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# ABSTRACT

Investigations on predation in natural communities indicate that predators are not all equal in their impact on ecosystems. Accidental and experimental perturbations of ecosystems suggest that top predators control the structure of communities. That appears to be true in fresh-water lakes, where planktivorous fish determine the size structure of planktonic communities without affecting biomass or the utilisation of this biomass. Among the small invertebrate carnivores of Heney Lake, Quebec, only the water mite _Piona constricta_ lacks a predator. As a result that particular species provides an ideal tool (1) to compare the role of small invertebrate and large vertebrate predators in the community, and (2) to assess the importance of trophic position in that regard.

The experimental work consisted of manipulating densities of the water mite _in situ_ to compare community response in enriched and non-enriched systems. To this end, twelve enclosures of 8000 litres in capacity were used to isolate water columns 10 meters in depth; four were kept as controls, while water mite densities were doubled in four others and tripled in the rest. The responses of the phytoplankton and zooplankton populations were followed for six weeks.

The initial enrichment resulted in a seven-fold average difference in water mite densities between the manipulated and control enclosures. Water mites were found to have a selective impact on herbivore biomass as four populations of zooplankters were significantly decreased by the enrichment. This results from differential escape abilities of the prey rather than from active selection by the mites. While water mites are found at relatively low densities, they have high predation rates per capita so that their cropping rate on zooplankton is comparable to that of most other invertebrate predators of the pelagic zone of lakes.

The reduction in herbivore densities resulted in increased phytoplankton volume, due to lowered grazing pressure on the edible algal fraction. Small but significant increases in inedible phytoplankton species richness were registered, likely due to shifts in nutrient availability following changes in phytoplankton volume. The results indicate that, in Heney Lake, invertebrate predators regulate zooplankton densities directly and phytoplankton volume and size structure indirectly. Community structure determines the extent to which water mites regulate the phytoplankton assemblage; if the phytoplankton is composed of a large fraction of small algae exploited by the herbivores, invertebrate predation will have an impact on the whole system. On the other hand, when large algae dominate the phytoplankton, the impact of the predator will be limited to regulating its prey.

Although Piona constricta plays a role in regulating plankton populations when the system is near equilibrium, major changes brought on by large shifts in nutrient availability override the impact of the mite.

Such results indicate that, although small invertebrate predators consume a very large proportion of the zooplankton production, their density is highly dependant on the presence of adequate prey, and therefore, on the size structure of the zooplankton assemblage. The latter is largely determined by the abundance of large vertebrate predators.

The trophic position of an invertebrate carnivore does not seem to determine the extent of its impact on the community but has implications for energy flow, since water mites, as top predators, reduce the zooplankton production available to planktivorous fish and fish larvae.

# RESUME

Nombre d'études sur le rôle des prédateurs en milieu naturel ont établi que l'impact de ceux-çi sur leurs systèmes n'est pas toujours semblable d'une espèce à l'autre. Les perturbations d'écosystèmes, qu'elles soient accidentelles ou expérimentales, suggèrent que la structure des communautés est controlée par les "top" prédateurs. Ainsi dans les lacs, ce sont les poissons planktivores qui déterminent la structure des communautés planktoniques, pour ce qui concerne la taille des organismes, sans affecter toutefois la biomasse ou l'utilisation de celle-çi. Parmi les petits invertébrés carnivores du Lac Heney, situé au Québec, seule la mite aquatique *Piona constricta* n'a pas de prédateur. Aussi cette espèce représente-t-elle un outil idéal pour (1) comparer le rôle des petits invertébrés et des vertébrés dans la communauté, et (2) pour évaluer l'importance de la position trophique sur ce plan. L'expérience consista à manipuler les densités de la mite *in situ* de façon à comparer les communautés enrichies à celles non-enrichies. A cette fin, douze enceintes de 8000 litres furent utilisées pour isoler des colonnes d'eau de 10 mètres de profondeur; quatre enceintes furent maintenues comme témoins, tandis que les densités des mites furent doublées dans quatre autres enceintes et triplées dans les quatre restantes. Ensuite les populations de phytoplankton et de zooplankton furent échantillonnées pendant six semaines.

L'enrichissement initial donna lieu en moyenne à des densités de mites sept fois plus élevées que les valeurs témoins. Les mites eurent un impact sélectif sur les herbivores puisque quatre populations de zooplankton furent réduites de manière significative suite à l'enrichissement. Ceci est du aux différences existant au niveau de la stratégie défensive des proies plutôt qu'à une sélection active des mites. Bien que les densités de mites soient faibles, leur taux de prédation par individu est élevé, si bien que le taux de consommation de zooplankton par la population de mites est semblable à celui d'autres prédateurs invertébrés de la zone pelagique des lacs.

La réduction des densités d'herbivores entraîna une augmentation du volume de phytoplankton, due à une réduction du broutage sur les algues comestibles. L'augmentation faible mais significative du nombre d'espèces de phytoplankton non-comestible est probablement due à un changement de la disponibilité des éléments minéraux suite à la hausse du volume de phytoplankton. Les résultats indiquent qu'au Lac Heney, les prédateurs invertébrés réglent directement les densités du zooplankton, et indirectement le volume et la structure du phytoplankton. La structure de la communauté détermine l'impact des mites sur le phytoplankton. Lorsque

celui-çi consiste essentiellement en algues comestibles exploitées par les herbivores, le prédateur aura un impact sur tout le système. Par contre, lorsque les algues non-comestibles dominent, l'impact sera limité aux herbivores.

Bien que *Piona constricta* joue un rôle dans la regulation des populations planktoniques quand celles-çi sont relativement stables, l'impact des mites est minime lorsque des changements majeurs ont lieu au niveau des éléments minéraux.

Bien que les prédateurs invertébrés consomment une proportion importante de la production du zooplankton, leur densité est fortement liée à la présence de proies adéquates, et ainsi à la composition du zooplankton, pour ce qui concerne la taille des organismes. Celle-çi est déterminée en grande partie par l'abondance de prédateurs vertébrés.

La position trophique d'un carnivore invertébré ne semble pas déterminer l'impact qu'il aura sur la communauté mais est importante pour le flux d'énergie. Ainsi la mite en tant que "top" prédateur, réduit la production de zooplankton disponible pour les planktivores et pour les larves de poissons.

# ACKNOWLEDGEMENTS

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## CONTENTS

## LIST OF TABLES

# LIST OF FIGURES

# Chapter I

# INTRODUCTION

## 1.1 PREDATION

Consumption of one organism by another for growth, metabolism and reproduction is the fundamental interaction in ecological systems. Indeed the network of all predator-prey links in a given environment will define the biological community of that environment. While the number and relative position of the links determine food web structure, the rate and direction of energy flow is a function of the intensity of interaction. Understanding the components of predation and their relation to community structure has now become a major goal of ecology.

Historically, interest in predation was stimulated by the observation of regular predator-prey cycles in nature and the potential for biological control of certain pest species by their predators. The first attempts to interpret predator-prey interactions mathematically are attributed to Lotka (1925) and Volterra (1926). Their early models exhibited neutral limit cycles where predator and prey populations oscillated indefinitely with an amplitude determined by the initial densities of the predator and the prey populations. If these models were innovative, they lacked realism in several ways. First, regular oscillations are more the exception than the rule in nature (Tanner 1975). Secondly, their equations did not incorporate density-dependant prey growth and assumed that prey capture and predator growth were a linear function of population density. Through greater realism and complexity, later models (Rosensweig and MacArthur 1963, Maynard Smith 1974, Hassel 1978) adequately described the behavior of simple predator-prey interactions. However, those remained limited in scope.

Holling (1963) took a more realistic approach which originated from his interest and experience in pest management. Using experimental component analysis, he identified the basic components of the functional response of predators to prey density, and determined how hunger,learning, inhibition by prey, interference between predators or avoidance by learning prey modified the response (Holling 1965, 1966). This approach has provided important insights on the outbreaks of certain insect pests (Peterman <u>et al</u>. 1979), the decline of commercial fish stocks (Peterman 1977), and human-host parasite systems (May 1977).

Unfortunately such models can only handle systems consisting of a small number of species and do not generate information about whole system behavior. Comprehension of the role of predation in community regulation and structure clearly requires a manipulative approach. Already the perturbation of natural ecosystems by accident or experimentation has yielded large amounts of information about the role played by certain species in the wild. Man's ability to inflict important damages on natural communities has given ecologists an opportunity to observe the response of ecosystems to stress.

For example, intensive selective fishery in the Great Lakes resulted in major changes in the fish stocks over the last 100 years. Heavy exploitation of lake sturgeon, lake trout, herring and whitefish accompanied by the introduction of the sea lamprey in the Great Lakes has led to the decline of these populations while chub, carp, smelt and alewives became the dominants in the system (Smith 1968).

Following the introduction of the ciclid, *Cichla ocellaris*, a native of the Amazon River, in Gatun Lake (Panama), the trophic structure of the lake community underwent major changes (Zaret and Paine 1973). The cyclid, now the top predator in the system, successfully invaded the whole lake and eliminated six of the eight native fish species. This in turn altered the zooplankton community structure, increased the population density of mosquitos and decreased that of fish-feeding birds.

The major role of predation in structuring intertidal communities is also well-known. Through bio-manipulations Paine (1966) demonstrated how a top predator, *Pisaster* ochraceus, can promote species diversity in an ecosystem. Following the removal of this sea star from a section of shoreline in the state of Washington, the intertidal zone became dominated by the mussel Mytilus californianus, the preferred prey of the starfish, at the expense of several other invertebrates that were ultimately excluded. These results were confirmed by the work of Lubchenco and Menge (1978) who found that predation by starfish and gastropods was the dominant interaction structuring the low intertidal zone community.

Sea otters (Estes et al. 1978, Duggins 1980) and lobsters (Breen and Mann 1976) are known to promote very diverse and productive kelp-dominated subtidal communities through intense predation on sea urchins. In this case the over-exploitation of the top predators has led to the complete elimination of most of the macrophyte beds and associated fauna by an exploding sea urchin population.

In the last twenty years numerous studies on lake plankton systems have demonstrated how fish predation is a very strong structuring agent of the zooplankton assemblage. Brooks and Dodson (1965) noted that lakes with the alewife Alosa pseudoharengus contained only small species of zooplankton while lakes without the fish had populations of large species. Following the introduction of alewife in a lake, the modal size of the zooplankton went from 0.784 mm to 0.285 mm. This indicates that Alosa selects prey of large size and thus determines zooplankton species composition.

In a similar vein Galbraith (1967) found that the introduction of rainbow trout in a lake resulted in the elimination of the largest Daphnia species along with a reduction of the average size of the zooplankton. Hall and his coworkers (1970) added fish to fishless ponds and followed the response of the zooplankton community. Although the fish had no effect on total biomass, they had profound effects on the diversity and size distribution of the plankton.

Such results suggest that predators at the top of food webs are the dominant structuring element in the community while the other predators play relatively minor roles. This may be a function of certain topological and dynamical properties of food webs , that is, the relation between feedback loop configuration and community stability. Or it may be a function of differential interaction strength; in other words, predators which shape communities may be simply those that are very large with respect to their prey and can thereby remove prey at high rates. Only through the selective manipulation of "target" species within a known food web can one determine the relative roles played by these factors.

This study will focus on top predators. It will compare the relative importance of small invertebrate and large vertebrate top predators in shaping the structure of lake plankton communities. This particular system offers several advantages: a) in a lake, whole communities can be isolated and experimentally manipulated with relative ease; b) the response time of the system is a matter of weeks, rather than years, due to the very short generation time of planktonic organisms; and c) a considerable amount of information is available on the feeding relationships of lake organisms.

## 1.2 LAKE PLANKTON COMMUNITIES

### 1.2.1 Predators of lake plankton

Since the early findings of Hrbacek (1962) that the size of zooplankton species in freshwater lakes or ponds is an inverse function of fish stock, the ability of planktivorous fish to structure zooplankton communities has been widely documented (e.g., Brooks and Dodson 1965, Galbraith 1967, Hall et al. 1970). In the absence of fish, other vertebrate planktivores such as salamanders (Dodson 1970) and birds (Dodson 1979) can play a similar role in structuring pond communities.

The other carnivores of the planktonic food web of lakes are microcrustaceans. These invertebrate predators probably play an important role in regulating community metabolism. In this respect investigators have focused their attention on the feeding behavior, mechanism, rate and selectivity of invertebrate predators, both in the laboratory (Fryer 1957a, 1957b, Mordukhai- Boltovskaia 1958, Confer 1971, Confer and Cooley 1977, Brandl and Fernando 1974, 1978, Kerfoot 1978) and in the field (Cummins _et al_. 1969, Anderson 1970, Fedorenko 1975a, 1975b, Brandl and Fernando 1979, Jamieson 1980, Kerfoot and Peterson 1980, Pastorok 1980, Williamson and Gilbert 1980). These investigations have isolated the components of the predation process and their impact on individual prey. However, because of the multidimensionality of real food webs, one cannot infer from simple cause and effect relationships the role played by predatory invertebrates in plankton community metabolism.

An alternate approach has been to apply multivariate statistical procedures on extensive field data. However, this approach has so far yielded more information about the physical and chemical characteristics of lakes than about their biology (Sprules 1977, 1980).

These studies have provided valuable information on the role played by invertebrate predators in determining the relative abundance of zooplankton species. To understand how invertebrate predators affect the whole system, experimental manipulations are required. Only by manipulating densities of invertebrate predators _in situ_ can one observe the response of all the components in the system and evaluate the importance of invertebrate predators in food-web dynamics. Very little has been accomplished in this regard, except for the recent manipulations of larvae of the phantom midge <u>Chaoborus</u> in an oligotrophic lake (Neill and Peacock 1980, Neill 1981), that have indicated that <u>Chaoborus</u> has relatively little impact on zooplankton community structure.

### 1.2.2 Heney Lake plankton community structure

The food-web of the pelagic zone of Heney Lake, Quebec, is described in figure 1. Although the lake is known to harbour over 25 species of fish (Faber 1982), only five are residents of the pelagic zone. The top predators are lake char and Northern pike, but it must be stressed that they are only occasional residents of the pelagic zone studied. The latter species is more closely associated with the weed beds of the littoral zone and the former, is only rarely found in the shallower basin of the lake (Delisle 1969) where the present study takes place.

The three other fish species represented are voracious planktivores that are present in the pelagic zone most of the year. They will be joined at certain times by the planktivorous life stages of littoral and benthic fish species (Scott and Crossman 1973). These planktivores may be responsible for maintaining the size structure of the zooplankton assemblage by preventing colonization by the larger species more susceptible to size-selective predation. The zooplankton species present in the pelagic zone are small and characteristic of lakes subjected to medium to high intensities of planktivorous predation pressure (Zaret 1980). The other carnivores in the system are invertebrates. Those are all subject, in varying degrees, to fish predation except for the water mite Piona constricta.

Of the 2800 species of water mites identified so far (Pieczynski 1976) almost all inhabit either ponds, streams or the littoral zone of lakes. Very few species have ever been regarded by limnologists as being associated with the pelagic zone of lakes (Hutchinson 1967). However, the recent work of Gliwicz and Biesadka (1975) on the water mite Piona limnetica in Madden Lake, Panama, has clearly showed the importance of this species in the pelagic zone, both in terms of population size and impact on the zooplankton community. Riessen (1980, 1981, 1982) has established that Piona constricta resides in the pelagic zone of Heney Lake and uses the zooplankton as its food source.

Both investigators emphasized that, thanks to peculiar adaptations, those water mites are not accidental plankters. Thus, Piona limnetica and P. constricta both have swimming setae on their legs that widen and flatten towards their distal ends, in order to increase swimming efficiency. P. constricta exhibits diel vertical migration which is probably an adaptation to maximize contact with cladoceran prey that follow the same migration pattern (Riessen 1980). Further, P. constricta has a life history pattern distinct from most other hydracarinids, which might be an adaptation to the pelagic environment (Riessen 1982). In the sequence from egg to adult, only the nymphs and adults are active predators. In most species the larvae search out an insect host which will serve as a food source and an agent of dispersal. In P. constricta the larvae do not need a host to develop successfully to the nymphal stage. This modification of the typical life history pattern has freed the mites from the need to find a littoral host species. The evidence thus indicates that certain water mites are true pelagic inhabitants.

Rejection of water mites by both invertebrate and vertebrate predators has long been recognized (Elton 1922, Cloudsley-Thompson 1947). In reviewing the ecology of water mites, Pieczynski (1976) concluded that they contribute very little to the food of invertebrate predators and fish in spite of reaching densities of thousands per m³. The share of water mites in the food of three species of fish, the tench, the carp and the crucian carp, represented less than 2% of the food biomass and was probably ingested accidently (Pieczynski and Prejs 1970). P. constricta is rejected by the planktivorous banded killifish Fundulus diaphanus (Riessen 1981), and its close relative, the pelagic water mite Piona limnetica has no known predator in Madden Lake, Panama (Gliwicz and Biesadka 1975). Elton (1922) was the first to suggest that the bright colours of some species of water mites may be related to their unpalatability. Although P. constricta is not brightly coloured but rather dark brown, it can be easily recognized by fish and thus avoided. Kerfoot (1982) demonstrated that fish rapidely learned to avoid mites as a food source. One may then conclude that P. constricta is probably devoid of any predator in the pelagic zone of Heney Lake.

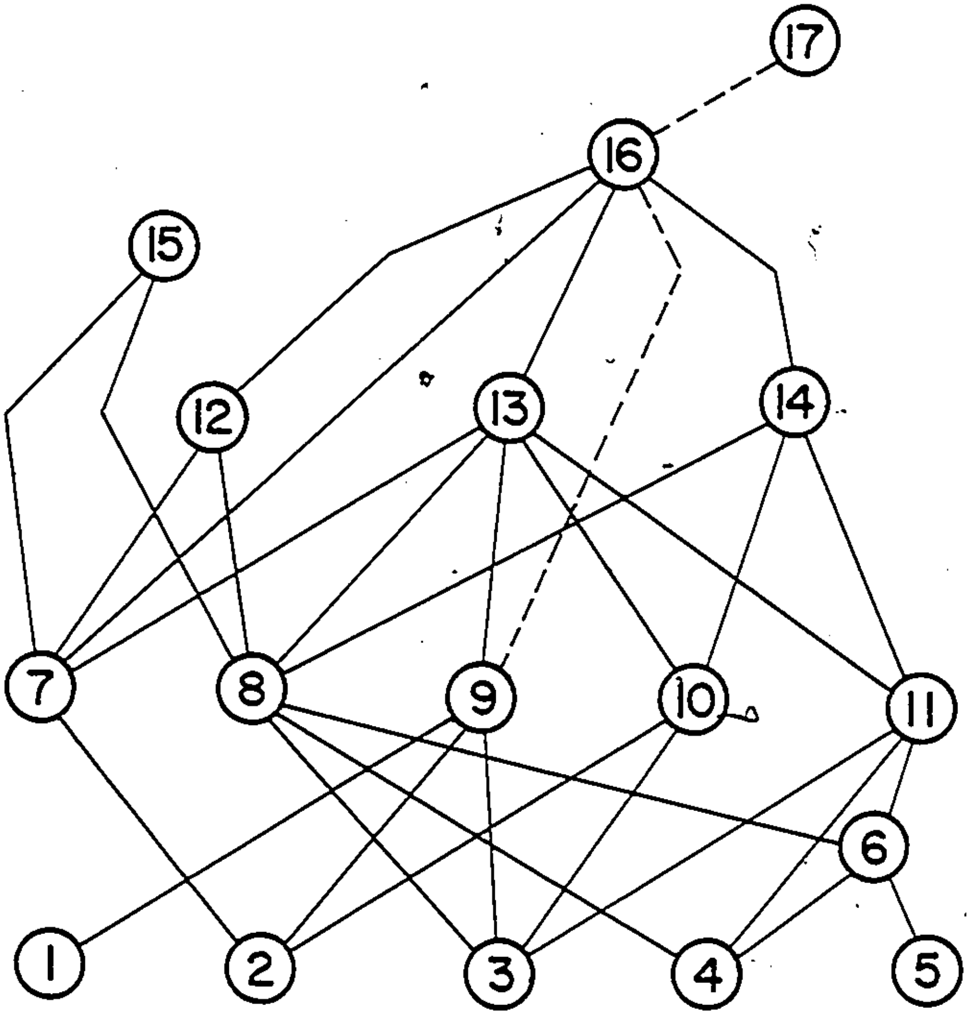
Thus, the mite Piona constricta appears remarkable in at least two respects: it is a true inhabitant of the pelagic zone of Heney Lake, and an invertebrate top predator. This makes it a highly suitable tool for this study which has two main objectives: (1) to compare the impact of an invertebrate predator on planktonic community structure to that of vertebrate planktivores, the presumed dominant structuring agent; (2) to assess the relative importance of trophic position, by comparing the impact of the invertebrate top predator in the system to the other invertebrate predators.

