoot 1975a) of zooplankton communities. In recent years ecologists have constructed models to predict the effects of predation on the zooplankton community structure (e.g. Gerritsen and Strickler 1977, Steele 1974). These models make assumptions on behavioural parameters, such as encounter radius (sensory range), swimming speed and predation rates, and will make realistic predictions only if accurate and precise information on the behaviour of zooplankters is available. In the higher trophic levels both the predator and the prey are often large enough for the act of predation to be observed easily. Animals in the lower trophic levels, however, are often of microscopic sizes. In the planktonic ecosystem detailed study of predation is further hindered by the fact that the animals do not use the visual sense upon which we rely heavily. So it is no surprise that detailed behavioural studies of predation among zooplankters is still badly needed.

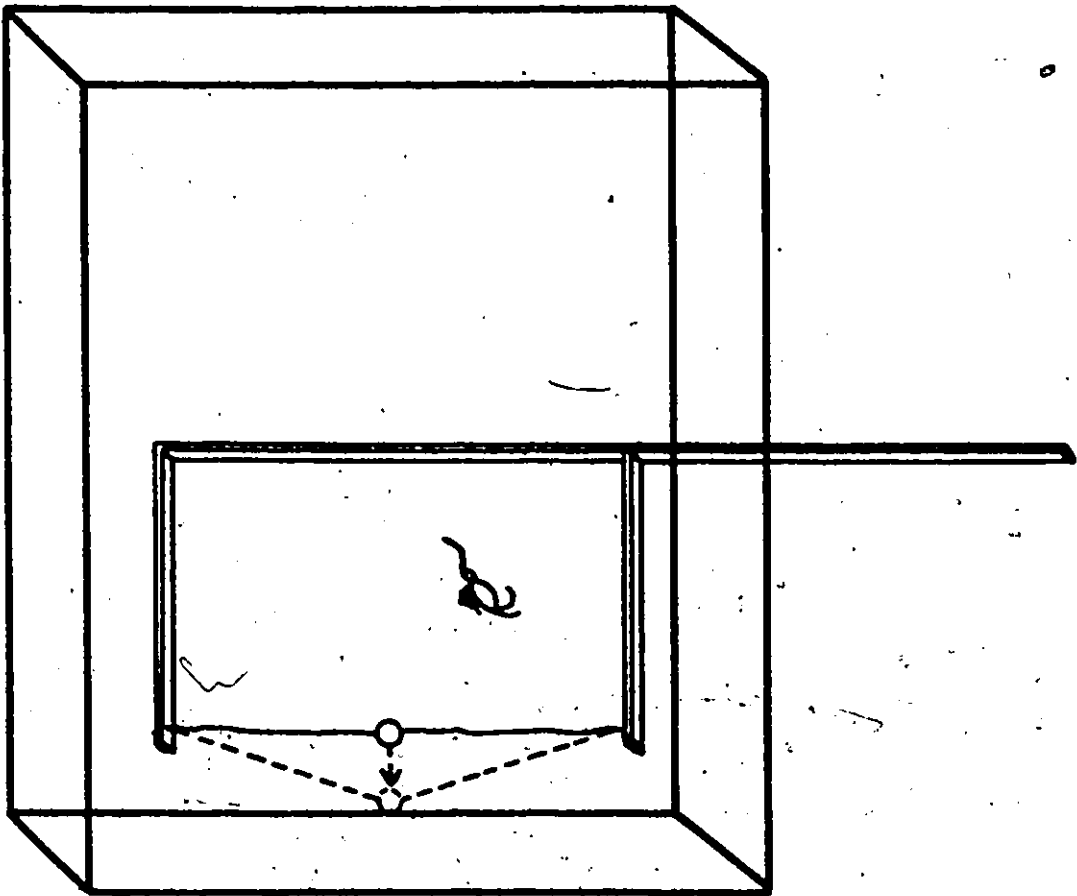
During predation, food is encountered, recognized, captured, and ingested, and each of these events may be governed by different sensory modalities. According to the Gerritsen and Strickler (1977) encounter model for 3-dimensional space with the animals distributed randomly and swimming in random directions, the encounter probability increases linearly with density and as the square of swimming speed and encounter radius. Thus the behaviour of an animal is manifested in its swimming speed and sensory range. It has long been noticed that zooplankters can sense small hydromechanical disturbances and respond by jumping away (Drenner et al. 1978, Gerritsen 1978, Strickler 1975, Szlauer 1964). A swimming animal produces water displacement and this results in a signal or active space (Bossert and Wilson 1968) whose size depends on the size, shape, and speed of the animal (Strickler and Twombly 1975). Previously, Strickler (1975) demonstrated that copepods detect other animals by mechanoreception. However, if detection is not followed by recognition, then the food chain would be determined by the capture and ingestion probabilities, and would appear more random. Additionally, predatory copepods which avoid each other but attack prey that are larger than themselves must occasionally encounter each other to mate. Therefore, the question is how do zooplankters recognize the signals of predators, prey, and mates. Katona (1973) demonstrated the importance of sex pheromones in the mating

behaviour of copepods, but other circumstantial evidence (Gerritsen 1978, Kerfoot 1977a, 1978, Landry 1978) suggests that mechanoreception is the major sense for prey detection by predatory copepods. Strickler and Bal (1973) found on copepods mechanoreceptors which may be excited when bent by water movement. However, studies of the responses of copepods to hydromechanical stimuli are relatively few, and quantitative information on the relationship between escape behaviour and the distance of the source of a hydromechanical signal is not available. The aim of this study is to quantitatively investigate the sensitivity and responses of copepods to hydromechanical disturbances, concentrating on the following questions: 1) From how far away will copepods avoid hydromechanical disturbances? 2) How is escape behaviour affected by the size, location, and direction of movement of a small moving object? Our method should prove useful in future studies of other small aquatic invertebrates which locate their food by mechanoreception.

4.2 MATERIALS AND METHODS

Copepods were collected from Meach Lake and Pinks Lake, Gatineau Park, Quebec. All experiments were carried out in a 9x4x2 cm chamber filled with filtered lakewater at 20°C. Observations of zooplankton behaviour were made with a horizontally mounted stereomicroscope at a power of 13.6X. Hydromechanical disturbances were created by the movement of small spheres made of iron filings encapsulated in paraffin wax. Two spheres of diameters of 0.8 mm and 1.2 mm were used. Each sphere was glued to the center of a loosely stretched hair, the ends of which were attached to the arms of a F-shaped clamp (Fig. 13). This allowed the sphere to be triggered to move horizontally over a distance of 3 mm by a manually operated magnet held outside the chamber. The stereomicroscope was focused on the sphere (depth of field=0.5 mm). The image of a grid of 1 mm squares was merged with that of the sphere by a beamsplitter (Alcaraz et al. 1979) placed between the lens and the chamber. The testing field consisted of 25 squares (5x5) left and above the sphere and 25 squares (5x5) left and below the sphere (see Fig. 14, 15). 20 to 40 Cyclops or Diaptomus were introduced into the chamber. The sphere was moved when an animal swam into the testing field in focus. The position and the response of the animal were recorded on a reference grid. This allowed us to display the data as a series of 5x5 matrices. To compare the responses between treatments (e.g.

Figure 13: Sketch of the experimental set-up for studying the escape responses of copepods. Hydromechanical disturbances were created when the sphere was triggered to move by a magnet (M).



M

response to a retreating sphere vs response to an approaching sphere), the total number of escape/number of trials was determined for each row and column. The angular transformations of these proportions were then subjected to a Chi-square test.

4.3 RESULTS AND DISCUSSION

4.3.1 Avoiding Predators

The escape probabilities of Cyclops and Diaptomus to a small sphere were measured when moving horizontally, directed towards them, or moving away from them. Two spheres of diameters of 0.8 mm and 1.2 mm were used. Diaptomus generally remain motionless, allow themselves to sink slowly for a while and then jump into a new position. When disturbed by the sphere, Diaptomus escape immediately by making several leaps of up to 1 cm. Cyclops, swimming in the hop and sink pattern, are also capable of escaping by long jumps. Usually, however, they move out of the disturbed region by simply making one or two hops similar to those used in normal swimming. Nevertheless, this escape behaviour can be easily distinguished from normal swimming because the duration of the sinking phase is greatly reduced. It is also important to note that although the direction of escape is random, it is always away from the sphere. The results, summarized in Figs. 14 to 20 show:

- 1) Both Diaptomus and Cyclops can detect a small moving sphere from distances of up to 4 mm. Additionally, escape occurs farther away from the large sphere (1.2 mm) than from the small sphere (0.8 mm) (Fig. 14, 15). A rapid drop from the 90% escape zone to the 50% escape zone is displayed for both species and both spheres, suggesting that certain

Figure 14: Escape probabilities of Diaptomus from a moving sphere. (A) sphere of 1.2 mm diameter, (B) sphere of 0.8 mm diameter, (C) sphere of 1.2 mm diameter in the presence of turbulence. Arrows indicate direction of movement of sphere. Scale=1 mm. Solid line indicates 50% escape probability, dotted line indicates 90% escape probability.

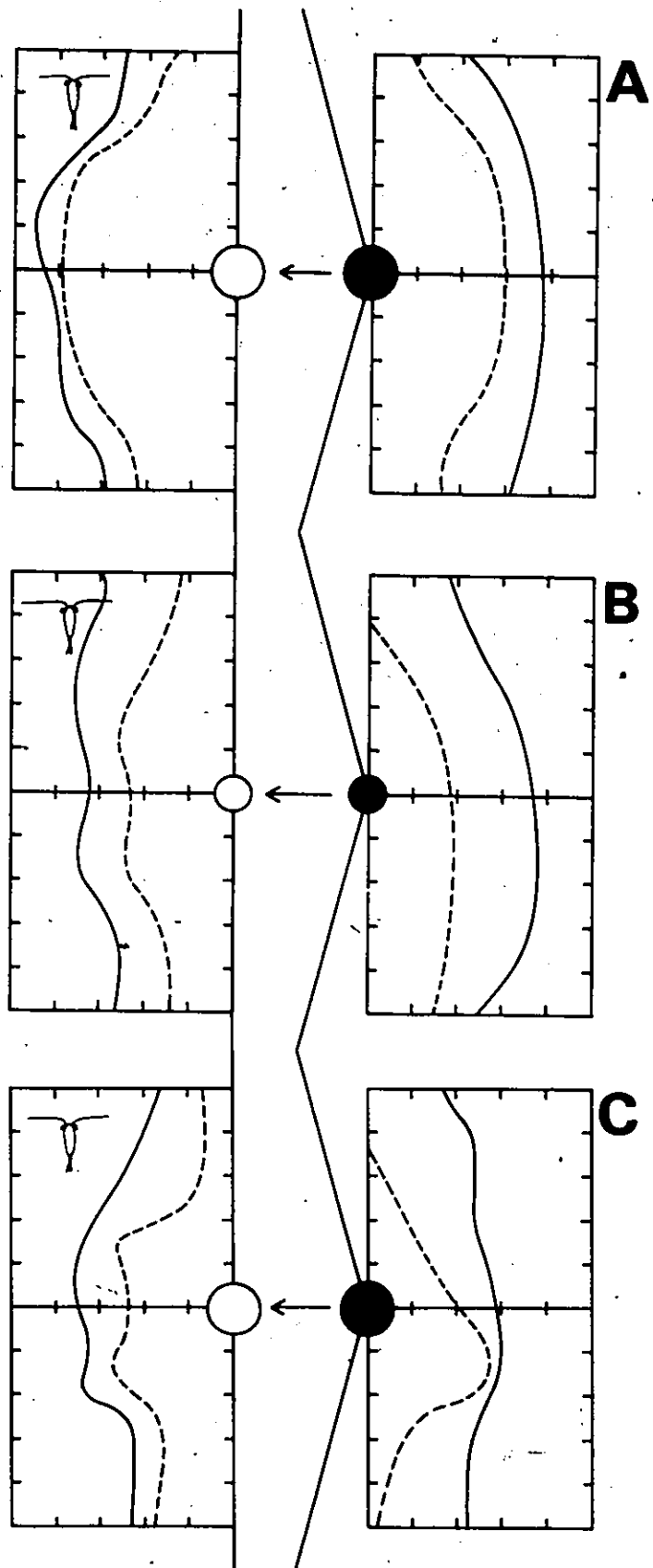
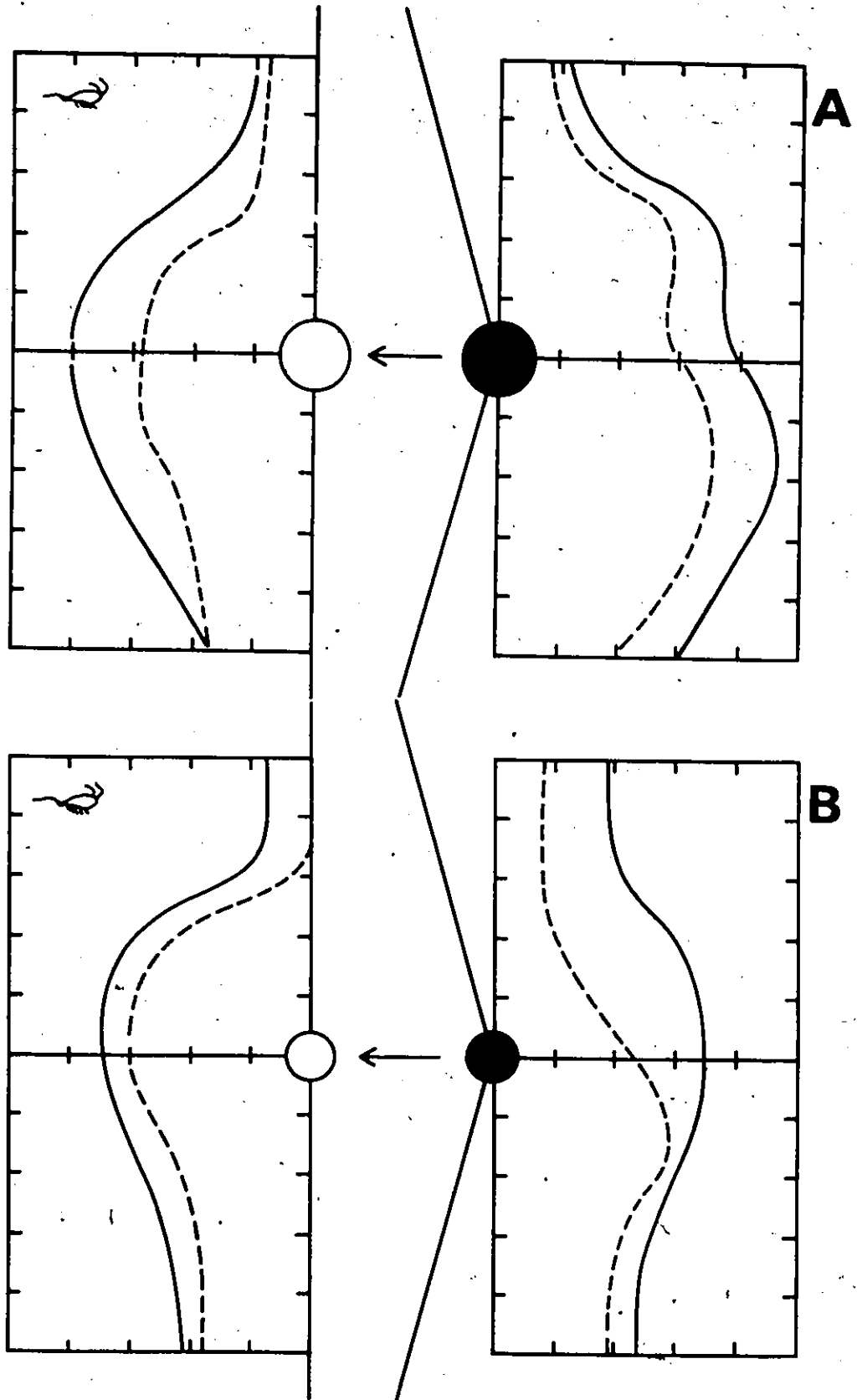