Labelling code:

(1) phytoplankton cells >30 um
(2) phytoplankton cells 10-30 um
(3) phytoplankton cells <30 um
(4) particulate organic matter
(5) dissolved organic matter
(6) bacteria
(7) Daphnia galeata mendota
D. retrocurva
Diaphanosoma leuchtenbergianum
Ceriodaphnia lacustris
(8) Bosmina longirostris
Chydorus sphaericus
Tropocyclops prasinus mexicanus
(9) Diaptomus (2 sp.)
(10) copepodites
(11) rotifers and copepod nauplii
(12) Leptodora Kindtii
(13) Chaoborus
(14) Epischura lacustris
Mesocyclops edax
Acanthocyclops vernalis
(15) Piona constricta
(16) Osmerus eperlanus mordax
Coregonus artedii
Coregonus clupeaformis
planktivorous life stages of littoral and benthic fish species
(17) Salvelinus namaycush
Esox lucius

Dotted lines represent probable but weak interactions.

Figure 1: Food web of Heney Lake pelagic zone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# Chapter II

# MATERIALS AND METHODS

## 2.1 HENEY LAKE

Heney Lake is situated in the province of Quebec (46°02' N, 75°55' W), approximately 100 kilometers north of Ottawa. This is a hardwater lake of low nutrient levels, with concentrations of $PO4^{3-}$ lower than 1 ug/l (Briand _et_ _al_. 1978). The pH varies between 7.8 and 8.8, and the hypolimnion is never anoxic, with oxygen concentrations rarely lower than 5 ppm (McCauley 1978).

Heney Lake exibits a phytoplankton successional pattern typical of northern temperate lakes of mesotrophic status. This pattern has been described by Wall (1980) and consists of three major biomass peaks: two diatom maxima, in spring and fall, and one blue-green maximum in late summer. The diatom biomass peaks are dominated by _Asterionella_ _formosa_, while the blue-green maximum is mostly the result of blooms of _Aphanizomenon_ _flos-aquae_ and species of the genus _Anabaena_. The chlorophytes, chrysophytes, cryptophytes and dinoflagellates contribute only a small percentage -about 30%- to total phytoplankton biomass, reaching their maximal seasonal highs in late spring, early summer and after the fall diatom maximum.

## 2.2 ENCLOSURES AND MANIPULATIONS

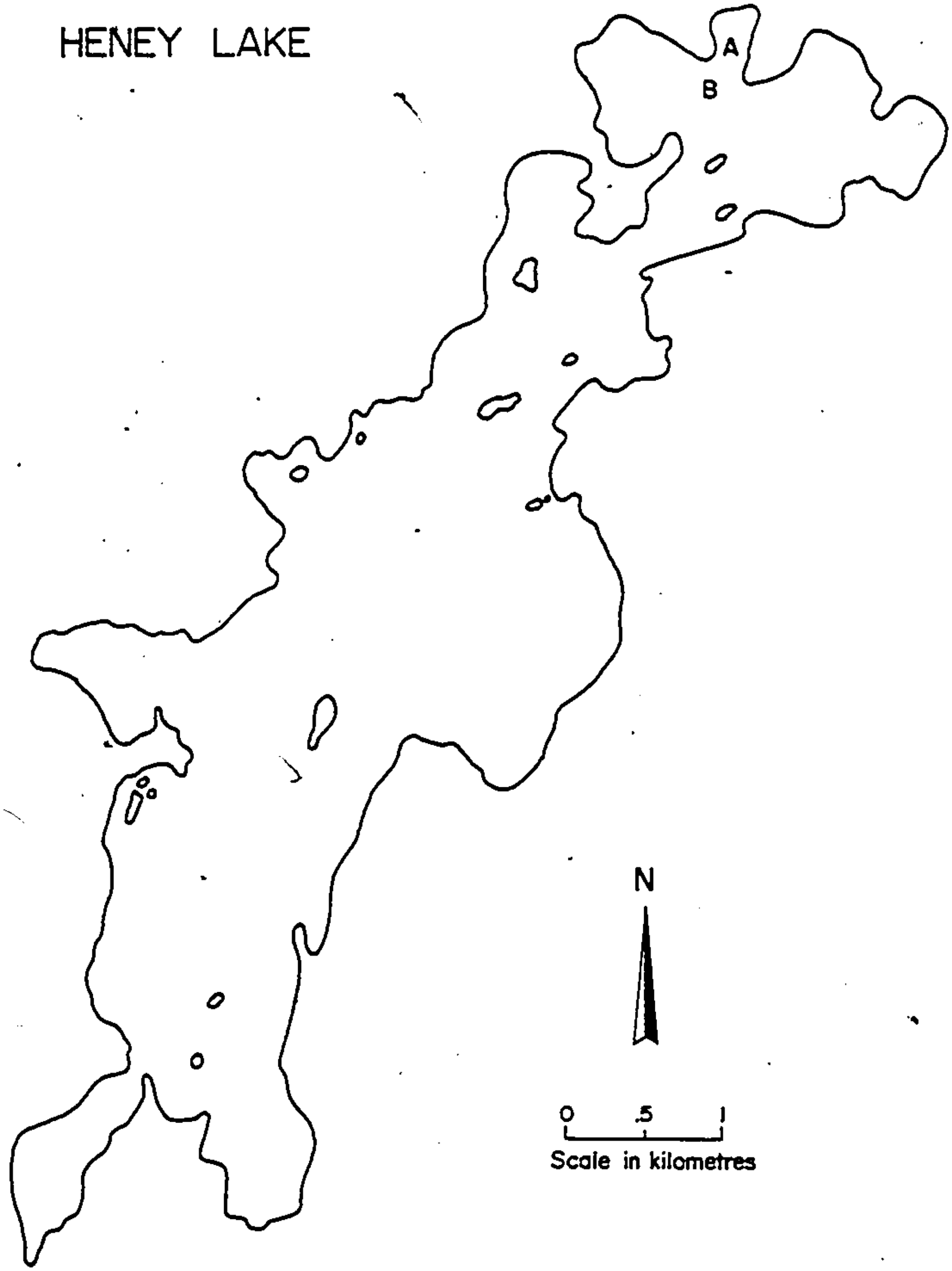
The experiments were run in the summer of 1978 in a small bay (fig.2, station A), 11 meters in depth, located at the northern end of the lake. Twelve enclosures, 1 meter in diameter and 10 meters long, were built out of clear polyethylene tubes sealed at the bottom and maintained open at the top by an aluminum ring. The enclosures were sunk in the bay on the 7th of July and then filled by towing vertically the opening of the tube through the water column. They were later filled to capacity with a gas-powered pump. The bottom of the enclosures was anchored with cement blocks while the opening was maintained above the water line with four carbuoys. Each enclosure held approximately 8000 liters of lake water. They were left unperturbed for one week before the manipulations to allow the plankton populations to return to equilibrium.

The enclosures were divided in three sets of four. The manipulation consisted of adding to each enclosure 600 water mites in the first set, 1500 in the second set, leaving the remaining set for control. The levels of mite enrichment were chosen so as to approximate levels two and three times greater than that of the controls. The water mites were collected the week previous to the manipulation from plankton tows taken from the pelagic zone of the lake (fig.2, station B). Only adult mites were collected for uniformity of treatment, using individual size as the main criterion for selection.

A: experimental area

B: area where water mites were collected

Figure 2: Contour map of Heney Lake, Quebec


HENEY LAKE
A
B
N
0
.5
1
Scale in kilometres

## 2.3 SAMPLING AND COUNTING PROCEDURES

The enclosures were sampled on the day preceeding the manipulation, and weekly thereafter. Phytoplankton samples were collected with a 2-litre Van Dorn bottle at depths of 0, 3, 6 and 9 metres. Subsamples of 100 ml from each of the depth samples were combined and preserved immediately in Lugol's solution. Then they were allowed to settle for three days, after which the top 300 ml were siphoned off. Phytoplankton cells were counted with a Zeiss inverted microscope, using the standard sedimentation procedure. A minimum of 400 cells were counted, which assures 95% confidence limits no larger than 10% of the count (Lund _et_ _al_. 1959). Taxa were identified down to the species level, whenever possible, and volume was determined using standard geometric shapes (Kovala and Larrance, 1966) and cell volumes (Wetzel, 1975).

Zooplankton populations were sampled by towing vertically through each enclosure a plankon net of 110 um mesh and 28 cm in diameter. As no more than 6% of the total volume of the enclosure was filtered in this way each week, it is assumed that sampling was not a major perturbation to the system. The samples were initially preserved in Lugol's solution to which formaline was later added. Ten per cent of each sample were then examined using a Wild M-7 stereomicroscope, and at least 1000 individuals counted; each was identified at the species level and, in the case of copepods, classified as adults or juveniles. Because of taxonomic difficulties all nauplii were grouped into one category.

# Chapter III

# RESULTS

## 3.1 WATER MITES

To evaluate and compare mite predation between enclosures through the whole experiment I simply computed the total number of mites counted in samples from each enclosure following enrichment (Table 1). Although such an index is not an absolute measure of predation pressure, it allows to quantify the relative importance of the water mites in each set of enclosures. As shown in table 1, the enrichment resulted in a substantial increase in water mite density, but there was no significant difference (t-test, P>>0.05) between the 2X- and 3X- treatments. Both groups were therefore lumped into a single one.

Since this new set of eight enclosures had a much greater variance in mite density than the control, it was decided to restrict further analysis of the enriched enclosures to those where the "predation pressure" index was within one standard deviation of the mean. This measure seriously alleviated the risk that the non-linearity of biological factors such as density-dependant predation and competition would obscure trends, and allowed to quantify more precisely predation pressure and its impact. Since the rejection of the outliers was done a priori, before the community response to the manipulation was tested, no personal bias was introduced. The new enriched group was thus limited to 5 enclosures, with a mean predation pressure index of 231.4 and a standard deviation of 20.5. The former value is seven times greater than that of the controls.

Mite densities in control and enriched enclosures were compared statistically *via* a two-factor analysis of variance, where the two factors were time and treatment. The distribution of the mite density data at time 0 was not significantly different (Kolmogorov-Smirnov Goodness of Fit test; $P>>0.05$) from a normal distribution.

Mean densities of water mites in the manipulated set were found to be significantly different from those in the control group (two-factor ANOVA, $F= 173.6$, $n=1$, $P<0.001$). Densities in the control set were never greater than $20/m^3$, while the experimental group increased to $35/m^3$ on day 7, then decreased to $25/m^3$ on 14 only to rebound to a maximum of $150/m^3$ on day 28 (fig. 3). After this maximum, mite densities declined to original levels. The initial enrichment thus resulted approximately in a 7-fold difference between the two groups throughout the experimental period.

TABLE 1

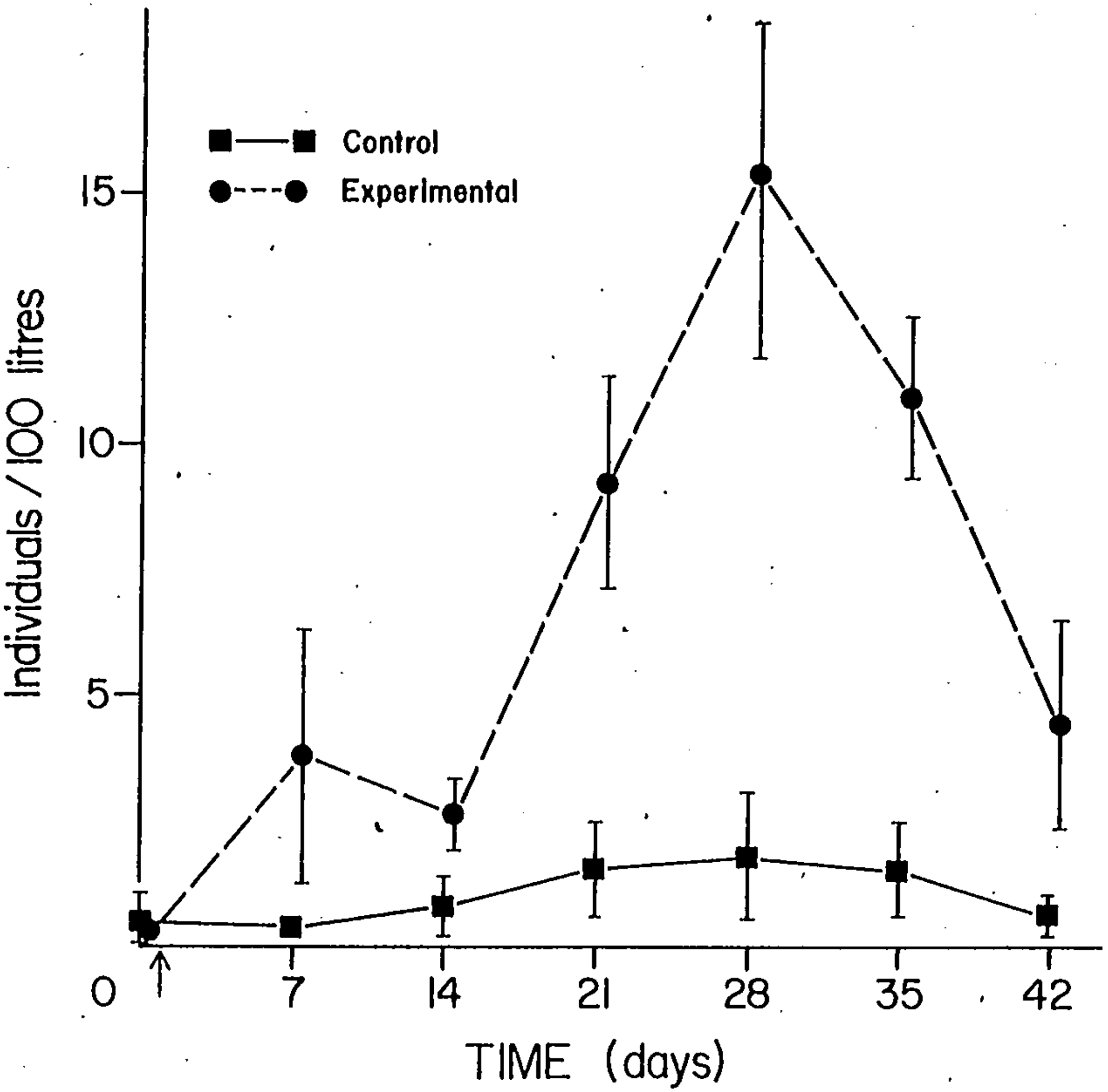
Index of water mite predation pressure

Total number of water mites sampled from each enclosure

<table>
<tr><th>REPLICATE</th><th>CONTROL</th><th>2X</th><th>3X</th></tr>
<tr><td>1</td><td>47</td><td>324</td><td>219</td></tr>
<tr><td>2</td><td>37</td><td>264</td><td>230</td></tr>
<tr><td>3</td><td>30</td><td>234</td><td>124</td></tr>
<tr><td>4</td><td>16</td><td>121</td><td>210</td></tr>
<tr><td>MEAN</td><td>32.5</td><td>183</td><td>196</td></tr>
<tr><td>S.D.</td><td>13.0</td><td>136.5</td><td>48.5</td></tr>
<tr><td>MEAN AFTER ELIMINATION OF OUTLIERS</td><td>32.5</td><td colspan="2">231.4</td></tr>
<tr><td>S.D.</td><td>13.0</td><td colspan="2">20.5</td></tr>
</table>

Mean water mite densities (±one standard deviation) in control (squares) and manipulated (circles) enclosures.

Figure 3: Water mite densities


Control
Experimental
Individuals / 100 litres
15
10
5
0
7
14
21
28
35
42
TIME (days)

## 3.2 ZOOPLANKTON

A total of 16 species of zooplankton were identified (Table 2). Of these, ten were cladocerans and six were copepods. The herbivores consisted mainly of cladocerans, two diaptomid species and one small cyclopoid copepod, Tropocyclops prasinus var. mexicanus. There were two cladoceran predators, Leptodora kindtii and Polyphemus pediculus, which were both rare in all enclosures. Only adults of the predacious calanoid species Epischura lacustris were found, and only in low numbers. The most numerous predators were the cyclopoid species, Mesocyclops edax and Acanthocyclops vernalis, in that order. In light of recent studies (Anderson 1970, Brandl and Fernando 1978, 1979, Jamieson 1980), copepodites I-III of both species were considered as herbivores, and only the latter stages as carnivores.

## TABLE 2

### Zooplankton species

List of zooplankton species encountered in this study, along with their feeding status.

| CLADOCERANS | HERBIVORES | CARNIVORES |
|---|---|---|
| *Bosmina longirostris* | + | |
| *Ceriodaphnia lacustris* | + | |
| *Chydorus sphaericus* | + | |
| *Daphnia galeata mendotae* | + | |
| *Daphnia retrocurva* | + | |
| *Diaphanosoma leuchtenbergianum* | + | |
| *Holopedium gibberum* | + | |
| *Leptodora kindtii* | | + |
| *Polyphemus pediculus* | | + |
| *Sida crystallina* | + | |
| COPEPODS | | |
| CALANOIDS | | |
| *Diaptomus* (2 species) | + | |
| *Epischura lacustris* | | + |
| CYCLOPOIDS | | |
| *Acanthocyclops vernalis* | | |
| ADULTS, COP. IV-V | | + |
| COPEPODITES I-III | + | |
| *Mesocyclops edax* | | |
| ADULTS, COP. IV-V | | + |
| COPEPODITES I-III | + | |
| *Tropocyclops prasinus* var. *mexicanus* | + | |

All zooplankton data were analysed via a two-factor analysis of variance, after they had been tested for normality and found not to be significantly different from a normal distribution (Kolmogorov- Smirnov goodness of fit test, $P>>0.05$).

Figures 4 and 5 respectively describe mean densities of carnivores and of herbivores through time in both sets. Carnivore densities in the enriched set were not significantly different from those in the control. The means in both sets of enclosures are very close for all sampling dates. Maximum densities of approximatly 320/100 litres are found initially and steadily decrease from then on. When compared to mite densities, the crustacean zooplankton clearly dominate the carnivore compartment of these communities for the first three weeks, after which mite densities approximate those of the other carnivores.