Figure 15: Escape probabilities of Cyclops from a moving sphere. (A) sphere of 1.2 mm diameter, (B) sphere of 0.8 mm diameter. Details see Fig.14



threshold sizes of disturbance are involved in eliciting an escape response.

2) The large sphere elicits more escapes from both Diaptomus and Cyclops than the small sphere (Fig. 16). Moreover, the effect due to sphere size is more apparent in Cyclops than in Diaptomus. Both Diaptomus and Cyclops escape from disturbances over certain threshold sizes. But, because a small signal may mean food for Cyclops, the escape threshold is lower in Diaptomus than in Cyclops.

3) For both Diaptomus and Cyclops the escape probability is higher when the sphere is approaching than when it is retreating (Fig. 17, 18). A swimming animal pushes water ahead of itself and pulls water in to fill the space it previously occupied (van Bergerjk 1964). Moreover, the signal strength of an approaching object increases with time, whereas that of a retreating object decreases with time. Thus the signal of an approaching animal is different from that of a retreating one. For a copepod a potential predator which is coming in imposes a much greater danger than one which is moving away. Strickler (1974) argued that for a copepod the energy needed for an escape reaction is 400 times that for normal swimming. Therefore, it would be adaptive for the animals to recognize and flee only from significant disturbances. In addition, for a predator such as Cyclops an animal which is

Figure 16: Effect of sphere size on the escape probability of (A) Daptomus and (B) Cyclops. Escape probabilities from large sphere (1.2 mm diameter) are always larger than those from small sphere (0.8 mm diameter). Numbers indicate probabilities of significance. Arrows indicate direction of movement of sphere.

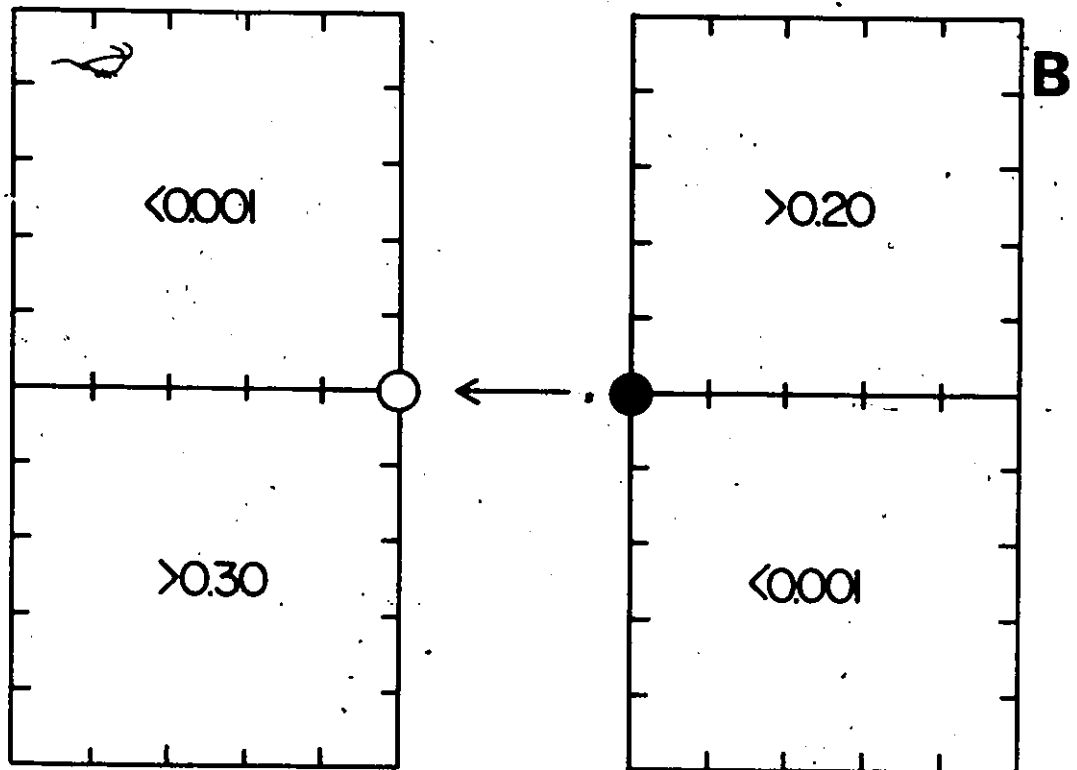
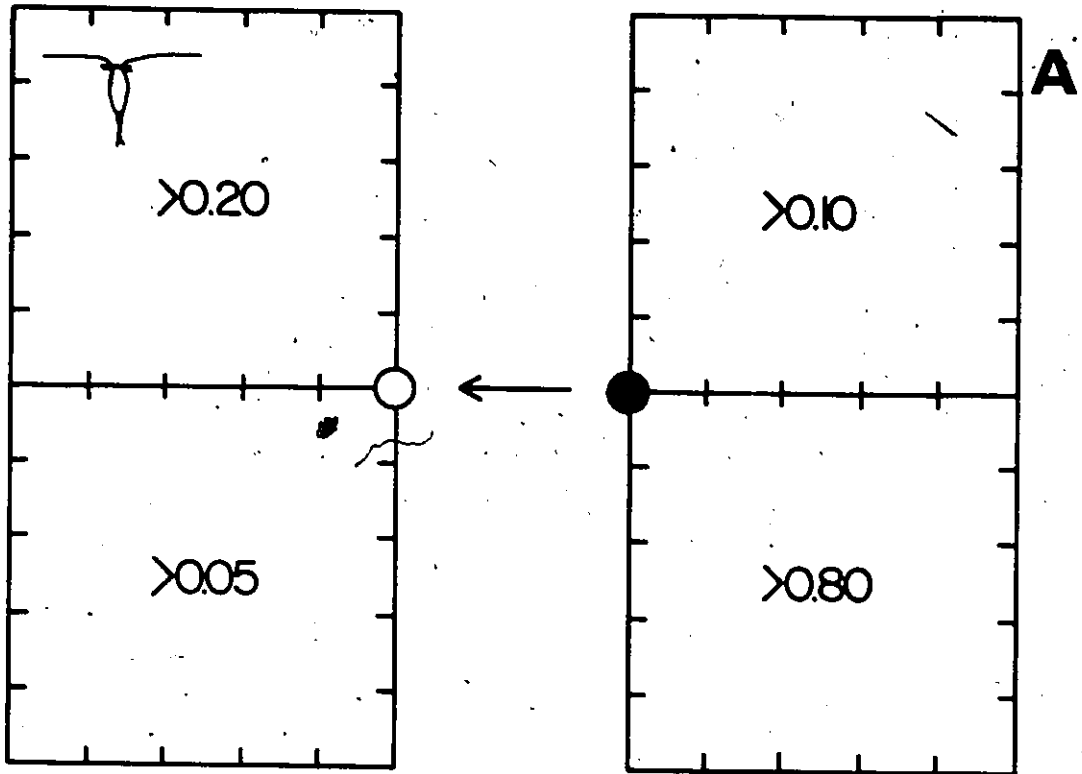


Figure 17: Effect of the location and direction of movement of the sphere on the escape probabilities of Diaptonus. Solid arrows point to situation of higher escape probabilities. Numbers indicate probabilities of significance. (A) sphere of 1.2 mm diameter, (B) sphere of 0.8 mm diameter, (C) sphere of 1.2 mm diameter in the presence of turbulence. Dotted arrows indicate direction of movement of sphere.