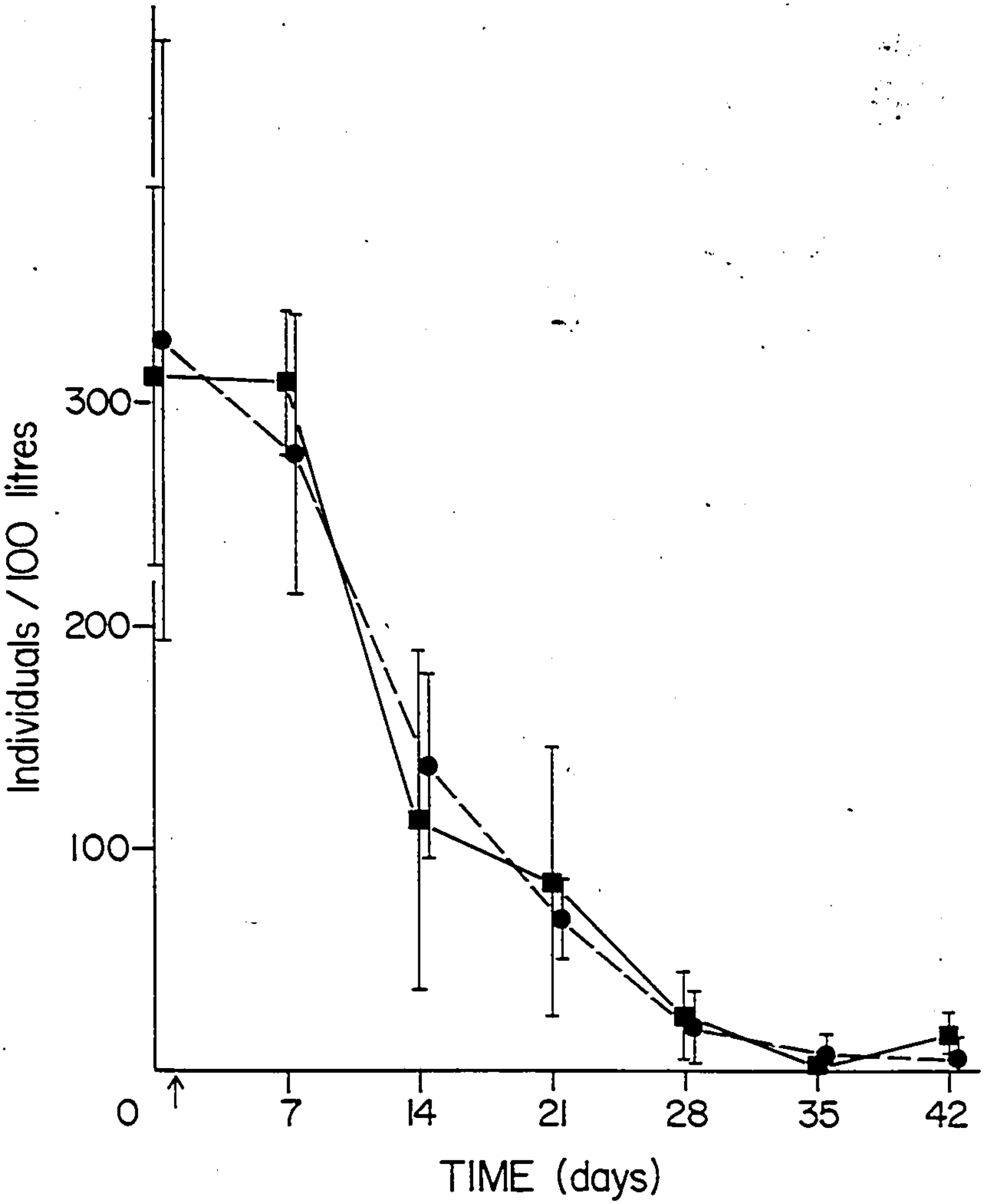
Total herbivore densities were significantly lower ($F=11.7$, $n=1$, $P<0.01$) in the enriched enclosures; mean densities were lower on all dates except on day 21 which corresponds to a peak in the number of nauplii with densities greater than 3000/100 litres in some enclosures, which represents 50 to 75% of the herbivore population (fig. 6).

As it is known that P. constricta can only effectively prey on a limited number of zooplankton species (Riessen 1981), the herbivore group was divided into two compartments, based on the susceptibility of the individual to predation by water mites. The group susceptible to predation (H1) consisted of four species of cladocerans: Dapnia retrocurva, Bosmina longirostris, Ceriodapnia lacustris and Chydorus sphaericus. All other herbivores were put into the second group (H2). The manipulation did not affect the density of the latter group, but resulted in a significant (F=29.9, n=1, P<0.001) reduction of group H1. The response of the whole herbivore compartment is due entirely to H1. Figure 7 shows how densities were lower at all dates in the enriched set, especially on days 7,14,35 and 42. Differences between both sets seemed to decrease on days 21 and 28.

If the effect of the manipulation is examined independantly for each species, one finds that differences between the control and enriched enclosures are statistically significant only for those species belonging to the group H1: D. retrocurva (F= 4.34, n=1, P<0.05), C. lacustris (F=12.3, n=1, P<0.001), B. longirostris (F=26.4, n=1, P<0.001) Ch. sphaericus (F= 52.9, n=1, P<0.001). Although D. retrocurva was already on the decline in controls at the start of the experiment, reaching densities near 0 by day 14 (fig. 8), it is almost completely eliminated one week after enrichment. B. longirostris (fig. 9) reaches its maximium mean density (650/100 L) on day 7 and steadily declines afterwards. The values in the enriched set are lower on all dates with the largest difference found on day 7. While C. lacustris (fig. 10) steadily increases in the control set to its highest mean density (770/100 L) on day 14, its mean density decreases steadily from day 0 in the enriched enclosures. Figure 11 shows Ch. sphaericus starting at levels near 0 in the controls and increasing to a maximum mean density of 2000/100 L on day 35 where the population stabilizes; the enriched set follows the same trend, always maintaining lower densities, but drops suddenly after day 28, where the difference between both sets becomes substantial.

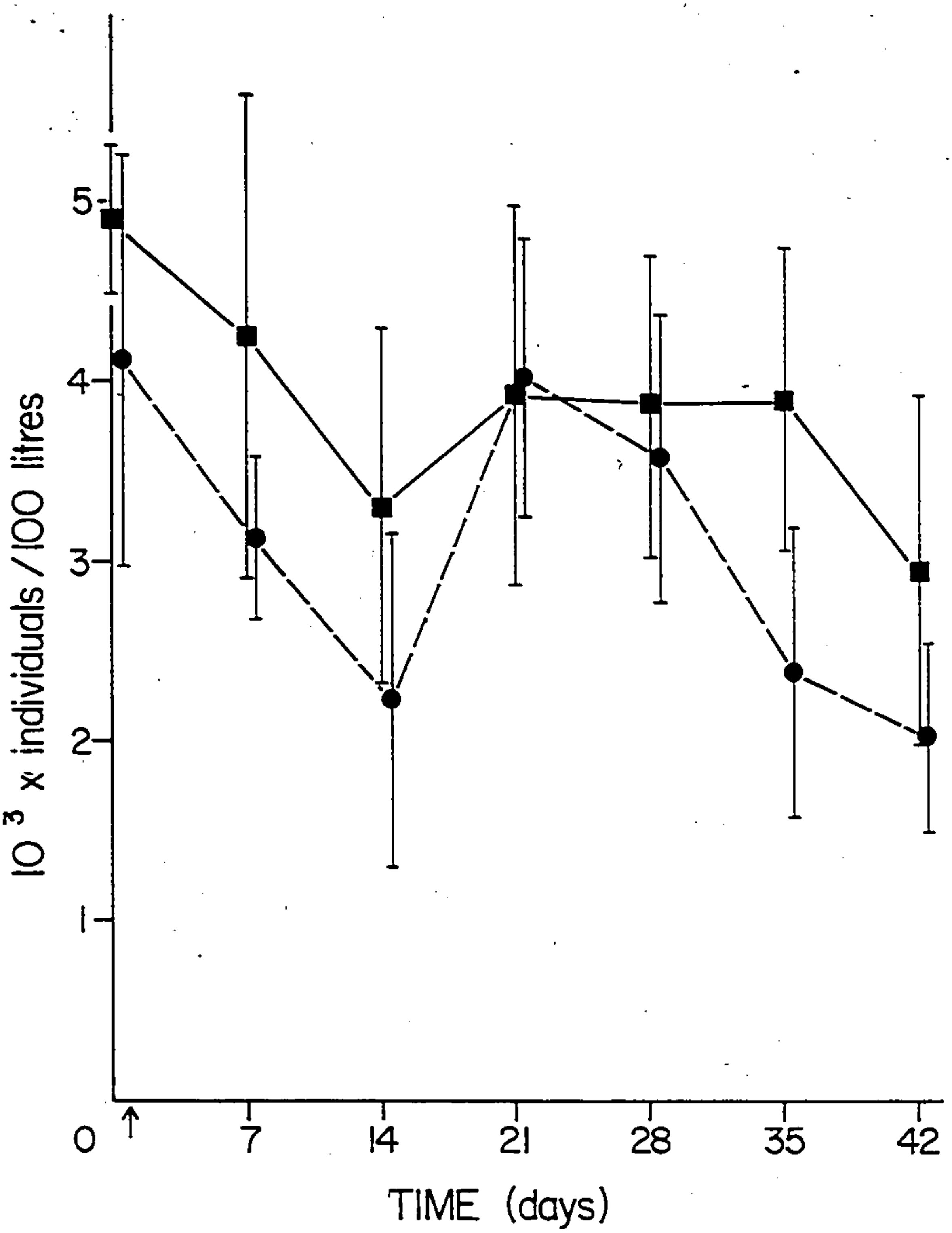
Mean densities of carnivores (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 4: Densities of carnivores (other than water mites)


Individuals / 100 litres
300
200
100
0
7
14
21
28
35
42
TIME (days)

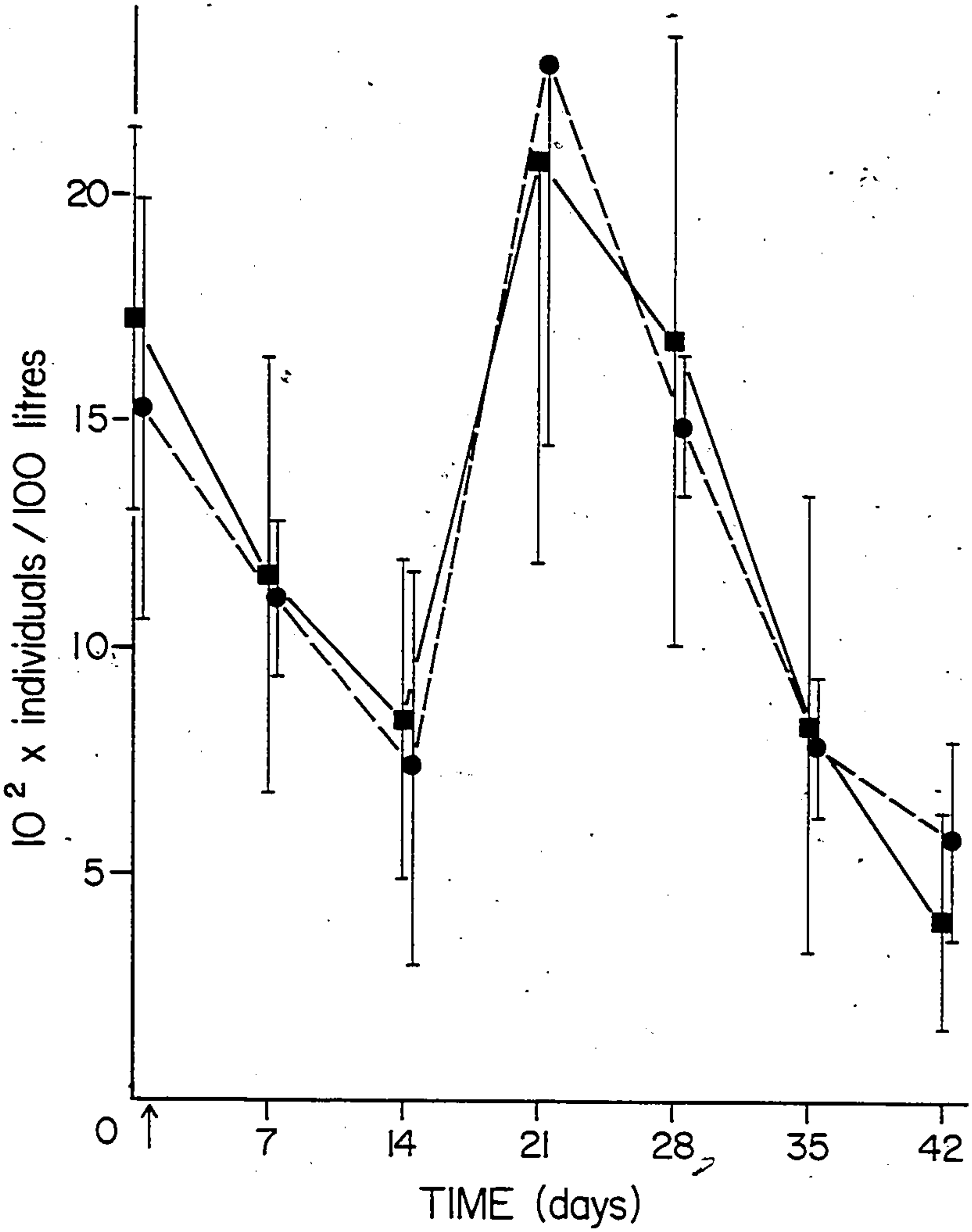
Mean densities of herbivores (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 5: Densities of herbivores


10 3 x individuals / 100 litres
5
4
3
2
1
0
↑
7
14
21
28
35
42
TIME (days)

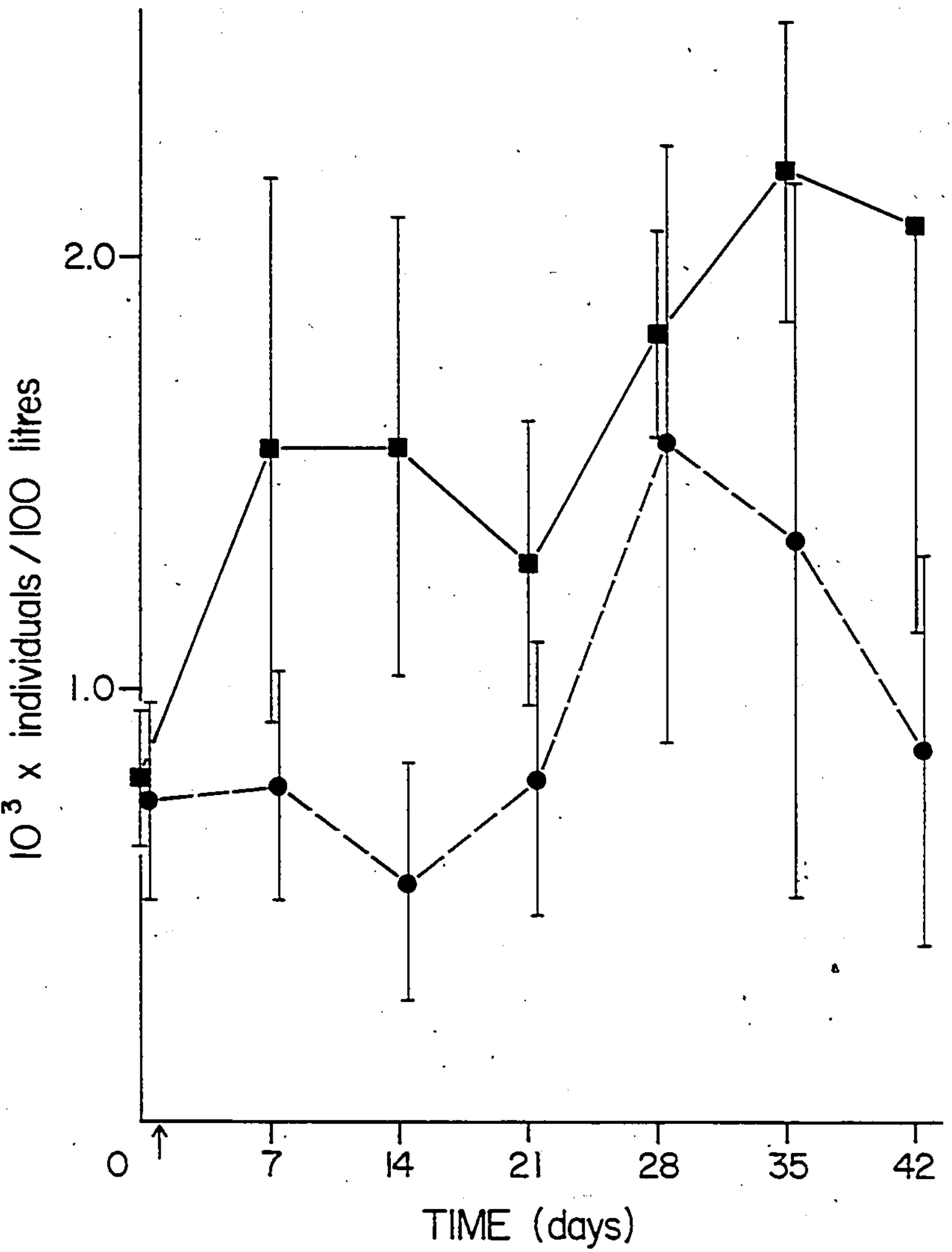
Mean densities of nauplii (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 6: Densities of nauplii


10 ² x individuals / 100 litres
20
15
10
5
0
7
14
21
28
35
42
TIME (days)

Mean densities of group H1 (±one S.D.) in control (squares) and manipulated (circles) enclosures.