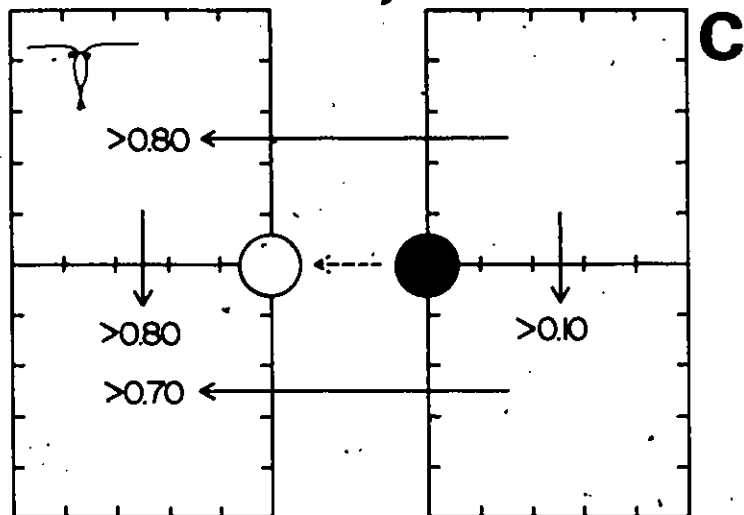
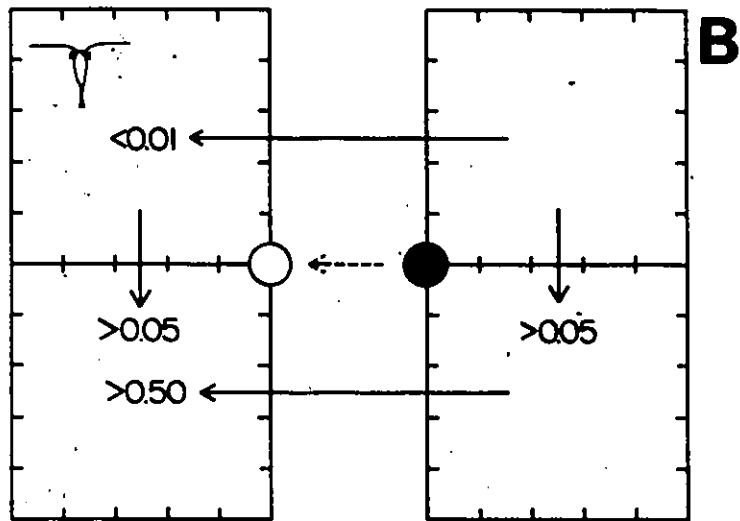
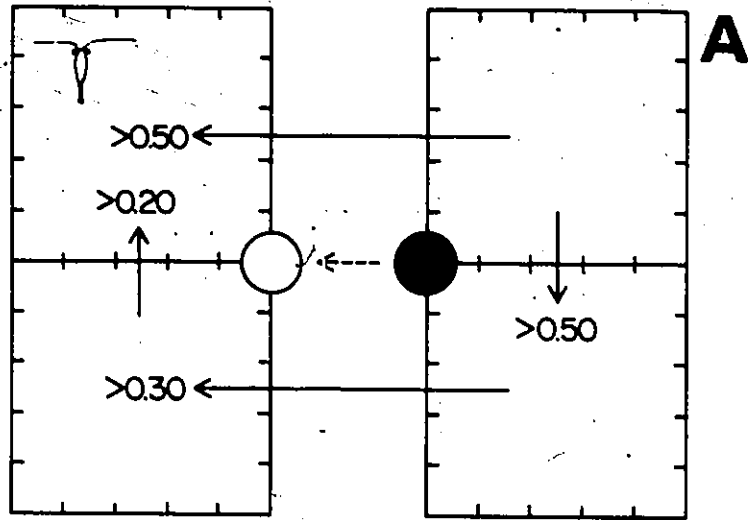
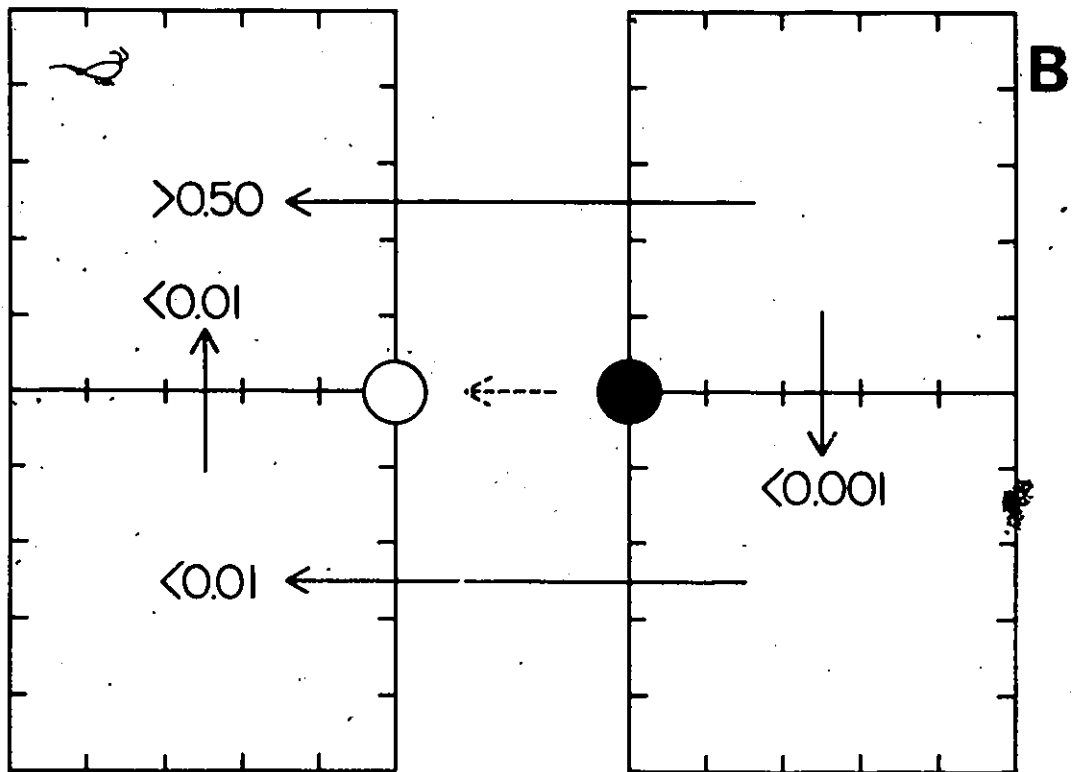
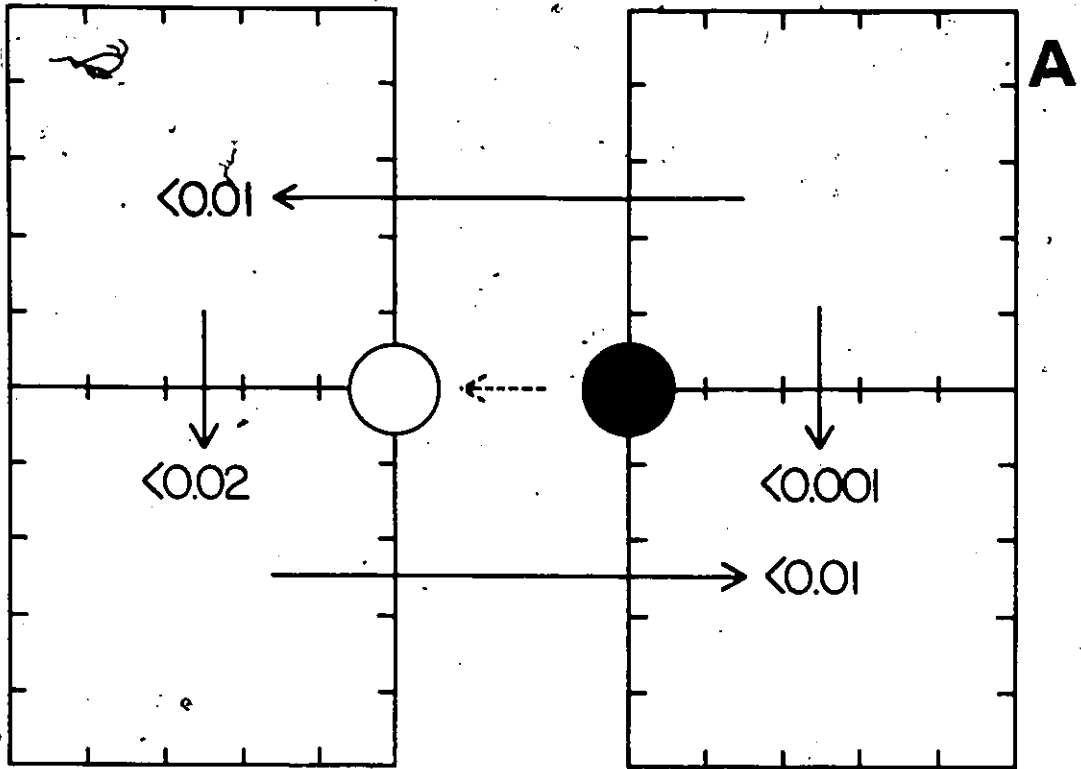


Figure 18: Effect of the location and direction of movement of the sphere on the escape probabilities of Cyclops. (A) sphere of 1.2 mm diameter, (B) sphere of 0.8 mm diameter. Details see Fig.17



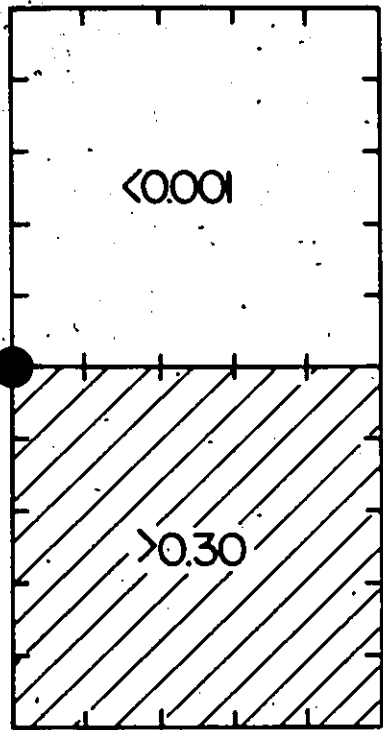
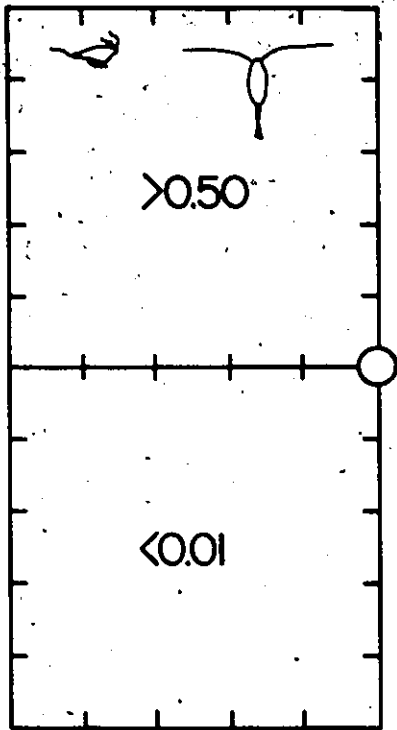
moving away could be a potential prey.

4) Both Diaptomus and Cyclops show higher escape probability when they are below the moving sphere than when they are above it (Fig. 17, 18). Since predatory copepods attack prey from above (Kerfoot 1977a, 1978, Strickler and Trombly 1975), the adaptive importance of this behaviour is obvious. Alternatively, because Cyclops swims with its first antennae pointed upwards (Fig. 3A, Strickler 1974) and Diaptomus hangs vertically right side up in the water, the result could be a bias of the position of the animals.

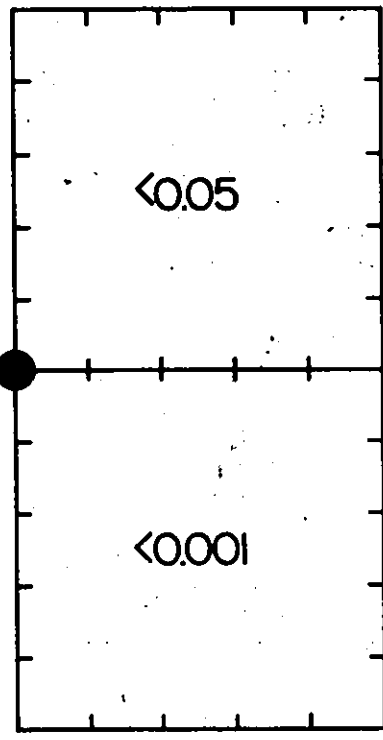
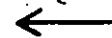
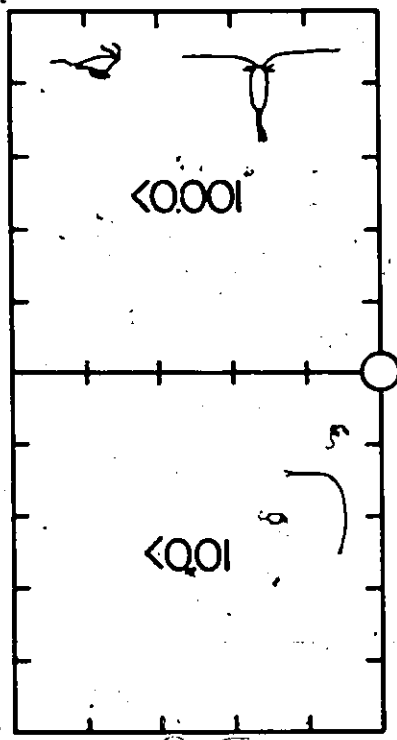
5) The escape probability for both Diaptomus and Cyclops is lowest when the sphere is below them and moving away from them. However, this observation is probably a direct result of the two previously mentioned behaviours.