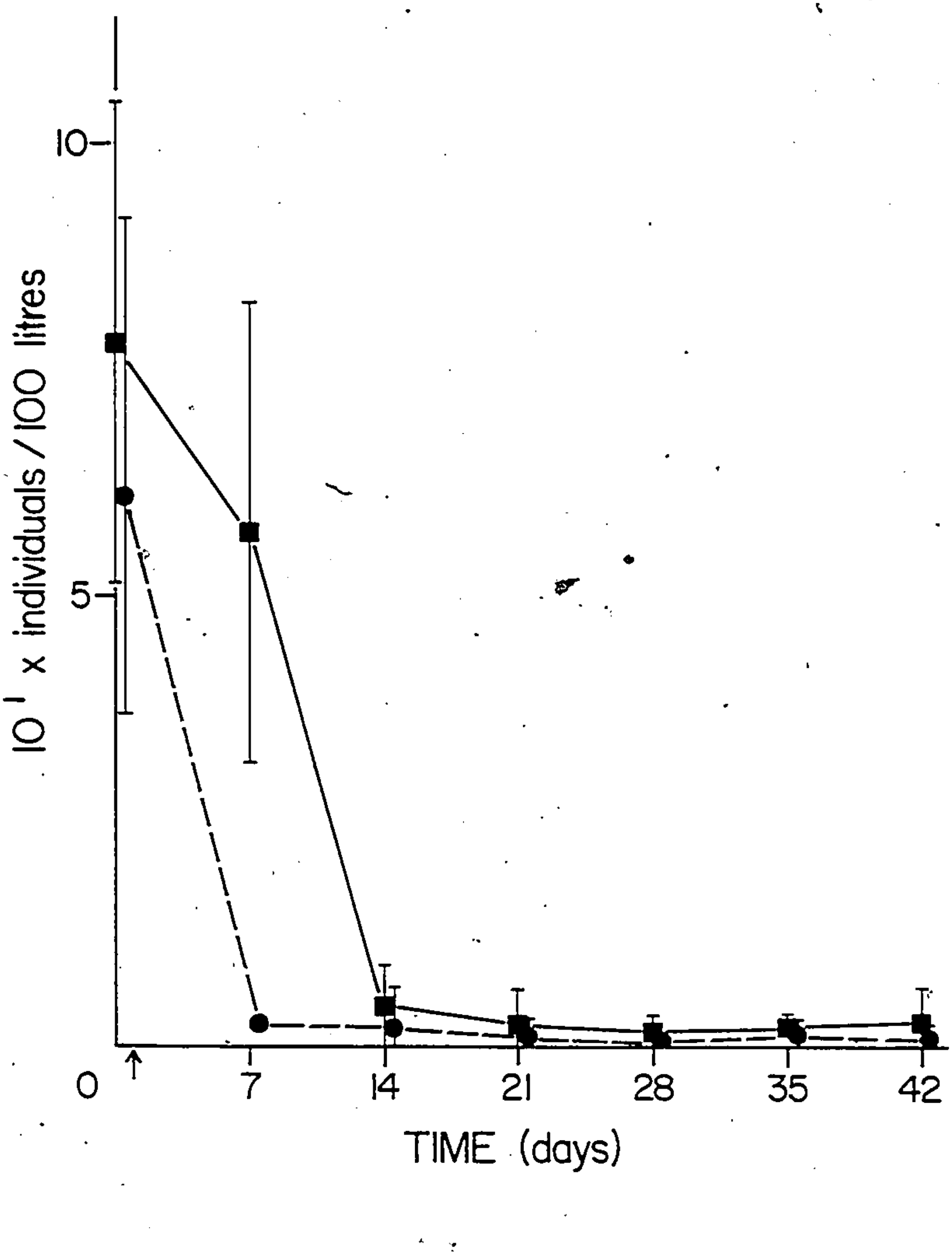
Figure 7: Densities of H1 group



2.0
1.0
10³ x individuals / 100 litres
0
↑
7
14
21
28
35
42
TIME (days)

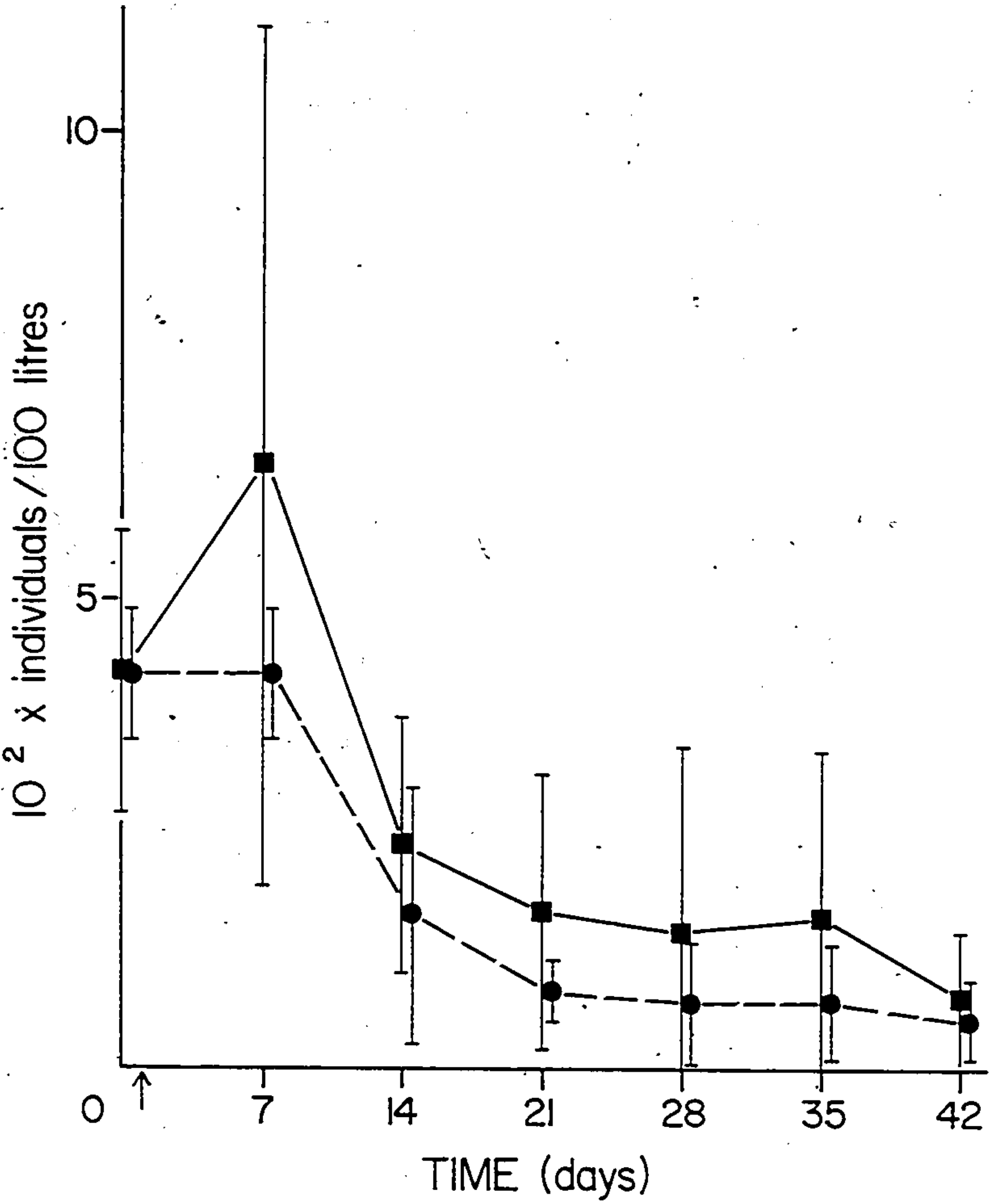
Mean densities of <u>Daphnia</u> <u>retrocurva</u> (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 8: Densities of <u>Daphnia</u> <u>retrocurva</u>


10
5
0
10¹ x individuals / 100 litres
↑
7
14
21
28
35
42
TIME (days)

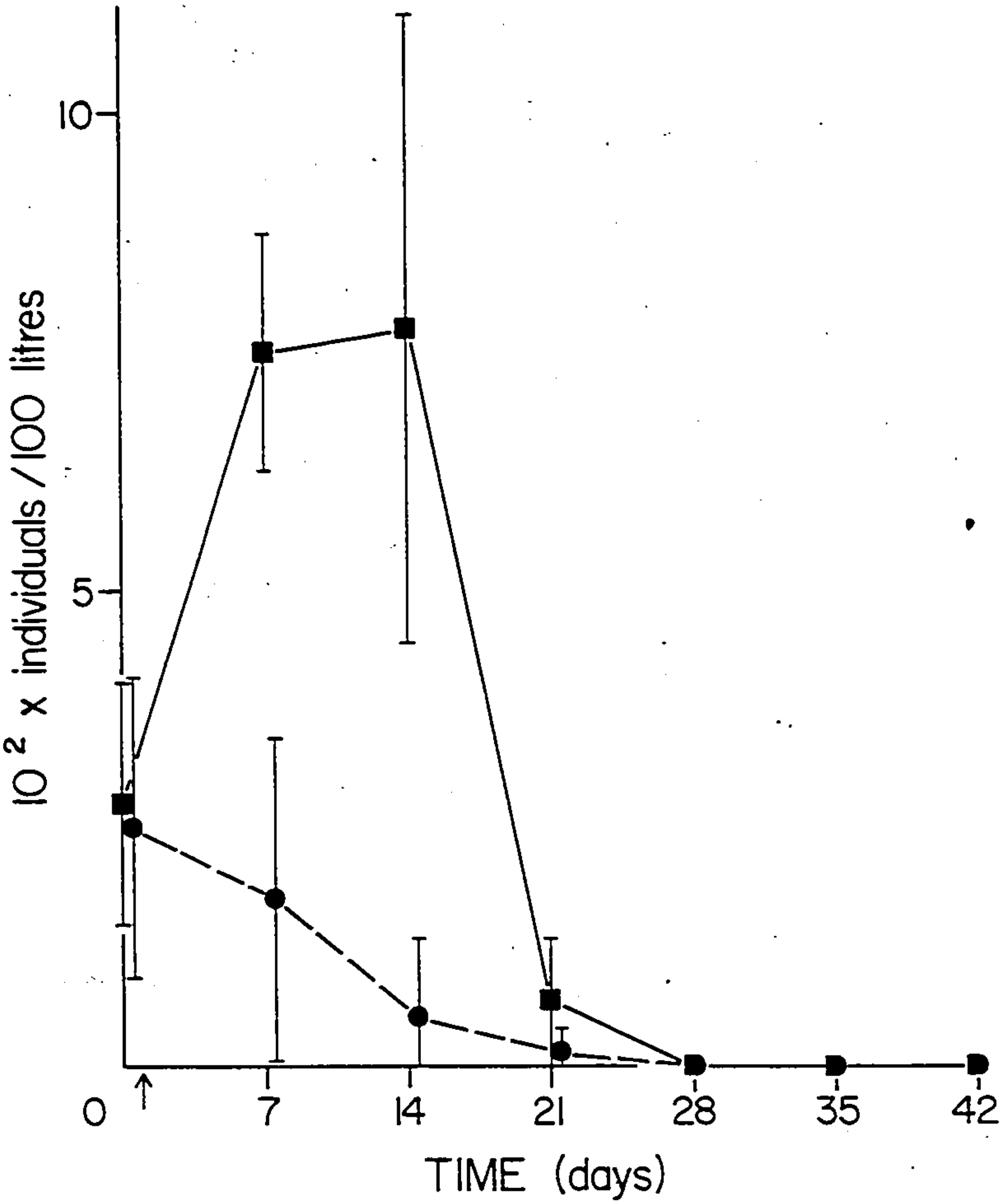
Mean densities of Bosmina longirostris (±one S.D.) in control (squares and manipulated (circles) enclosures.

Figure 9: Densities of Bosmina longirostris


10² x̄ individuals/100 litres
10
5
0
7
14
21
28
35
42
TIME (days)

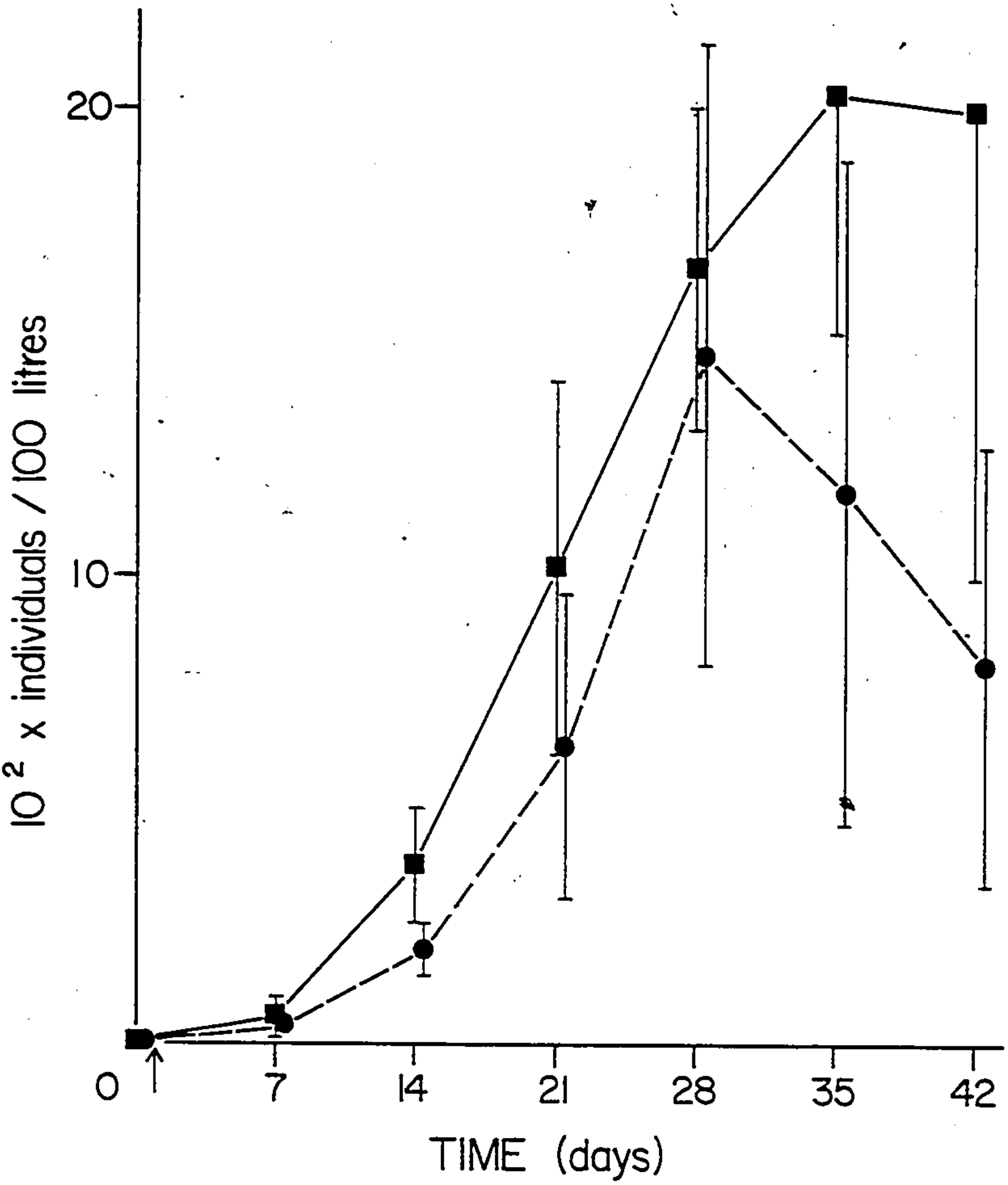
Mean densities of Ceriodaphnia lacustris (±one S.D.) in control (squar
and manipulated (circles) enclosures.

Figure 10: Densities of Ceriodaphnia lacustris


10² x individuals /100 litres
10
5
0
↑
7
14
21
28
35
42
TIME (days)

Mean densities of Chydorus sphaericus (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 11: Densities of Chydorus sphaericus



10 ² x individuals / 100 litres
20
10
0
7
14
21
28
35
42
TIME (days)

## 3.3 PHYTOPLANKTON

Ninety species of phytoplankton were recognized in the counts and include 17 blue-greens, 27 diatoms, 39 greens, 5 chrysophytes and 2 dinoflagellates. Because of their small size, flagellates were difficult to identify and were thus counted as either small (<10 um in diameter) or large (>10 um) flagellates.

Cell counts were converted to volumes as to provide a realistic evaluation of biomass (Lund and Talling 1957, Vollenweider 1969). Since the range of phytoplankton volumes spanned up to five orders of magnitude and the coefficient of variation (= standard deviation/mean) was as high as 95% in some cases, the data were transformed logarithmically (Zar 1974). The statistical procedures consisted of two-way analyses of variance.

Figure 12 shows the evolution of total phytoplankton volume through time in both sets. Alhough the enriched enclosures have almost always higher volume, they do not differ significantly from the control. The total volume was subdivided into four taxonomic groups (blue-greens, greens, diatoms, others) to find whether the treatment had affected phytoplankton volume along taxonomic lines. There was no statistically significant difference between the control and enriched set for any of the taxonomic divisions.

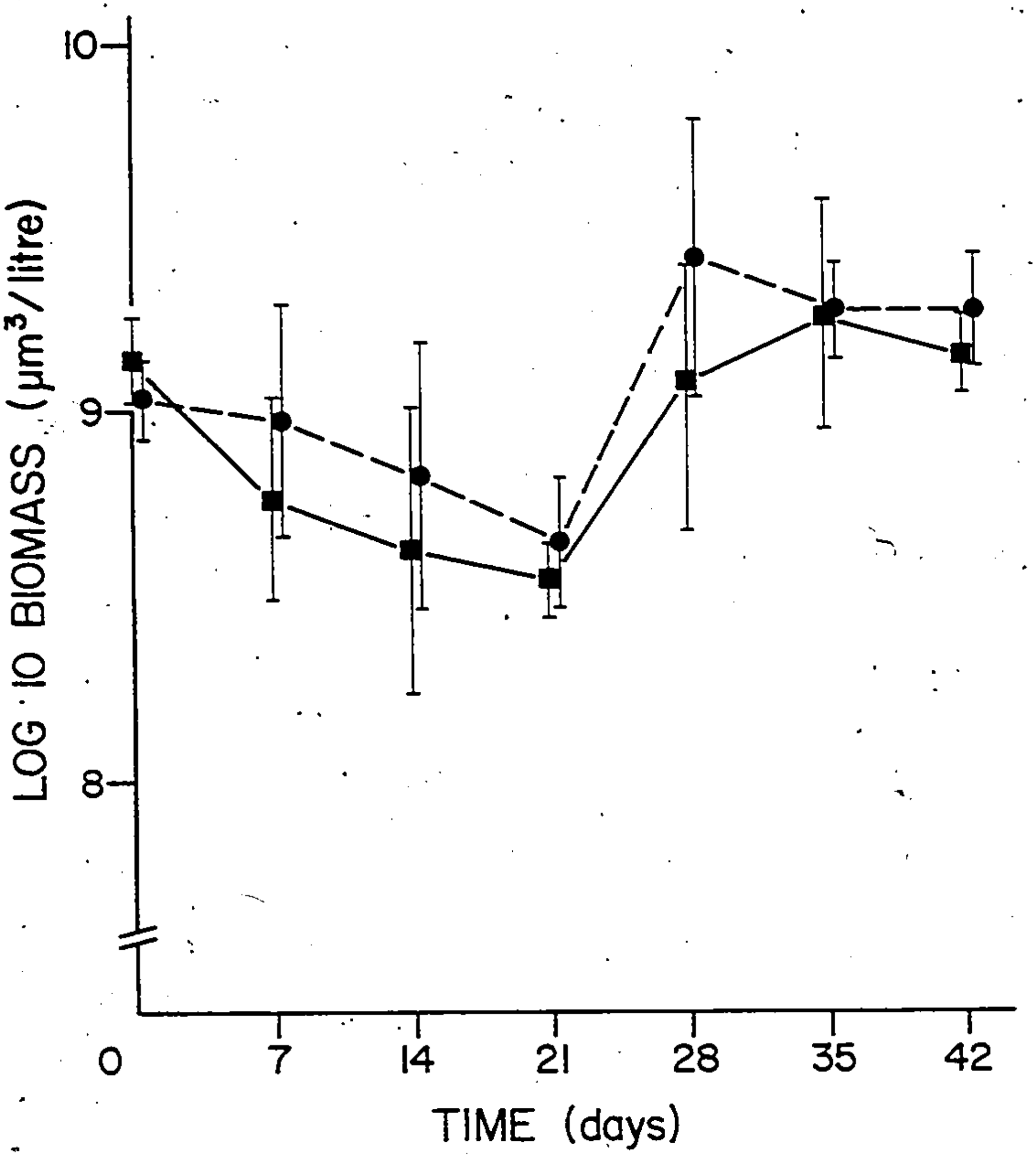
There is ample evidence (Burns 1968, Porter 1973, Weers and Zaret 1975, Nadin-Hurley and Duncan 1976) that zooplankters selectively graze on the smaller fraction of the phytoplankton biomass. Zooplankton grazing is also known to affect the size composition (Gliwicz 1975) and taxonomic composition (McCauley and Briand 1979) of phytoplankton communities. Large phytoplankton inhibit zooplankton feeding (Webster and Peters 1978) and this inhibition can drive zooplankton succession in lakes (Gliwicz 1977). Empirical analysis of biomass data from thirteen lakes (McCauley and Kalff 1981) demonstrates the constancy of the ratio of zooplankton biomass to nannoplankton biomass, irrespective of total phytoplankton biomass. For these reasons it was decided to examine the phytoplankton size structure. Species smaller than 30 um were classified as edible and the others as inedible. Although blue-greens have been shown to decrease survivorship and reproductive output in cladocerans (Arnold 1971, Porter and Orcut 1980), there is recent evidence that they are ingested (De Bernardi _et_ _al_. 1981); therefore they were not excluded from the edible group.