6) Escape probability for Diaptomus is higher than that for Cyclops (Fig. 19). Diaptomus is a herbivore and its tactic is to flee quickly from all signals over certain crucial sizes. Being a predator, Cyclops, however, must obtain more information from a signal in order to distinguish between predator and prey. Cyclops frequently exhibits the 'stop and listen' behaviour (Gerritsen 1978) before an escape. On several occasions, we have observed that Cyclops attacked

Figure 19: Comparing escape probability of Diaptomus and Cyclops from (A) sphere of 1.2 mm diameter, (B) sphere of 0.8 mm diameter. Numbers indicate probabilities of significance. Arrows indicate direction of movement of sphere. Shaded area indicates the only situation where Cyclops has higher escape probability than Diaptomus.



A

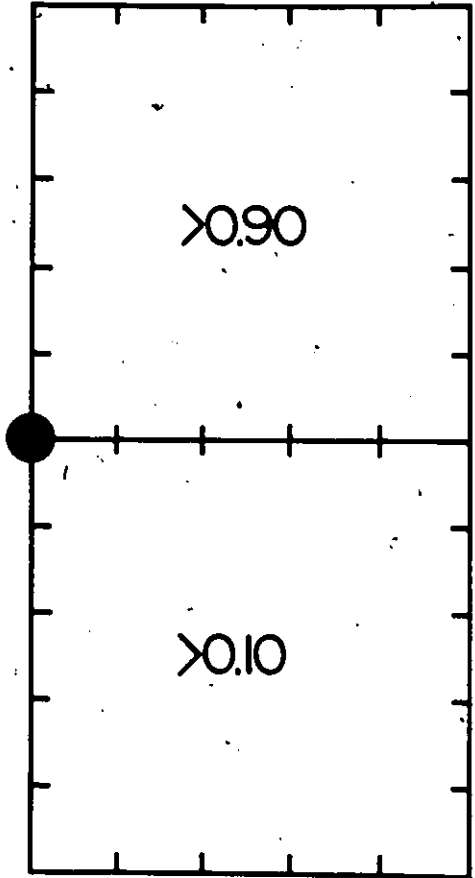
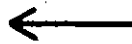
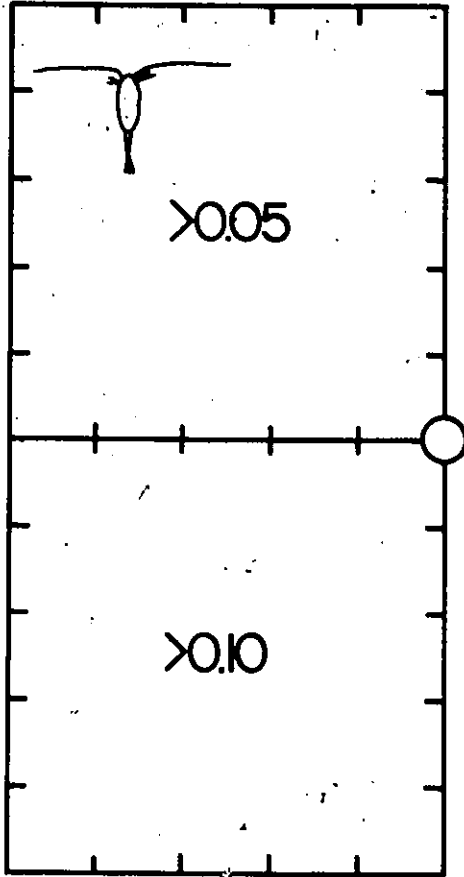


B

and grasped the moving sphere. Since an escape was scored only if it happened as soon as the sphere was triggered to move, escape frequency in Cyclops is probably being underestimated. On the other hand, since Diaptomus has longer first antennae to scan a larger volume of water, it is possible that it has a larger sensory range than Cyclops.

7) The results we have reported so far, and other studies which demonstrate that copepods can react to hydro-mechanical signals (Drenner et al. 1978, Gerritsen 1978, Strickler 1975), were all carried out in calm water. Thus there is still no evidence for believing that the same is true in a lake or ocean where turbulence is continuously created by the transfer of wind and heat energy into the water. To test if copepods can detect the hydromechanical signal of a small moving object against ambient turbulence, the escape probability of Diaptomus to a horizontally moving sphere (1.2 mm) was determined while ambient turbulence was created by bubbling air slowly through the water. The results presented in Fig. 14c show clearly that Diaptomus can detect the moving sphere even in the presence of background disturbances. Furthermore, the escape probabilities in turbulent water are not significantly lower than those in calm water (Fig. 20). This is similar to the results of Taylor (1968) who demonstrated that the sensitivity of crayfish to water displacement produced by moving objects does not decrease in turbulent water.

Figure 20: Effect of turbulence on the escape probabilities of Diaptomus. Sphere of 1.2 mm diameter was used. Numbers indicate probabilities of significance. Arrows indicate direction of movement of sphere.



4.3.2 Predator-Prey Interactions

Although Cyclops avoided the small moving spheres, they frequently attacked and grasped the hairs that the spheres were attached to. Kerfoot (1977a) pointed out that the attack probability of Cyclops on Bosmina is size dependent and the predators avoid Bosmina over certain crucial sizes. These observations suggest that copepods avoid hydromechanical signals over certain sizes and recognize small signals as prey. The consequence of this is that a potential prey may release fewer signals, thereby decreases the probability that it will be detected by a predator. Indeed, copepod nauplii suffer low mortality from Chaoborus (Gerritsen 1979) and Epischura (Chapter 1) because they remain motionless. Following an unsuccessful attack by a copepod, Bosmina lowers the probability of being recovered by the predator by stopping swimming and sinks passively (Kerfoot 1977a, 1978, Zaret and Strickler 1976). When hair tethered Bosmina was introduced into a chamber with starved Cyclops, detection by the predator occurred only when the Bosmina flapped its antennae (J.R. Strickler, per. comm.). Moreover, when attacked, Bosmina tucked its antennae, but continued to move the filtering legs. Since movements of the filtering legs probably do not cause as much disturbances as flappings of the antennae, it is obvious that the entire behaviour pattern of Bosmina serves to reduce the hydromechanical signal and not the chemical or visual signals. How-

ever, since Cyclops locates and eats other dead zooplankters, chemoreception may also be involved in prey detection. But because chemicals diffuse slower than the speed of a swimming copepod (Strickler 1975), chemoreception is probably used only for prey detection at very close range and for prey recognition after contact. Nevertheless, the fact that Cyclops will attack small inert objects such as a hair indicates clearly that chemicals are not required to elicit attack behaviour in Cyclops.

It is clear that a major concern for a prey is to escape detection by predators. Epischura and Cyclops detect Bosmina long before the prey becomes aware of the predator (Kerfoot 1978). Other zooplankton prey, however, can perceive a nearby predator and avoid it by swimming away. Diaptomus, which has a larger sensory range than Cyclops, may perceive the predator and initiate evasive reactions before the predator can launch an attack. So, it is easy to see that the predators have a problem rather similar to that of their prey--they must release few signals and be less detectable to potential prey. High speed movies of Cyclops attacking Bosmina (J. R. Strickler), reveal that the predator senses the prey while in the sinking phase of the hop and sink swimming pattern. A sinking Cyclops causes so little disturbances that a Bosmina usually will not react by performing the dead-man-response until the predator actually touches it. Also, the large disturbances associated with

the hopping movement of Cyclops would probably mask the small disturbances produced by a Bosmina from a distance. Taylor (1968) reported that the response to water vibration by crayfish is physiologically inhibited when the animal is moving the walking legs. A similar relationship may exist in Cyclops.

The behaviour of the animals is reflected further by the anatomy of their sensory systems. The ratio of mechanoreceptors to chemoreceptors in the first antennae of the herbivorous Diaptomus oregonensis and D. minutus is close to 1:1, whereas that for the carnivore Cyclops vernalis is almost 10:1 (Y. Barrientos, per. comm.). Herbivorous copepods perceive algae by chemoreception (Alcaraz et al., 1979, Friedman and Strickler 1977). Therefore, Diaptomus needs chemoreceptors for locating algae and mechanoreceptors for detecting predators. Cyclops, on the other hand, can rely on its mechanoreceptors to detect both predators and prey.

Chapter V

CONCLUDING DISCUSSION

Most research on predator-prey interactions in the freshwater ecosystem has suggested that size is the most important factor in prey selection by predaceous zooplankters (Anderson 1970, Brandl and Fernando 1975, 1978, Confer 1971, McQueen 1969). Size selective predation has been considered critical in determining the size composition of the freshwater zooplankton communities (Allen 1973, Brooks and Dodson 1965, Kerfoot 1975a). However, recent studies, most particularly those of Dodson (1974b), Kerfoot (1977a, 1978) and Li and Li (1979) have demonstrated that prey characteristics such as swimming behaviour, carapace thickness, and shape are also important in determining the selective process.

Chapter 1 of this thesis examines the predatory behaviour of Epischura lacustris. The predation rate is very heavy on Bosmina, moderate on Ceriodaphnia, and very low on Diaptomus. However, in this instance equating the predator's nonrandom diet to the predator's food preference makes no sense. Epischura shows no true behavioural inclination for one of the prey. Rather, it attacks all the prey it can detect, and the nonrandom diet is a result of the differences in the effectiveness of prey defenses. Kerfoot et al.

(1979) classified prey defenses against invertebrate predation into primary (pre-capture) and secondary (post-capture) responses. Copepods sense other animals by mechanoreception (Strickler and Bal 1973). Thus a prey which causes little disturbances has a low encounter rate with the predators. Indeed, my results show that Diaptomus nauplii, which do not move much, experience lower predation rates from Epischura than copepodites which are larger, faster, and move more often. Many small cladocerans (e.g. Bosmina, Chydorus) make themselves less detectable by performing the dead-man response (Kerfoot 1978). For animals which depend on fleeing rather than on crypsis, the earlier the detection of the predator the higher the probability of escape. Detection ability increases with the number of detectors. While cladocerans have few sensory organs over their thick carapace, the exoskeleton of copepods is covered by chemo- and mechanoreceptors (Kerfoot et al. 1979). Both cyclopoid and calanoid copepods can sense a predator from distances up to 4 mm. Because copepods have a greater sensory range than cladocerans, during an encounter the copepod predator will sense the cladoceran prey before the prey is aware of the predator. Strickler (1974) found that copepods can escape at speeds of up to 20 cm/s. On the other hand, most cladocerans have limited locomotory abilities, and cannot outrun or outmaneuver an attacking copepod (Kerfoot 1978, Kerfoot et al. 1979). Thus it seems obvious that cladocerans which

cannot utilize escape response to avoid a copepod predator must rely heavily on secondary responses to reduce the ingestion probability once they are captured. Slow-moving cladocerans (e.g. Bosmina, Chydorus) are adorned with a thick chitinous exoskeleton. In some forms (e.g. Daphnia, Bosmina) the exoskeleton is further reinforced by the development of spines and stout protuberances. Daphnia develops helmets and spines to hinder handling by invertebrate predators (Dodson 1974b, O'Brien et al. 1979). In places where predatory calanoid copepods are common, Bosmina develops an enlarged mucral spine and larger antennules (Kerfoot 1975a, 1977a, O'Brien 1979b). In Pinks Lake, Bosmina undergoes increase in mucral spine length during the summer at a time when the adults of Epischura appear. Since Bosmina showing this cyclomorphic change are less susceptible to Epischura predation than similar-sized individuals without the adaptation, my results are consistent with Dodson's (1974b) hypothesis that cyclomorphosis is an adaptation against invertebrate predation. Selection clearly has not favoured the development of secondary-morphological defenses in copepods since they rely on early detection and rapid evasion to reduce the efficiency of the predators. This explains why copepods are invariant in body shape (Kerfoot et al. 1979) and why cyclomorphosis in copepods is not as conspicuous as that in cladocerans.

Although prey defense mechanisms co-evolve with predator hunting strategies (Gilbert and Raven 1975), it is wrong to assume that every prey will acquire defense mechanisms to protect it totally from predation. Any individual animal must maximize its reproductive success, but it can do it in many different ways and some are more efficient than others. Evolving defense mechanisms against predator is only one of the ways. In addition, the development of any prey defense device may incur appreciable costs and influence the life history of a species. For instance, in Bosmina the development of protective defenses against copepods results in decreased brood sizes and reduced competitive ability (Kerfoot 1977b). Similarly, the life history of a species may determine whether natural selection will favour a particular defense mechanism or not. The copepodites of Cyclops and Diaptomus are susceptible to Epischura predation during the summer. In both cases natural selection has favoured escape strategies that minimize encounter with the predator. Cyclops escapes by going into diapause (Strickler and Twombly 1975), whereas Diaptomus speeds up growth to reduce the duration of the vulnerable copepodite stages. Future studies should consider the role of life history variables, which has been ignored in most studies (exception, see Lynch 1980), as the determining factor in the evolution of predator-hunting strategies and prey defense mechanisms.

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