No significant difference was found between the inedible phytoplankton volume of the control and the enriched sets (fig. 13). Both show similar means throughout the experiment. On the other hand mean edible phytoplankton volume is significantly greater (F=10.8, n=1, P<0.002) in the enriched than in the control enclosures (fig. 14). This difference is consistent for all dates and maximal on day 7. The evolution of volume values over time was similar in both sets with values decreasing to a low on day 21, but increasing after that date. Examination of all 90 species revealed that only four species were significantly affected by the treatment: <u>Cyclotella</u> sp. (P<0.002), <u>Sphaerocystis Schroeteri</u> (P<0.01), <u>Chlorochromonas minuta</u> (P<0.05) and <u>Selenastrum</u> sp. (P<0.009). Figures 15 and 16 show that mean volume was greater in the experimental group for all species except <u>S. Schroeteri</u> which reacted negatively to the treatment.

The total number of phytoplankton species, i.e. species richness, was significantly higher (F= 4.8, n=1, P<0.05) in the enriched enclosures. Although the pattern is erratic over time (fig. 17), species richness is higher in the enriched set on four of the six dates after treatment. When total species richness is divided into edible and inedible species richness (figures 18 and 19) a statistically significant difference (F=4.5, n=1, P<0.05) between the treatment and the controls is found only for the inedible species richness. The patterns for both the inedible and edible species richness are again very erratic.

Mean log phytoplankton volume (±one S.D.) in control (squares) and manipulated (circles) enclosures.

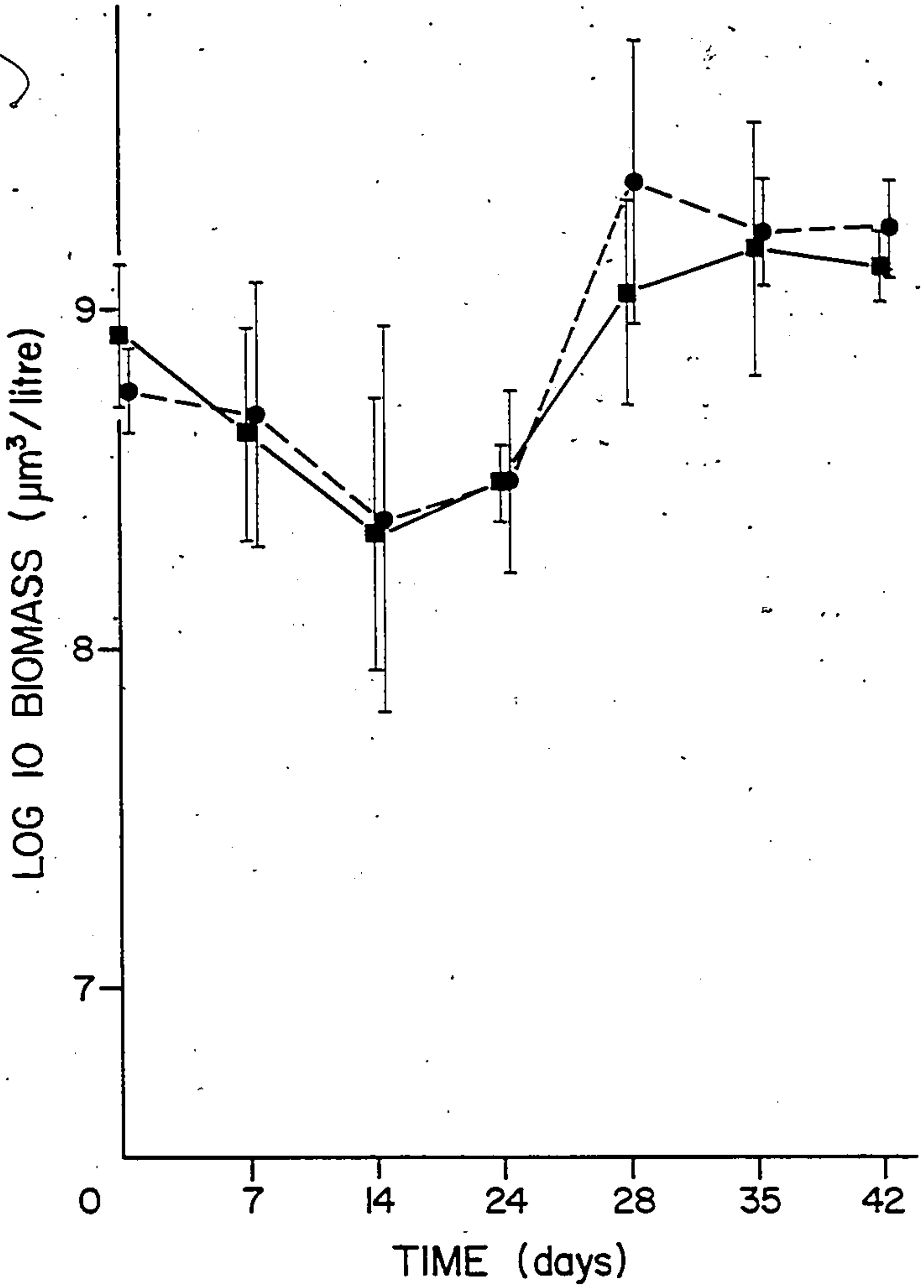
Figure 12: Total phytoplankton volume



LOG 10 BIOMASS (μm³/litre)
10
9
8
0
7
14
21
28
35
42
TIME (days)

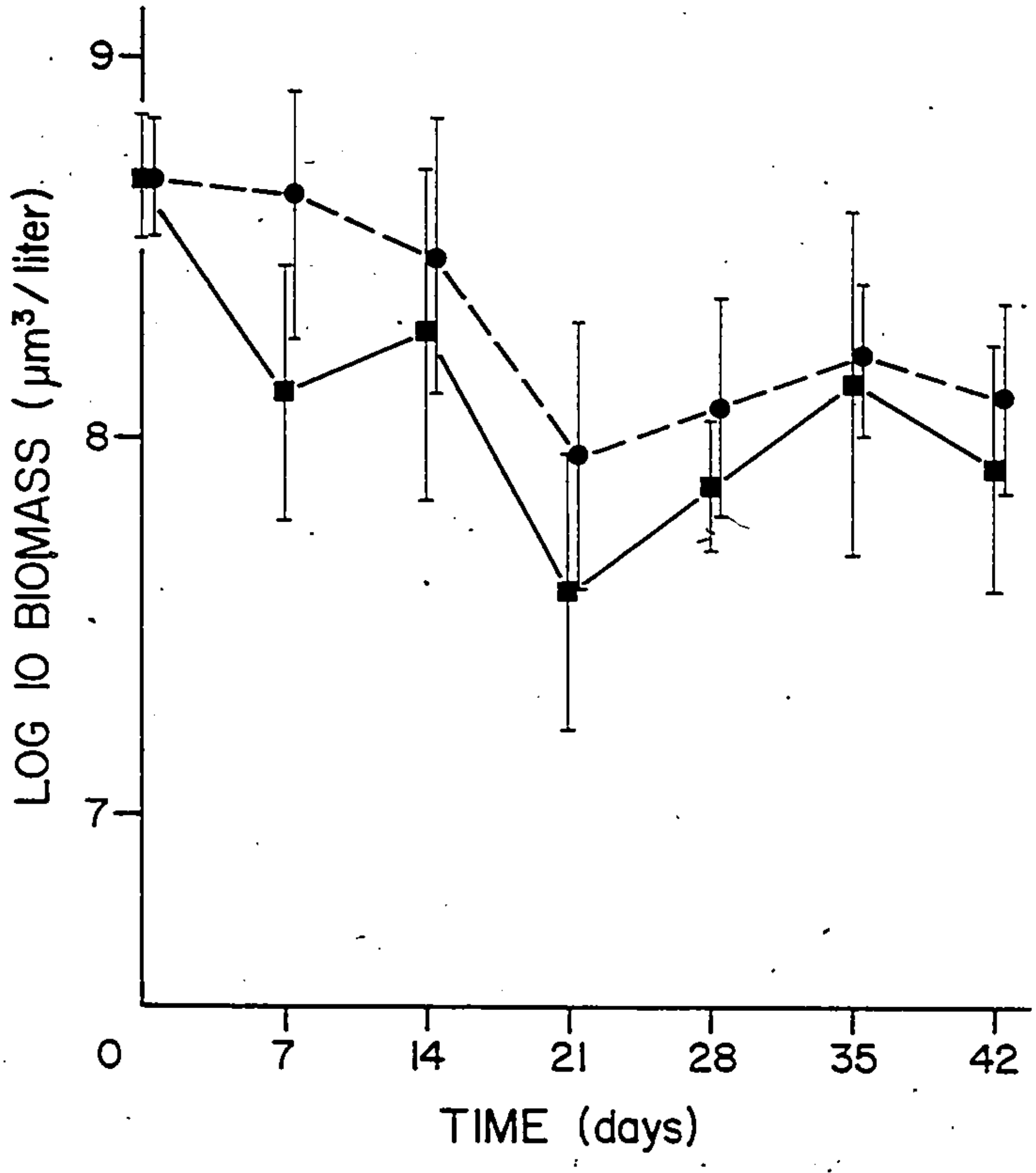
Mean log inedible phytoplankton volume (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 13: Inedible phytoplankton volume


LOG 10 BIOMASS (µm³/litre)
9
8
7
0
7
14
24
28
35
42
TIME (days)

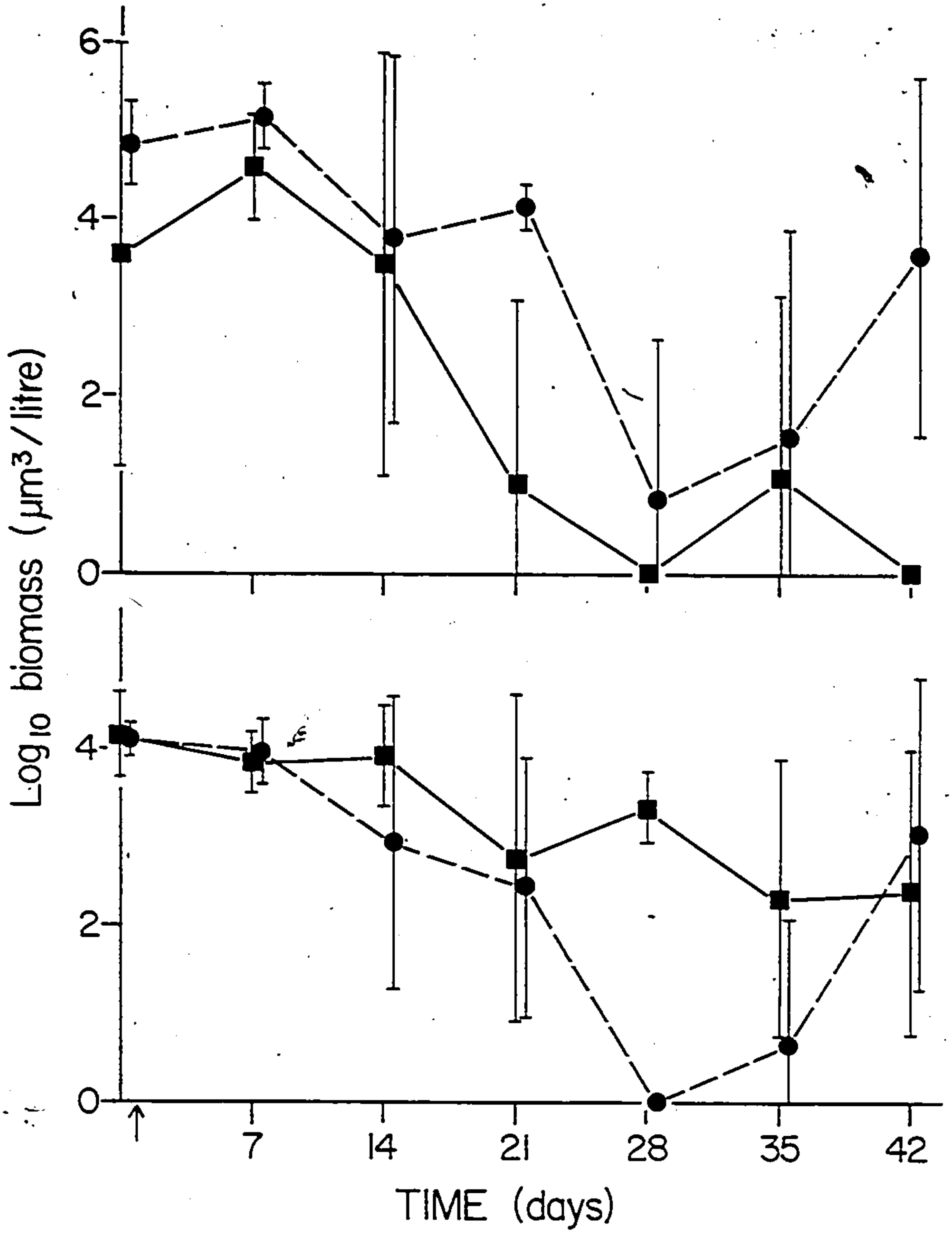
Mean log edible phytoplankton volume (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 14: Edible phytoplankton volume


9
8
7
LOG 10 BIOMASS ($\mu m^3$/liter)
0
7
14
21
28
35
42
TIME (days)

Mean log volume (±one S.D.) of _Cyclotella_ sp. (upper) and _Sphaerocystis_ _Schroeteri_ (lower) in control (squares) and manipulated (circles) enclosures.

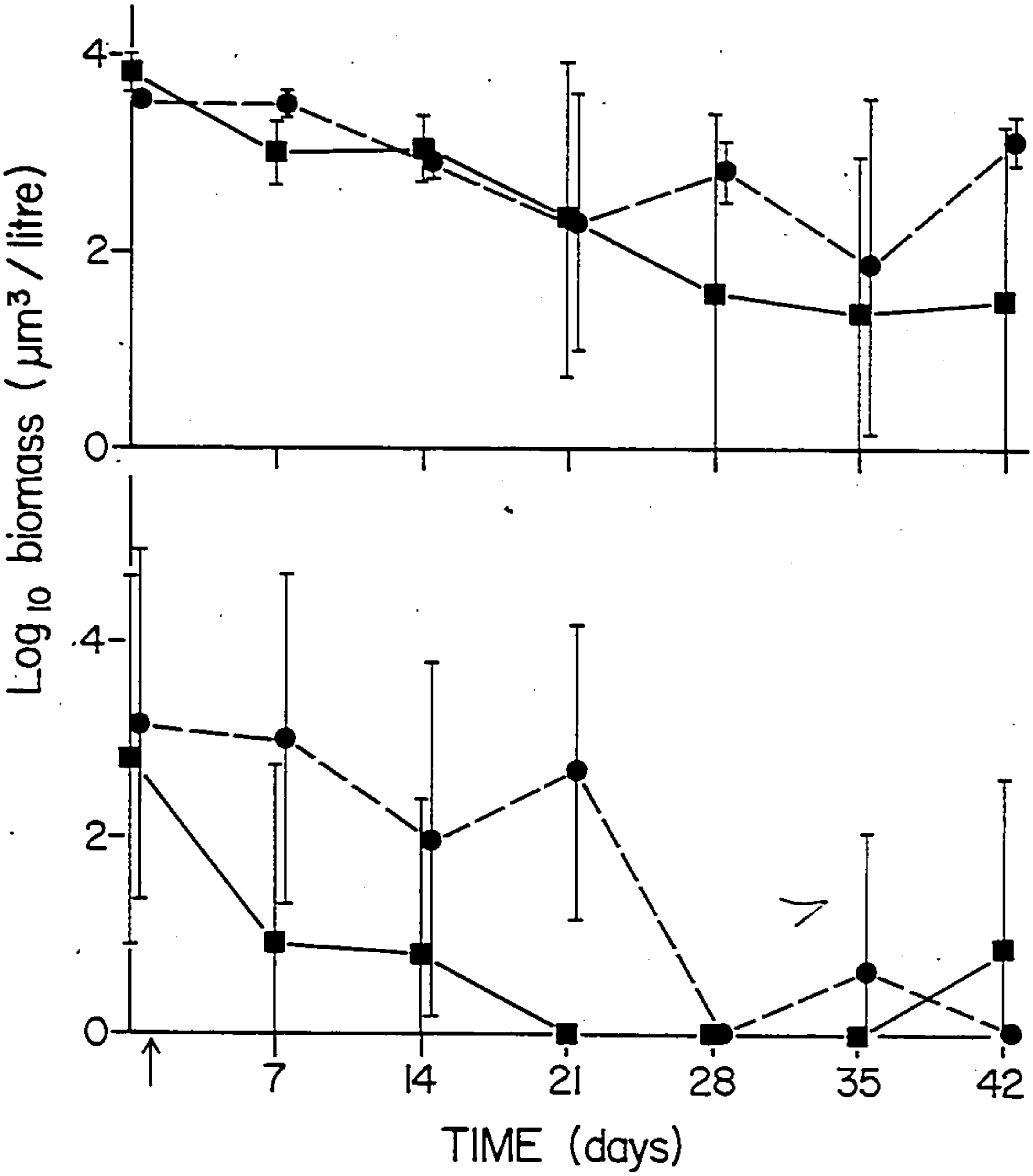
Figure 15: Biomass of _Cyclotella_ sp. and _Sphaerocystis Schroeteri_



6
4
2
0
4
2
0
Log10 biomass (µm3/litre)
↑
7
14
21
28
35
42
TIME (days)

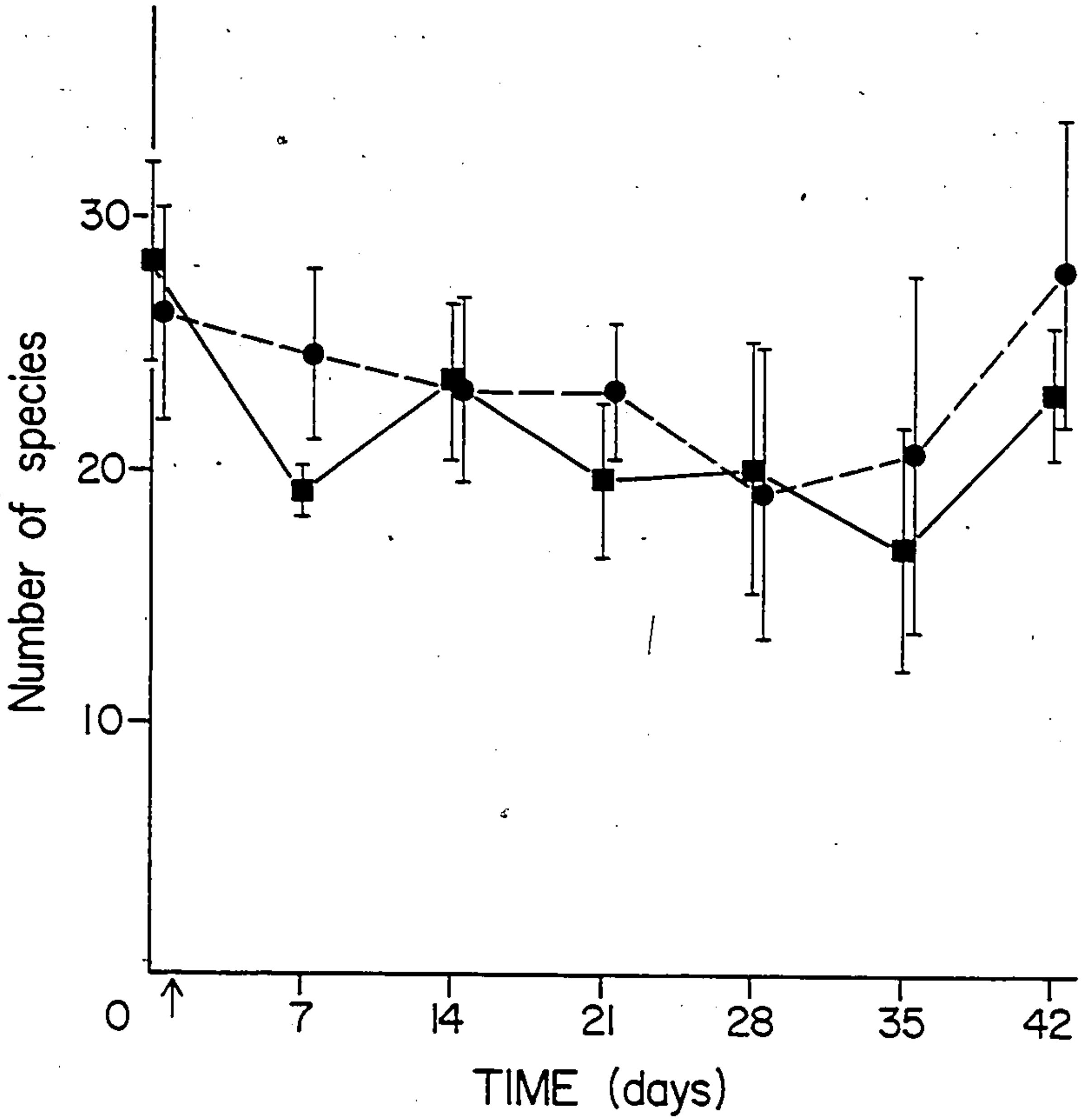
Mean log volume (±one S.D.) of Chlorochromonas minuta (upper) and Selenastrum sp. (lower) in control (squares) and manipulated (circles) enclosures.

Figure 16: Biomass of Chlorochromonas minuta and Selenastrum sp.


Log10 biomass (μm3 / litre)
4
2
0
4
2
0
7
14
21
28
35
42
TIME (days)

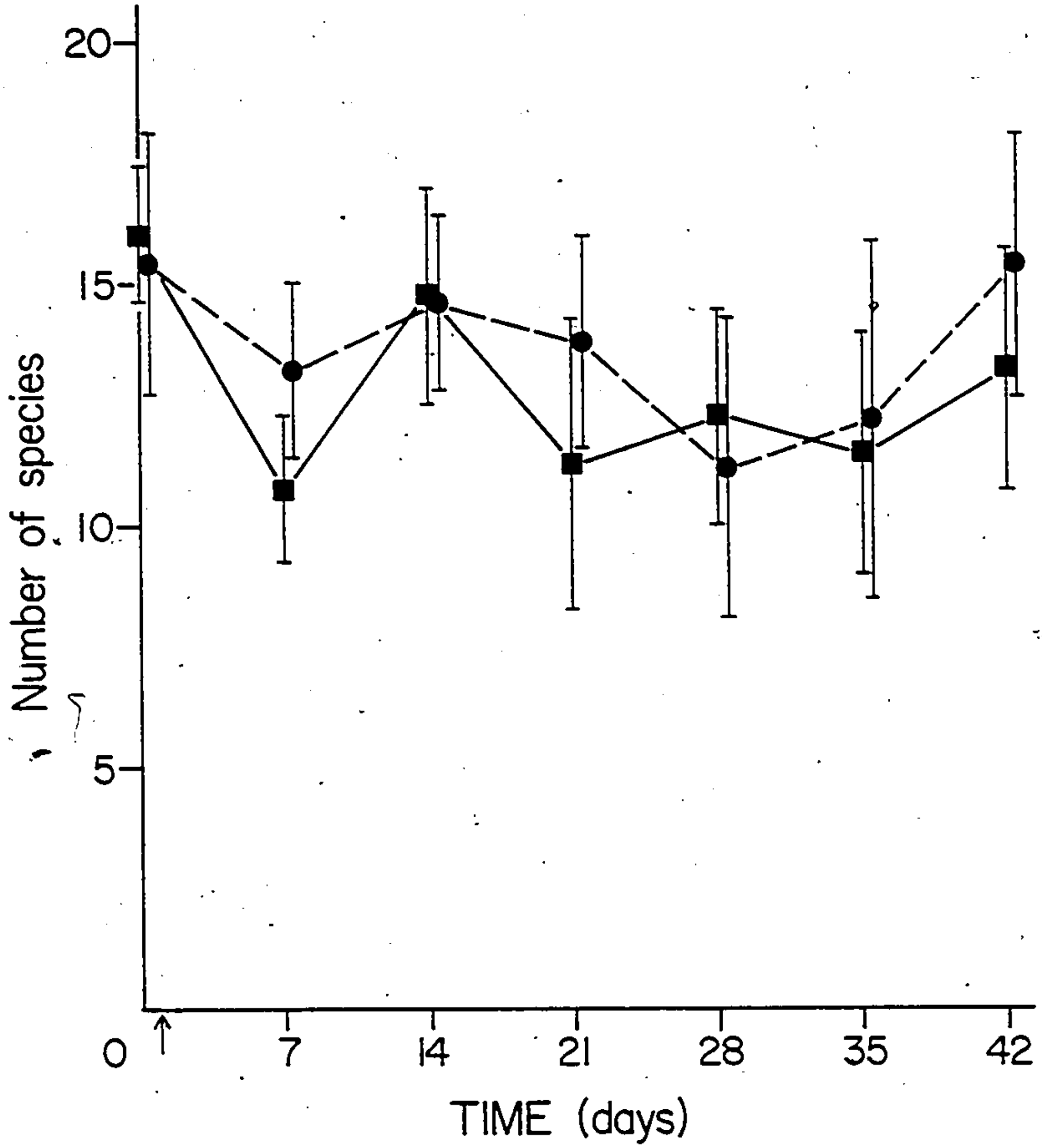
Mean phytoplankton species richness (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 17: Total phytoplankton species richness


Number of species
30
20
10
0
↑
7
14
21
28
35
42
TIME (days)

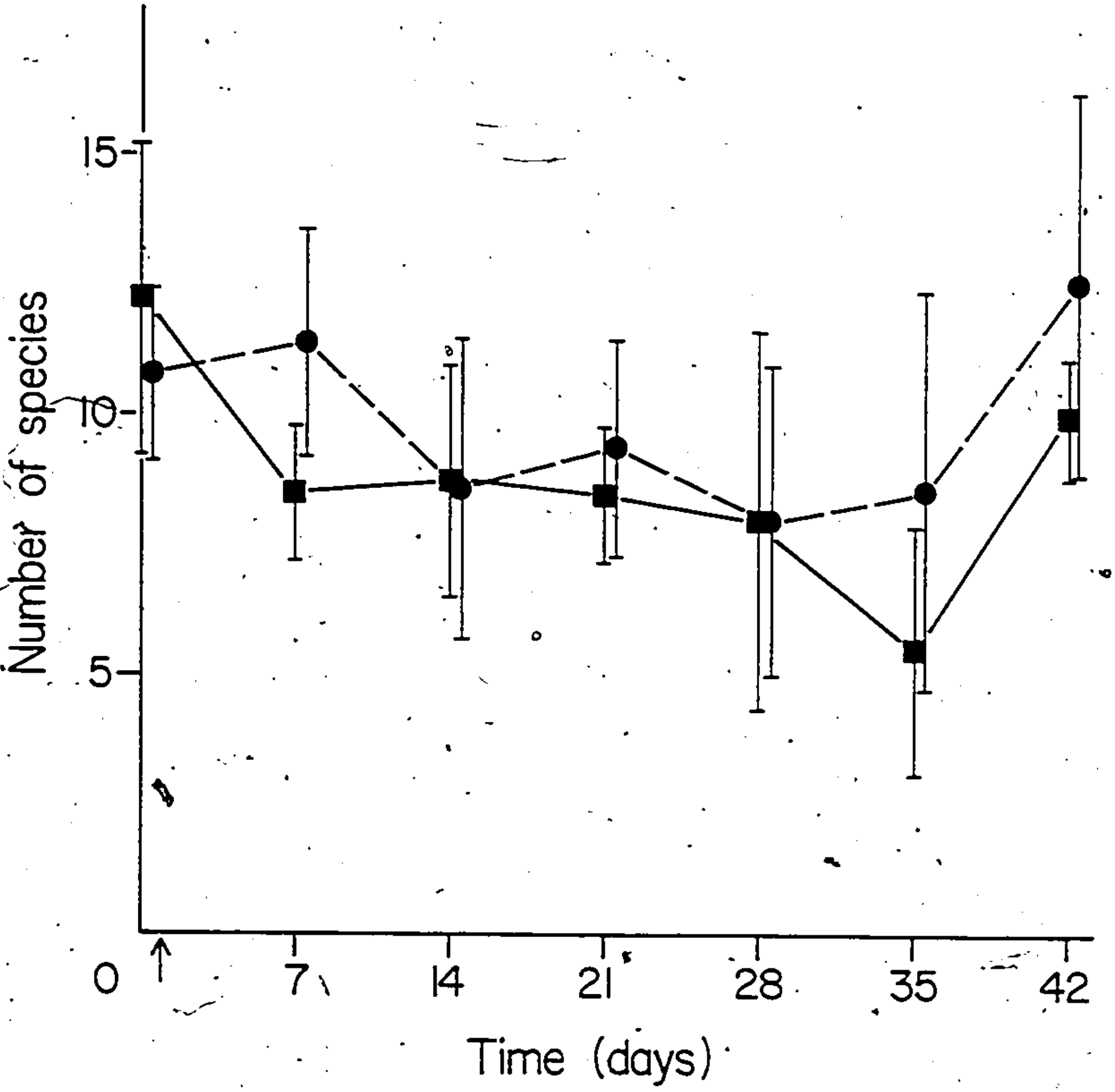
Mean edible phytoplankton species richness (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 18: Edible phytoplankton species richness


20
15
10
5
0
7
14
21
28
35
42
Number of species
TIME (days)

Mean inedible phytoplankton species richness (±one S.D.) in control (squares) and manipulated (circles) enclosures.

Figure 19: Inedible phytoplankton species richness


15
10
5
0
Number of species
↑
7
14
21
28
35
42
Time (days)

# Chapter IV

# DISCUSSION

## 4.1 METHODS

Although the use of medium scale enclosures *in situ* for this study is more realistic than laboratory or small scale microcosms, a number of problems are associated with this approach. Steele (1979) reviewed work done with experimental ecosystems and found that advantages such [illegible]ncreased duration of experiment and greater sensitivity to stress due to the larger number of variables, have the drawbacks of both a lack of control over the processes by the experimenter and decreased understanding of cause and effect. Therefore, before any conclusions can be drawn from the results, the importance of a number of factors linked with this approach must be weighed.

In order to extrapolate the results of this work to a real lake situation, the lake plankton system must be replicated to some degree in the enclosures. Zooplankton seasonal dynamics were studied in Heney Lake during the experimental period by Riessen (1981) and comparison with population densities in the control enclosures showed that the densities were very similar, with enclosure levels identical or slightly lower than lake levels. Population densities over time showed exactly the same trends, except that in the last two weeks of the experiment, diaptomid, cyclopoid and daphnid populations were substantially lower in the enclosures.

Although data on lake phytoplankton biomass are lacking to make a similar comparison, previous work on enclosed water columns (Takahashi et al. 1975, Oviat et al. 1980) showed that they behaved similarly to the outside environment. However, in one case the phytoplankton communities did start to diverge from the external community after 20 days (Takahashi et al. 1975). After working with enclosures of 1300 $m^3$ in volume, Reeve and his co-workers (1981) have suggested that this type of experiment should not last more than 50 days because communities become "unnatural". If one takes into account the divergence of the zooplankton community in the control enclosures after day 28, four weeks might be as long as these enclosures are representative of the lake community. Factors such as lack of advection, build-up of populations —such as periphyton and hydra— on the container wall and loss of nutrients are probably the cause of the divergence.

Researchers using enclosures in fresh water (Neill 1978, Neill and Peacock 1980, Kerfoot and DeMott 1980) have neglected replication of single treatments, which prevents the statistical estimation of variance. Their conclusions were drawn from graphical presentations of the data without regard for possible inherent variations in community structure. However, investigation of the problem of replication in marine enclosures (Takahashi _et_ _al_. 1975, Oviatt _et_ _al_. 1980, Reeve _et_ _al_. 1981, Woolcott _et_ _al_. 1981) has led to the general conclusion that they are highly replicable. The zooplankton data in this study seemed to be well replicated within treatment groups. The problem associated with the high variability in phytoplankton volume between enclosures is probably due to an inadequate sampling regime. Oviatt and his co-workers (1980) found that apparent divergences between replicates within treatments were caused by the phasing of plankton blooms and declines. Takahashi and his co-workers (1975) showed better apparent replication of plankton communities when phytoplankton was sampled every two days. He recommended that sampling intervals not be longer than 2 or 3 times the generation time of the organism being studied.

## 4.2 WATER MITE-ZOOPLANKTON INTERACTIONS

### 4.2.1 Predator selectivity

The discrepancy between the original 2- to 3-fold enrichment and the resulting 7-fold difference in water mite densities between groups can be explained by the fact that mature adult water mites were added to the enclosures. The experiment started at the exact time when water mite females layed their eggs that year (Riessen 1980), which contributed to a large population increase in the enriched enclosures. This is evidenced by adult:nymph ratios of 4 before day 14 and 0.25 after day 14.

The emergence of nymphs in the enclosures is due to the laying of eggs by females at the beginning of the experiment. This is supported by development times for *P. constricta* determined by Riessen (1981). Because female water mites deposite their eggs on a substrate, this could have occurred at any depth on the wall of the enclosures. Since temperatures in the lake at that time ranged from 14°C to 23°C, egg development times ranged from 8 days to 22 days while development time from emergence of larvae to emergence of nymph ranged from 9 to 28 days. Therefore total development time from egg to emergence of nymphs could have taken between 17 and 50 days, depending on the depth of deposition of the eggs. Hence the maximum density of mites recorded on day 28 could be the result of egg laying by females immediately after treatment.

The treatment of enclosures with additions of the water mite P. constricta resulted in significant effects on the zooplankton community. The results showed the mite to be highly selective in the capture of its prey. This is in agreement with the experimental work of Riessen (1981) who showed that adult P. constricta had the following prey preference: Bosmina > Daphnia, Ceriodaphnia > Chydorus >> Diaphanosoma, Diaptomus > Mesocyclops. Gliwicz and Biesiadka (1975) found that Piona limnetica had a very strong preference for cladoceran prey. This has also been found to be true of other species of the genus Piona (Pieczinski 1976).

The shift in the dominant life stage in the population of P.constricta corresponds to a change of its impact on the prey. Figure 7 shows how the difference between mean prey densities in the two sets decreased over time to a low on day 28 and increased again after that date regardless of relatively consistent differences in water mite densities between control and enriched enclosures. This is due to differences in adult and nymph predation rates, adults having rates 5 times greater than that of nymphs (Riessen 1981). In addition, the predation rate of nymphs is an increasing function of age and prior feeding experience. Thus, the smaller difference in prey densities between control and enriched enclosures on day 28 is probably due to the replacement of adults by nymphs emerging from their larval stage. The resulting low predation rate cannot keep in check the rapidly growing population of Chydorus sphaericus.

As well as affecting the densities of the prey, increased predation can change their relative abundance in the plankton. If water mite predation has equal effects on each prey species, the proportions of the latter should not differ between the control and enriched enclosures. This was tested by comparing observed proportions of each species —in the manipulated enclosures— to expected values —in the control— using chi-square analysis. Table 3 shows that the manipulation significantly affected the relative abundance of prey species on days 7, 14, 21 and 28. Figure 20 illustrates how the proportion of Ceriodaphnia lacustris is depressed in the manipulated enclosure while those of the other species were either unaffected or increased.

Three hypotheses can be advanced to account for such results: the proportion of prey eaten is an increasing function of prey density, prey capture rates are a function of prey type, or water mite predation differentially affected the reproductive rates of its prey. Because water mite swimming speeds are much greater than those of their prey, their encounter radius small, their search pattern randomn (Riessen 1981) and their prey handling time relatively long, their functional response curve is probably of Type 2 (Holling 1965). Thus, the curve describing the number of prey killed as a function of prey density for a given number of predators is characterized by a curvilinear approach to a plateau. This implies that the proportion of prey killed will decrease with increasing prey density.

The second hypothesis appears most plausible since predation rates are a function of prey defense "strategies" (Riessen 1981); Ceriodaphnia lacustris is larger than Bosmina and Chydorus, and thus probably more easily detected by the water mite and easier to grasp. On the other hand, Bosmina and Chydorus, when detecting a predator, execute a "dead-man response" (Kerfoot 1977,1978), which makes them difficult to detect by the water mite. Thus the pattern seen in figure 20 is very likely due to the differential capture of prey by the predator.

The last hypothesis involving a direct effect of predation on prey reproductive rate is highly unlikely, although indirect mediation of prey competitive interactions may well affect prey proportions, as rare opportunistic herbivores might take advantage of the increased resource base.

## TABLE 3

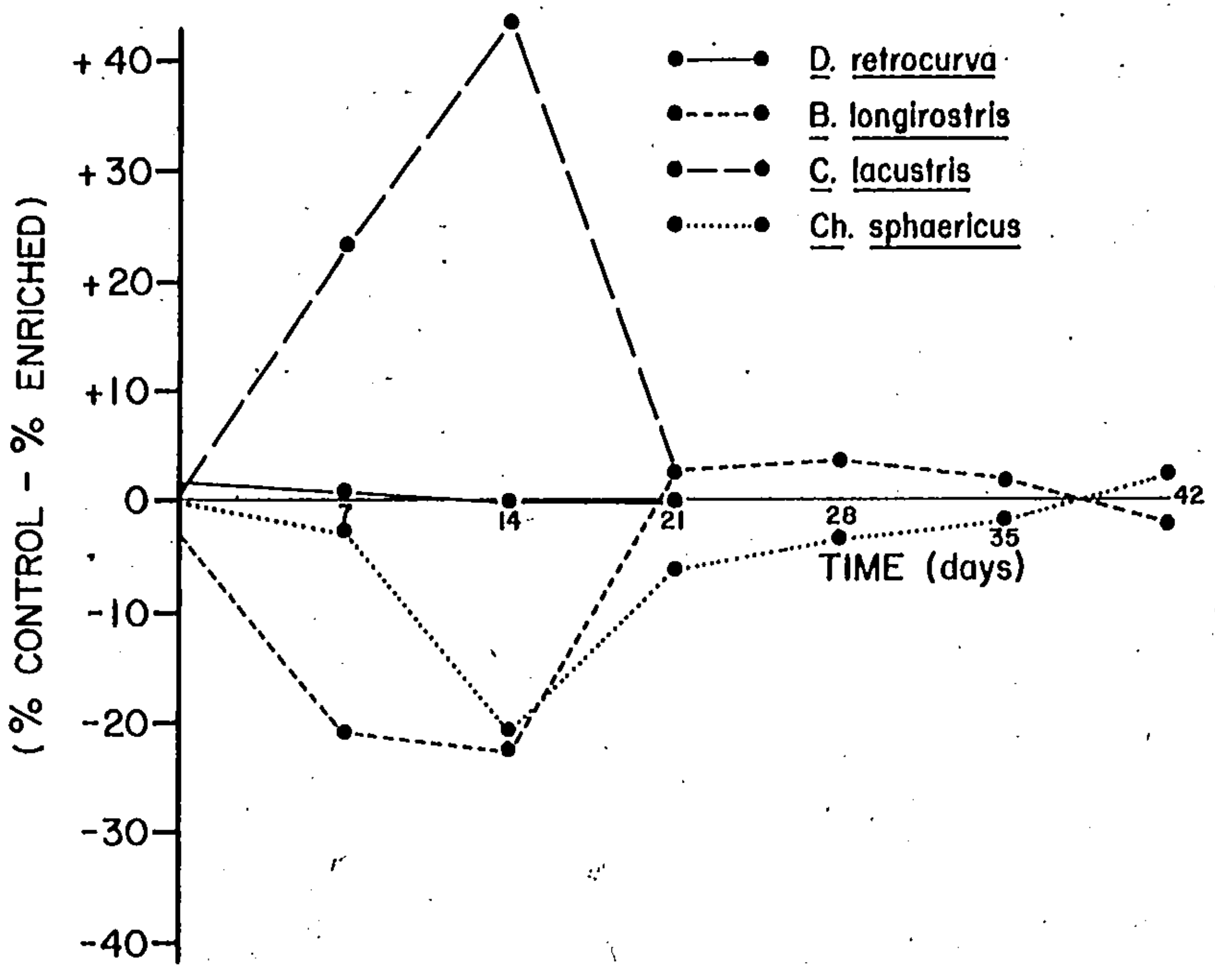
## Observed vs. expected proportions of prey

Observed (O) and expected (E) relative abundance of prey assuming non-selective predation. The chi-square analysis was performed on the absolute, and not on the relative values. shown in the table.

| | TIME (DAYS AFTER TREATMENT) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | | 7 | | 14 | | 21 | | 28 | | 35 | | 42 | |
| | E | 0 | E | 0 | E | 0 | E | 0 | E | 0 | E | 0 | E | 0 |
| <u>DAPHNIA RETROCURVA</u> | 10.0 | 8.2 | 3.8 | 3.0 | 0.4 | 0.4 | 0.2 | 0.2 | - | - | - | - | - | - |
| <u>BOSMINA LONGIROSTRIS</u> | 53.6 | 56.7 | 43.1 | 64.1 | 17.1 | 9.6 | 13.5 | 11.0 | 8.0 | 4.5 | 7.3 | 5.6 | 3.6 | 5.8 |
| <u>CERIODAPHNIA LACUSTRIS</u> | 35.1 | 33.7 | 49.8 | 26.7 | 55.4 | 12.0 | 5.5 | 2.5 | - | - | - | - | - | - |
| <u>CHYDORUS SPHAERICUS</u> | 1.3 | 1.3 | 3.3 | 6.1 | 27.1 | 48.0 | 80.8 | 86.3 | 92.0 | 95.5 | 92.7 | 94.4 | 96.4 | 94.2 |
| $X^2$ | 1.1 | | 324.1 | | 680.7 | | 73.8 | | 9.38 | | 0.98 | | 2.14 | |
| P | NSD | | 0.001 | | 0.001 | | 0.001 | | 0.001 | | NSD | | NSD | |

Relative abundance of the various prey in manipulated enclosures compared to control.

Figure 20: Selectivity of water mite predation


D. retrocurva
B. longirostris
C. lacustris
Ch. sphaericus
(% CONTROL - % ENRICHED)
+40
+30
+20
+10
0
-10
-20
-30
-40
7
14
21
28
35
42
TIME (days)

### 4.2.2 Cropping Rates

The work of Riessen (1981) showed that P. constricta has predation rates averaging 10 to 15 prey/predator/day for adults and 2 to 3 prey/predator/day for nymphs. These rates are much higher than those exhibited by predatory copepods encountered at Heney Lake, which range from 0.07 to 1.3 diaptomid copepodites/predator/day for *Mesocyclops edax* (Confer 1971) and 2 daphnids/predator/day for *Acanthocyclops vernalis* (Brandl and Fernando 1974).

Predation rates are determined in the laboratory and, used alone, do not reflect the ability of a predator population to remove prey. However they can be used to estimate cropping rates of prey in the enclosures (Table 4). The cropping rate C was calculated using the following relationship:

$$C=((P\times Npred)/Nprey)\times 100$$

where P is the predation rate of water mites on their prey, Npred is the density of predators and Nprey is the density of the prey. Table 4 shows that on average there is a difference of one order of magnitude between cropping rates of *P. constricta* prey in control and enriched enclosures. This difference is due to increased mite densities and decreased prey densities in the enriched enclosures. Cropping rates of the dominant predacious copepod in the enclosures, Mesocyclops edax, determined using a predation rate P of 1 prey/predator/day (Confer 1971, Brandl and Fernando 1978), range from 10 to 30% of prey standing stock. Thus, in spite of a much smaller predation rate, the maximum cropping rate of M. edax is five times greater than the maximum cropping rate of P. constricta. This is easily explained by the 100-fold difference between the densities of the two predators.

The maximum cropping rate of 6.4% of the prey population per day by P. constricta is very close to the value of 7.5% found for P. limnetica on cladoceran prey in Madden Lake, Panama (Gliwicz and Biesadka 1975). These rates for water mites are within the range estimated for various predacious copepods. Brandl and Fernando (1979) found that in three lakes in Ontario, Mesocyclops edax cropped between 8.6 and 13.6% of the total zooplankton standing stock per day while Confer (1971) calculated that predation by the same species removed 1 and 6% of the standing crop of Diaptomus copepodites per day in two lakes in Florida. Using the data of McQueen (1969) one can estimate that Cyclops bicuspidatus thomasi was removing nauplii in Marion Lake British Columbia at a rate of 5 to 8% of the standing stock per day. Fedorenko (1975b) found that the larvae of the phantom midge

_Chaoborus_ _trivittatus_ consumed between 2 and 9% of their prey standing-crop daily. It thus seems that low densities and high predation rates of water mites combine to result in cropping rates comparable to the more numerous pelagic crustacean predators.

# TABLE 4

Cropping rates of water mites on their prey

Percentage of the prey population consumed by the water mite population per day.

|  | TIME (DAYS AFTER TREATMENT) |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  | 7 | 14 | 21 | 28 | 35 | 42 |
| CONTROL SET | 0.3 | 0.7 | 0.3 | 0.2 | 0.2 | 0.1 |
| ENRICHED SET | 6.4 | 6.1 | 2.9 | 2.4 | 2.0 | 1.3 |

### 4.2.3 Water Mites and Zooplankton Community Structure

The impact of the manipulations on zooplankton biomass was considerable. The initial two- to three-fold increase in water mite density resulted in a 7-fold difference in concentrations between control and enriched enclosures. This in turn decreased prey densities to values 44% lower on average than those of the controls. This decrease translates in an average drop of total herbivore density by 23%. The consequence of such a reduction in herbivore densities on the phytoplankton community will be discussed in the following chapter.

Although generally ignored in the analysis of zooplankton communities, water mites are found here to be at least as important as the other invertebrate predators in the pelagic zone. There is growing evidence that invertebrate predation plays a major role in the regulation of herbivore biomass (Hall _et al_. 1970, De Bernardi and Giussani 1975, Fedorenko 1975b, Hillbricht- Ilkowska _et al_. 1975, Neill and Peacock 1980). Lane (1979) argues that the major cause of death for Gull Lake zooplankton is invertebrate predation. Although fish are more efficient planktivores, the invertebrate predators are much more numerous and thus have a greater impact on zooplankton biomass. Such results tend to agree with the findings of this study and those of Gliwicz and Biesiadka

(1975) which indicate that water mites have a significant impact on their cladoceran prey.

The important reduction of herbivore biomass by invertebrate predators can potentially lead to competitive interactions between co-occuring predators. In Heney Lake there are five numerically important invertebrate predators in the pelagic zone: *Mesocyclops edax*, *Acanthocyclops vernalis*, *Epischura lacustris*, *Leptodora kindtii* and *Chaoborus*. If they compete for food with water mites, artificially increased densities of the latter should result in lower recruitment of the other predators. Unfortunately the long generation time characteristic of these species does not allow us to detect whether there was a competitive effect during the experiment. However, examination of the degree of overlap between respective diets may indicate whether there is a potential for competition.

Although invertebrate predators, as opposed to vertebrate planktivores, will usually select small sized prey, they seem to be highly selective within this spectrum. The selection of prey has been shown to be a function of the sex, age and density of the predator, and of the swimming motion, the size and the defense tactics of the prey (Jamieson 1980, Williamson and Gilbert 1980, Zaret 1980). Table 5 summarizes all prey preferences of the five major invertebrate predators in the pelagic zone of Heney Lake. Because of temporal and spatial segregation in the distribution of predators and prey (Makarewicz and Likens 1975), the overlap in the diet will not be as high as it seems from Table 5. Fedorenko (1975a) found that predator prey distribution in time and in space was the primary factor determining the composition of the diet of Chaoborus larvae. Thus diet overlap is not sufficient to infer competition between the predators present, particularly since all six occurred in the plankton throughout the most productive period of the lake (Riessen 1981). Only a careful study of the spatial and temporal distribution of both density and growth, along with a knowledge of predation rates and predator selectivity as a function of prey composition could answer this question.

It would appear that the species most likely to compete with water mites are Chaoborus sp. and Leptodora kindtii, since they are the only ones that can prey on species as large as D. galeata mendotae, D. retrocurva or Ceriodaphnia lacustris. In addition, L. kindtii seems to be limited, like P. constricta, to cladoceran prey. Although it is not possible to infer competition between water mites and the other invertebrate predators from the data, L. kindtii would probably be the species most affected by increased water mite densities if resources were limiting. The tracking of prey both temporally and spatially by P. constricta (Riessen 1981) and the absence of predation on the latter suggests that prey availability will be of major importance in regulating its population. Therefore, competition with other invertebrate predators along with factors determining the relative abundance of herbivorous prey species may have a major impact on the water mite population in the pelagic zone of Heney Lake.

TABLE 5

Prey choice of the five invertebrate carnivores

|  | ROTIFERS | NAUPLII | SMALL CLADOCERANS | COPEPODITES | LARGE CLADOCERANS | COPEPODS |
|---|---|---|---|---|---|---|
| CYCLOPOIDS | + | + | + | + |  |  |
| *Epischura* | + | + | + | + |  |  |
| *Chaoborus* | + | + | + | + | + | + |
| *Leptodora* |  |  | + |  | + |  |
| *Piona constricta* |  |  | + |  | + |  |

## 4.3 ZOOPLANKTON-PHYTOPLANKTON INTERACTIONS

The difference in phytoplankton volume between the two sets of enclosures is due entirely to the edible fraction. On day 7, mean edible phytoplankton volume in the enriched set is more than three times greater than that of the control. This results most likely from lower grazing pressure. At that time the herbivore fraction is composed mostly of nauplii that feed essentially on bacteria and detritus (Hillbricht-Ilkowska 1977), and thus have little impact on the edible phytoplankton. Then, the relative decrease of edible algae in the control set is most likely due to the relative increase of group H1. This point is supported by the relative contribution of nannoplankton to total phytoplankton volume (fig. 21). Only on day 7 do I find a significant decrease in relative edible volume in the control enclosures when compared to the treated enclosures (t-test, $P<0.01$).

All four of the phytoplankton species significantly affected by the treatment belong to the edible group. Of these, three are more abundant in the manipulated enclosures, most probably as a result of reduced grazing pressure. The fourth species, <u>Sphaerocystis</u> <u>Schroeteri</u>, shows a trend towards decreasing abundance with low herbivore densities. This is consistent with the findings of Porter (1973,

1976) that the abundance of Sphaerocystis Schroeteri is enhanced by grazing as this green gelatinous alga can survive gut passage, where high nutrient levels increase the growth and productivity of the cells.

The results indicate that, in Heney Lake, nannoplankton biomass is controlled in part by grazing. Other experimental (Hurlbert *et al*. 1972, O'Brien and de Noyelles 1974, Gliwicz 1975, Lynch and Shapiro 1981) and empirical studies (McCauley and Kalff 1981) have shown a similar strong link between herbivore and nannoplankton biomass.

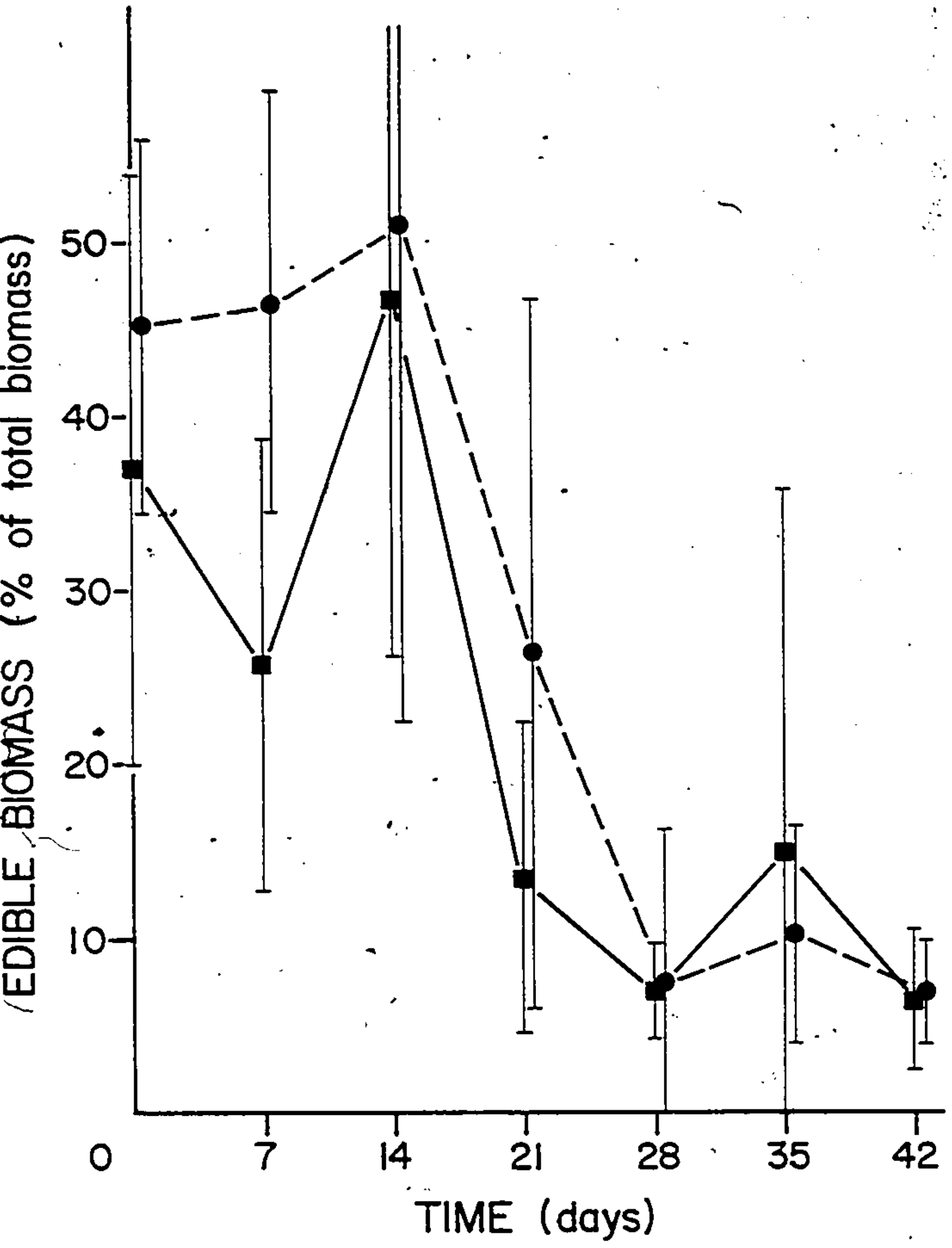
Different herbivore levels lead to differences in algal biomass which in turn determine the availability of nutrients in the water column; the greater the amount of nutrients locked up in biomass the less is available for growth (Gliwicz 1975). In addition, availability of nutrients and their ratios are very important in determining competitive superiority of one species over another (Titman 1976, Tilman 1977, Kilham and Tilman 1979). Therefore, one would expect that the differences in volume lead to differences in the relative abundance of edible phytoplankton species between both sets. However, I find that out of the 23 most abundant species, only four (see Table 6) significantly differed in relative abundance between both sets (two-way analysis of variance). Three of these were edible while the fourth was inedible. Except for the small flagellates each of the species affected was relatively more abundant in the enriched enclosures.

These results might indicate that the smaller species benefited from the treatment. However, one cannot separate the effect of changing nutrient conditions from that of reduced grazing pressure. That the species which responded are edible or, in the case of Dinobryon, close to the edible size criterion and that their relative abundance increased with reduced grazing in most cases, tend to indicate that edible phytoplankton species are not all equally susceptible to grazing. This is confirmed by the greater relative abundance of the small flagellates in the control enclosures; they are possibly not effectively grazed because of their small size and could be favored in an environment characterized by greater herbivore densities.

Along with the changes in relative abundance, one might predict that the increase in volume will be paralleled by a higher species richness of the edible group, simply through biomass increase of the rare species. I find however that the number of species present increased only in the inedible group (see figure 19). Analysing the frequency of occurrence of phytoplankton species in each set reveals what is responsible for such an increase (see Table 7). On days 7 and 21, the average species richness was higher in the enriched enclosures due to certain species found more frequently. The difference in species richness between both sets is not due to new arrivals but to differences in the frequency of occurence. However on days 35 and 42, not only do I find that certain species are found more frequently in the enriched set but that the latter has many more "endemic" species than does the control group. Of the thirteen species responsible for the observed higher species richness observed in the treated enclosures, only 4 ever contribute more than 10% to inedible phytoplankton volume. Therefore the inedible phytoplankton response to the manipulation consisted only of an increase in the frequency of occurrence of species generally contributing very little to net phytoplankton volume. Such results cannot be a direct consequence of reduced herbivore pressure. The only alternative explanation is a possible response of larger species to changes in nutrient conditions in the enclosures.

Contribution of edible phytoplankton to total phytoplankton volume in control (squares) and manipulated (circles) enclosures.

Figure 21: Proportion of edible over total algal volume



EDIBLE BIOMASS (% of total biomass)
50
40
30
20
10
0
7
14
21
28
35
42
TIME (days)

# TABLE 6

Dominance structure of phytoplankton community

|  | EDIBLE PHYTOPLANKTON | INEDIBLE PHYTOPLANKTON |
|---|---|---|
| NO. OF SPECIES CONTRIBUTING 10% OR MORE OF GROUP BIOMASS IN AT LEAST ONE ENCLOSURE AT LEAST ONCE | 25 | 12 |
| NO. OF SPECIES DOMINANT IN AT LEAST ONE ENCLOSURE AT LEAST ONCE | 12 | 11 |
| SPECIES WITH RELATIVE ABUNDANCES SIGNIFICANTLY DIFFERENT BETWEEN THE TWO SETS OF ENCLOSURES | SMALL FLAGELLATES<br>(F= 8.8, N=1, P= 0.005)<br>*CYCLOTELLA* SP.<br>(F= 4.73, N=1, P= 0.03)<br>*ACHNANTES LANCEOLATA*<br>(F= 6.5, N=1, P=0.013) | *DINOBRYON DIVERGENS*<br>(F= 4.7, N=1, P= 0.034) |

## TABLE 7

Frequency of occurrence of inedible phytoplankton species

|  | TIME (IN DAYS AFTER ENRICHMENT) |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | 0 |  | 7 |  | 21 |  | 35 |  | 42 |  |
|  | CN | TR | CN | TR | CN | TR | CN | TR | CN | TR |
| TOTAL NUMBER OF SPECIES IDENTIFIED IN ONE SET | 19 | 17 | 17 | 19 | 17 | 18 | 12 | 17 | 17 | 24 |
| NUMBER OF SPECIES FOUND EXCLUSIVELY IN ONE SET | 4 | 2 | 2 | 4 | 2 | 3 | 1 | 6 | 1 | 8 |
| SPECIES WHICH DIFFER BY AT LEAST TWO ENCLOSURES IN FREQUENCY OF OCCURENCE: |  |  |  |  |  |  |  |  |  |  |
| CN < TR |  |  |  |  |  |  |  |  |  |  |
| *ANABAENA FLOS-AQUAE* | 2 | 4 | 2 | 4 |  |  | 1 | 3 | 1 | 3 |
| *SYNEDRA ULNA* |  |  | 1 | 3 | 2 | 5 | 2 | 4 |  |  |
| *STAURASTRUM QUEBESCENCE* |  |  |  |  | 1 | 3 | 0 | 2 |  |  |
| *NITZSCHIA LINEARIS* |  |  |  |  |  |  | 0 | 2 | 0 | 4 |
| *MELOSIRA GRANULATA* | 0 | 2 |  |  |  |  |  |  |  |  |
| *OEDOGONIUM* SP. |  |  | 1 | 5 |  |  |  |  |  |  |
| *ASTERIONELLA FORMOSA* |  |  | 1 | 4 |  |  |  |  |  |  |
| *TABELLARIA FENESTRATA* |  |  | 2 | 5 |  |  |  |  |  |  |
| *OSCILLATORIA LIMNETICA* |  |  | 2 | 5 |  |  |  |  |  |  |
| *PERIDINIUM* SP. |  |  | 0 | 2 |  |  |  |  |  |  |
| *ANABAENA* SP. |  |  |  |  |  |  | 0 | 2 |  |  |
| *SCHROEDERIA SETIGERA* |  |  |  |  |  |  |  |  | 1 | 3 |
| *APHANIZOMENON FLOS-AQUAE* |  |  |  |  |  |  | 1 | 4 |  |  |
| CN > TR |  |  |  |  |  |  |  |  |  |  |
| *MOUGEOTIA* SP. | 3 | 0 |  |  |  |  |  |  |  |  |
| *OEDOGONIUM* SP. | 2 | 0 |  |  |  |  |  |  |  |  |
| *ASTERIONELLA FORMOSA* |  |  |  |  |  |  |  |  | 3 | 1 |
| *ANABAENA* SP. |  |  | 2 | 0 |  |  |  |  |  |  |

## 4.4 COMMUNITY RESPONSE TO THE MANIPULATION

Because of the complexity and dynamic character of planktonic systems, the effects of the manipulation on the primary producers can only be interpreted if one distinguishes different periods of the experiment.

The results observed and discussed in the preceeding sections clearly indicate that the sequence of events in the enclosures can be divided into three distinct periods. The variables most influencing community interactions and the resulting impact of the water mites on these variables are very different from one period to the next. The characteristics of these three phases are summarized in Tables 8 to 10.

### 4.4.1 Sampling Days 7 and 14

During the first two weeks, the control enclosures are characterized by relatively high nannoplankton volume and high densities of large and efficient cladoceran grazers. This state of the plankton community is comparable to that of oligotrophic lakes described by Nilssen (1978) and to the early summer successional stage of the plankton as described by Gliwicz and Hillbricht-Ilkowska (1972). The smaller edible algae have the ability to monopolize nutrients much faster than the large algae because of higher surface:volume ratios, thus allowing greater growth and turnover rates of their populations. This allows larger, more efficient, herbivores to dominate their trophic level in the community (Gliwicz 1977).

The maintenance of high nannoplankton volume through reduction of herbivore densities in the enriched enclosures has two consequences for species richness. First, lower grazing pressure allows the rare species of nannoplankton to become detectable (see figure 18). Second, more nutrients are locked up in biomass and so less are available in the water column. Because zooplankton supply 10 times more phosphorus and 3 times more nitrogen to the epilimnion during thermal stratification than all external sources combined (Lehman 1980), lower herbivore densities will mean less nutrient regeneration in the water column. Such a change in nutrient availability may lead easily to a shift in the competitive ability of the species present and allow some rare large species to grow as was observed on day 7 (fig. 19). While grazing determines phytoplankton biomass, it is nutrient availability and ratios that determine in the end which phytoplankton species will be present, as suggested by Lynch and Shapiro (1981).

### 4.4.2 Sampling Days 21 and 28

This period is characterized by rapid changes in a number of variables in the community. Nilssen (1978) has proposed that the ability of small algae to lock up nutrients in biomass during rapid population growth reduces available nutrients to very low levels and consequentely leads to the the population crash of nannoplankters. He argued that this in turn would favor large and slow-growing algae. This nutrient loss from the system is compounded by the "enclosure effect" described by Briand and McCauley (1978) who showed that sealing the enclosures at the bottom prevents nutrient input from the sediments and from the surrounding waters. This seems to explain the trend observed in the control enclosures. During the second period the relative volume of nannoplankton drops from approximately 45% to less than 10% of the total volume. Not only do the large algae become dominant in relative terms, but their volume increases 5-fold between day 14 and day 28. During that time the large filamentous green alga Mougeotia becomes the dominant species of the whole phytoplankton assemblage. Although this species is not truly pelagic but rather periphytic, its appearance and subsequent impact is consistent with the hypothesis formulated above and in the rest of the discussion.

The increase in net phytoplankton in the enclosures is paralleled by a decrease in the large grazers and by a rapid increase in the abundance of the small grazer Chydorus sphaericus. This is in agreement with the work of Gliwicz (1977) who showed that increased abundance of large algae interfered with the filter feeding apparatus of cladocerans. This results in reduced filtering rates, feeding rates and fecundity of the large herbivores. Under such circumstances small herbivores such as Chydorus sphaericus are the superior competitors.

Higher densities of water mites during this phase had a very limited effect on herbivore density and no significant effect on phytoplankton volume and species richness. Because of the rapid increase in the population of Chydorus sphaericus, the predator is swamped. Thus the difference in herbivore densities between both sets is relatively small. Although nannoplankton volume is consistently greater in the manipulated enclosures, this difference is very small. Overall, it seems that the changes in the phytoplankton community structure brought on by changes in the nutrient regime of the enclosures are overwhelming and consequently override and mask the impact of the predator additions.

### 4.4.3 Sampling Days 35 and 42

During this last sampling period the community structure appears relatively stable, compared to the previous period. The phytoplankton is characterized by high volume values and a very large fraction of net phytoplankton. The latter is dominated by the large filamentous green Mougeotia. Because of the high algal volume, one can assume that nutrient availability is low. This environment favours the maintenance of a large population of the small grazer Chydorus sphaericus.

The effect of increased predation on this system is to significantly reduce herbivore levels. Indeed, the dominant grazer in the enclosures, Chydorus sphaericus, is subjected to heavy predation by the water mite nymphs; this contrasts with the previous period where the growth of the population was much greater than the cropping rate.

Ch. sphaericus is too small a herbivore to effectively graze the edible phytoplankton. It feeds most efficiently on particles smaller than 10 um (Gliwicz 1980) and usually on bacteria and detritus (Hillbricht-Ilkowska 1977). For this reason, the phytoplankton structure in this last period is most favorable for Ch. sphaericus. The large fraction of ungrazable algae contributes largely to an increasing amount of particulate organic matter and dissolved organic matter which favour the growth of bacteria (Gliwicz and Hillbricht-Ilkowska 1972). One can predict that reduced *Ch. sphaericus* densities will not lead to changes in nannoplankton volume. This is exactly what is observed (fig. 14), as the differences between the two sets are at their minimum.

Because herbivores are less abundant in the manipulated enclosures we expect lower nutrient regeneration to the water column and thus lower nutrient availability (Lehman 1980). This shift in nutrient regime allows a change in the competitive ability of the phytoplankton species and allows an increase in species richness, as rare inedible species become more frequent in the enriched set of enclosures (see figure 19)

# TABLE 8

## Community response to the manipulation: sampling days 7 and 14

|  | CONTROL SET | EFFECT OF ENRICHMENT |
|---|---|---|
| ZOOPLANKTON | _ HIGH DENSITY OF LARGE EFFICIENT GRAZERS | _ LOWER DENSITY OF LARGE EFFICIENT GRAZERS |
| PHYTOPLANKTON | _ RELATIVELY HIGH PERCENTAGE OF EDIBLE PHYTOPLANKTON BIOMASS | _ HIGHER PERCENTAGE OF EDIBLE BIOMASS<br>_ HIGHER ABSOLUTE EDIBLE BIOMASS<br>_ HIGHER EDIBLE SPECIES RICHNESS (TREND)<br>_ HIGHER INEDIBLE SPECIES RICHNESS (SIGNIFICANT) |

## TABLE 9

Community response to the manipulation: sampling days 21 and 28

|  | CONTROL SET | EFFECT OF ENRICHMENT |
|---|---|---|
| ZOOPLANKTON | _ DECREASING DENSITY OF LARGE EFFICIENT GRAZERS<br>_ INCREASING DENSITY OF SMALL GRAZERS | _ RELATIVELY SMALL IMPACT ON ZOOPLANKTON |
| PHYTOPLANKTON | _ LARGE DECREASE OF RELATIVE EDIBLE BIOMASS<br>_ INCREASING BIOMASS OF THE LARGE FILAMENTOUS ALGA *MOUGEOTIA* | _ NO EFFECT |

TABLE 10

Community response to the manipulation: sampling days 35 and 42

| | CONTROL SET | EFFECT OF ENRICHMENT |
|---|---|---|
| ZOOPLANTON | _ HIGH DENSITY OF SMALL GRAZERS | _ LOWER DENSITY OF SMALL GRAZERS |
| PHYTOPLANKTON | _ HIGH PERCENTAGE OF INEDIBLE ALGAE<br>_ DOMINANCE OF THE LARGE FILAMENTOUS ALGA *MOUGEOTIA* | _ NO CHANGES IN BIOMASS<br>_ NO CHANGES IN RELATIVE ABUNDANCE<br>_ HIGHER SPECIES RICHNESS OF INEDIBLE ALGAE |

## 4.5 SUMMARY AND CONCLUSIONS

During the whole experiment the impact of increased water mite densities on the community was only noticeable during certain periods: the first two sampling dates and the last two. During both phases, the community was relatively stable with respect to species composition, relative abundance and size structure of the components of the food web. In the first two weeks the plankton community can be generally described as a "grazing" food web (Hillbricht-Ilkowska 1977) where a large fraction of the phytoplankton biomass is edible and effectively grazed and controlled by herbivores. During this period the increased water mite densities have a marked impact on herbivore densities and phytoplankton biomass. In the final two weeks of the experiment the plankton community can be described as a "detrital" food web where almost all of the phytoplankton biomass is unavailable to grazers which feed mainly on bacteria and detritus. The community utilizes the energy available less efficiently and in consequence the impact of water mites limits itself only to controlling the herbivore compartment.

During these two different but relatively stable states of the plankton community the water mites play a significant role in the direct regulation of herbivore densities and indirect control of phytoplankton biomass when the latter is efficiently utilized by the grazers. During the transition period however, when the community undergoes radical changes due to major shifts in nutrient availability, the impact of the water mites is insignificant. The effects of water mite predation are simply overwhelmed by those of shifting nutrient availability. Changes in absolute and relative nutrient levels bring about a radical change in the size structure of the phytoplankton biomass and, in consequence, a shift in the herbivore species composition. In the face of such large-scale changes, the impact of water mites was negligible.

### 4.5.1 Water mites vs. other invertebrate carnivores

The insignificance of water mite predation when large scale changes occur in the community is not atypical of invertebrate predators. Those, like Piona constricta, have been termed size-dependant predators (SDP) by Zaret (1980) and are characterized by a bell shaped prey size electivity curve (fig. 22a). The left hand side of the curve indicates a preference for larger prey but the right hand side shows the increasing difficulty of handling prey with increasing prey size. This implies that the occurence of each species of invertebrate carnivore will be limited to those times when its optimum prey is present in large enough numbers;

this indeed has already been suggested for P. constricta (Riessen 1981). For his part Neill (1981) showed that increased densities of the invertebrate Chaoborus in enclosures had no long-term effects on the zooplankton community and that the changes were obliterated when favourable conditions allowed for the rapid growth of prey populations. Therefore, as with the water mites in this study, invertebrate predators will probably not have more than a quantitative impact on their prey populations. They regulate their prey densities without actually altering the structure of the community.

### 4.5.2 Water mites vs. vertebrate planktivores

This is in contrast to the effects of gape limited predators (GLP) like fish or salamanders which are characterized by the prey size electivity curve in figure 22b. This curve indicates a preference for large prey, with the maximum prey size being determined by the gape or maximum diameter of the mouth of the predator. The role of fish in determining the size structure of zooplankton has been extensively recorded (Brooks and Dodson 1965, Galbraith 1967, Hall et al. 1970, Hrbacek 1962). These studies showed conclusively that planktivorous fish maintained zooplankton populations of small-sized individuals. Their introduction in fishless lakes or ponds led to the elimination of large-sized zooplankton species and their replacement by small species; however the total zooplankton biomass did not change.

The strong structuring effects of nutrients and vertebrate planktivores on the pelagic plankton community do not relegate Piona constricta to a minor role. The water mite plays an important regulatory part in determining herbivore densities and thus the flow of energy from the primary producers. Hillbricht-Ilkowska (1977) found that invertebrate predators frequently consumed close to 100% of the herbivore production, with 20% of the latter transformed into predator biomass, while "...fish communities less efficiently utilize the production of zooplankton in natural conditions..." although "...fishes constitute a strong structure forming factor, through selective feeding on zooplankton...".

### 4.5.3 Importance of trophic position

Among the invertebrate carnivores of Heney Lake, the unique position of Piona constricta in the food-web, as a top predator, does not give it a more important role in the organisation of the community. This study has shown that it differs very little from the other invertebrate carnivores in its inability to structure the community. This is in contrast with the impact that planktivorous fish have on the system, whether they are top predators or not. The structuring role played by fish is probably related to the strong size-selective pressure which they put on the competitively dominant zooplankton species; this, in turn, favours the presence of smaller species and their associated invertebrate predators which are highly dependant on the availability of specific prey. Recently Paine (1980) suggested that, in intertidal communities, strong interactions between a predator and competitively superior prey can generate subsystems composed of species co-adapted to one another. This appears also true for pond communities structured by salamanders (Dodson 1970, Giguere 1979) and might explain the finding that in 16 swedish lakes, the water mite <u>Piona carnea</u> is never found in the absence of fish (Eriksson <u>et al</u>. 1980).

Whereas the precise determination of interaction strength in food-webs will be ultimately necessary to understanding how communities are structured, topology is essential in determining the path of energy flow through the system. In fresh-water pelagic communties, carnivorous invertebrates effectively reduce by 20 to 25% the zooplankton production available to planktivorous fish and fish larvae because of the losses involved in the transfer of energy from one trophic level to the next (Sprules 1980). In Heney Lake, <u>P. constricta</u> not only consumes part of the zooplankton production, but its own resultant production is made unavailable to higher trophic levels. This may have important implications for fisheries management in lakes.

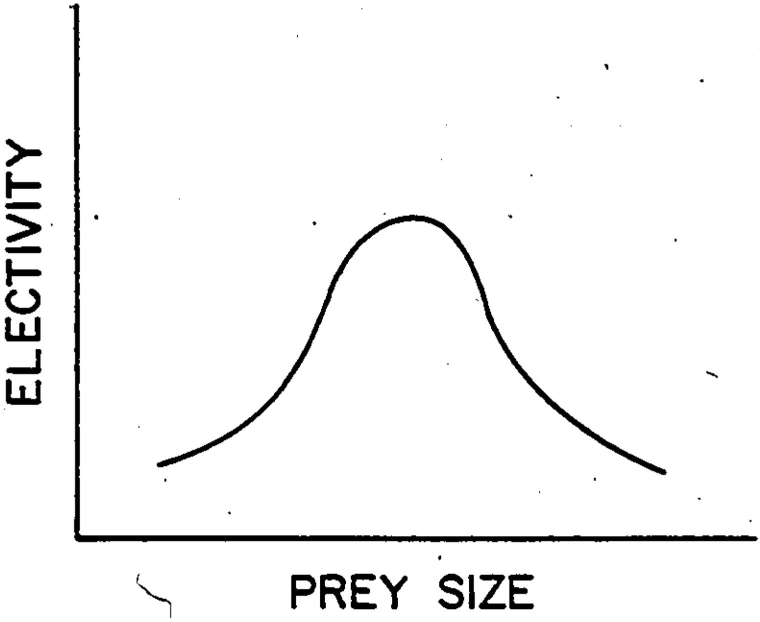
A: size electivity curve of size dependant predators

B: size electivity curve of gape-limited predators

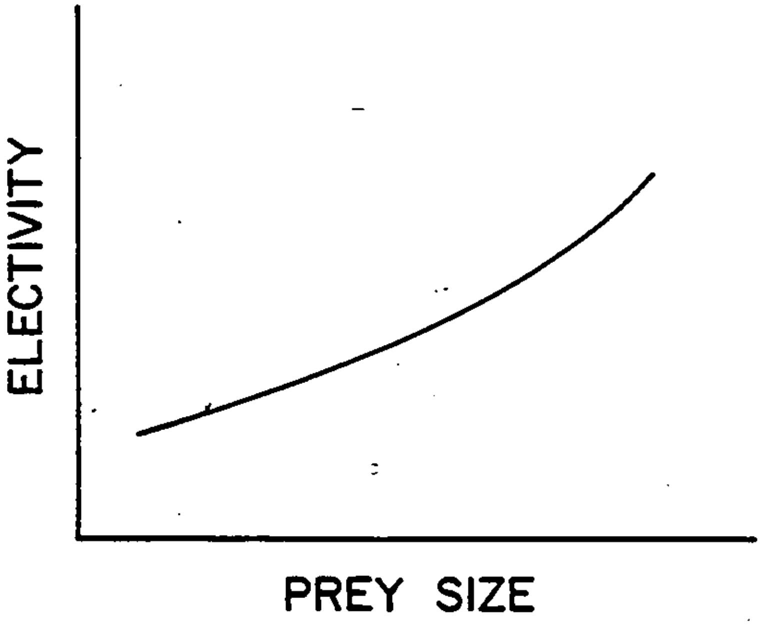
from Zaret (1980)

Figure 22: Size electivity

A



B



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