EFFECTS OF MACROGRAZERS AND MICROGRAZERS ON ENCLOSED, IN SITU PHYTOPLANKTON ASSEMBLAGES IN A NEWFOUNDLAND LAKE

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EFFECTS OF MACROGRAZERS AND MICROGRAZERS ON ENCLOSED, *IN SITU* PHYTOPLANKTON ASSEMBLAGES IN A NEWFOUNDLAND LAKE.

By

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ABSTRACT

The effects of macrograzing and micrograzing on enclosed, *in situ* phytoplankton assemblages were examined in a Newfoundland lake. Chambers, with inner and outer compartments, were deployed in Hogan's Pond during three experiments each lasting 13 days. Samples were collected every other day from both chamber compartments and the lake water. In two experiments, the macrograzer *Diaptomus minutus* (Copepoda) was initially added to the outer compartment of the grazed chamber, and in a third experiment *Bosmina longispina* (Cladocera) was added. Macrograzer metabolites were able to pass through fine gauze between the two compartments. Thus the chemical effects of the macrograzers were observed in the inner compartment while the physical effects were the dominant treatment in the outer compartment. Micrograzer effects were investigated in chambers without added macrograzers in all three experiments.

Micrograzing effects, the physical effects of macrograzers, and the chemical effects of macrograzer metabolites on phytoplankton assemblages were evaluated. Grazing effects were examined in each experiment by *a priori* comparisons of phytoplankton densities between the chamber compartments and the lake water.

Densities of some of the desmid species were depressed by the physical effects of macrograzers. Some individual taxa, such as *Arthrodesmus triangularis* var. *rotundatus* and *Mesotaenium* sp., were augmented under the chemical effects of the macrograzer metabolites. Physical effects of macrograzers were more marked than the micrograzer effects on the Chlorophyceae and the microflagellates. Micrograzers may affect the species composition and abundance of the

chlorophycean taxa within phytoplankton assemblages.

With the exceptions of *Synedra* sp. and *Tabellaria fenestrata* var. *lacustris* the diatoms were unaffected by the grazers. The Chrysophyceae were little affected by micrograzing and physical effects of macrograzers, in contrast to chemical effects of macrograzer metabolites that were evident for individual species. Several of the Cyanophyceae were augmented in the presence of micrograzers; some individual species, *e.g.*, *Microcystis aeruginosa*, were augmented by both physical and chemical effects of macrograzers.

Key words: Macrograzers, micrograzers, phytoplankton, assemblages, Newfoundland, lake.

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INTRODUCTION

Phytoplankton abundance and its ecological impact in aquatic environments is influenced by grazing, a broad term describing the activity of animals feeding on living plants. The rest of the aquatic animal community depends to a large extent on the algivorous zooplankton (Round 1984).

Algivorous zooplankton may be classified into two groups based on size: macrograzers (larger than 125 μm, usually large enough to be seen with the naked eye), such as post-juvenile copepods and cladocerans, are typically larger than the largest phytoplankter they encounter. Micrograzers (125 μm and smaller), such as rotifers and protozoans, are often similar in size to the larger phytoplankton.

Aims of the investigation

The main aim of this investigation was to examine responses of individual phytoplankton species within natural assemblages to different grazing regimes. The study evaluated micrograzing effects separately from both the physical effects of macrograzers and the chemical effects of their metabolites on phytoplankton assemblages. The study was conducted on phytoplankton assemblages enclosed in grazing chambers (each with two compartments), *in situ*, in a Newfoundland lake during the summer of 1985. There is a limited literature on the biology of the fresh waters of Newfoundland and much of the work previous to that of Davis (1972a) consists only of species lists. Earle *et al.* (1987) related environmental factors to phytoplankton distribution in a large number of Newfoundland lakes. The current study is the first to examine the effects of zooplankton grazers on enclosed phytoplankton species in a Newfoundland lake, although similar studies have been conducted elsewhere.

Rigler (1975) distinguished two distinct schools of limnological thought; the Holists, who deal with properties of the intact system, and the Reductionists, who study isolated components of the system. This study involves some careful manipulation of algivorous grazers and provides a situation where the ideas of both schools of limnology may be drawn together. The responses of individual phytoplankton taxa within phytoplankton assemblages under the influence of macrograzing and micrograzing effects were examined. Enclosed phytoplankton assemblages were exposed to grazing regimes in a holistic manner, while the responses of individual taxa to the various grazing effects were examined in a reductionistic manner.

Macrograzing

Grazing studies have tended to concentrate on the effects of food on the biology of macrograzers. Such studies have typically examined the effects of different foods and food densities on filtering (Burns and Rigler 1967, Thompson *et al.* 1982, Richman and Dodson 1983) and feeding rates (McMahon and Rigler 1965, Kersting and van der Leeuw 1976, DeMott 1982, Price and Paffenhöfer 1986), respiration (Porter *et al.* 1982, Richman and Dodson 1983), fecundity (Slobodkin 1954, Frank 1957, Hebert 1978, Carvalho and Hughes 1983) and feeding behaviour (Berman and Richman 1974, Gophen *et al.* 1974, Horton *et al.* 1979) of various macrograzer species.

There has also been a focus on selective feeding. Food selection is the ability of animals either to ingest preferentially or to avoid some kinds of foods, and may depend on the animals' ability to detect food and on functional specialization of feeding appendages (Bloem and Vijverberg 1984, Omori and Ikeda 1984).

Nutritional requirements may be an indirect cause of food selection (Taub and Dollar 1968, Horton *et al.* 1979), but they are unlikely to facilitate food selection. Both size (Burns 1968, Lampert 1974) and abundance of available food (Berman and Richman 1974) are important factors in food selection.

Much of the evidence for selective grazing has come from studies involving analyses of zooplankton gut contents. These studies allow direct comparison of phytoplankton consumed with those available in the water. However, such studies tend to underestimate easily digested forms such as flagellates, and overestimate algal cells that escape digestion, including the silica frustules of many diatoms (Bacillariophyceae) and mucilaginous members of the Chlorophyceae such as *Sphaerocystis schroeteri* (Porter 1976). This has been recognised by a few authors (*e.g.*, Ferguson *et al.* 1982) who did not regard the presence of recognisable algal remains in the animals' guts as necessarily implying that the algal taxa represented a major nutritional source for the animals.

The influence of grazing zooplankton on phytoplankton assemblages has received less attention than the effects of different foods on zooplankton biology. Gauld (1950) reported that the lack of response from the phytoplankton to the distribution of fertilizers in a sea-loch was, at least on some occasions, due to the effects of zooplankton grazing. Round (1984) stated that "grazing undoubtedly influences the specific composition of algal assemblages though there are few data on this aspect" of algal ecology.

Grazing does not always have a negative influence on individual species. Bergquist *et al.* (1985) assessed the responses of phytoplankton to two different body-sized zooplankton communities. They found that large phytoplankters (>

100 μm), *e.g.* , *Aphanocapsa* spp. and *Dinobryon* spp., increased in density when exposed to large grazers, dominated by *Daphnia pulex* and *Diaptomus oregonensis*, *cf.* macrograzers of this study. Small algae (< 25 μm), *e.g.* , chlorococcales, increased in density in response to grazing by small grazers which included small copepods, *Bosmina longirostris*, and rotifers.

Micrograzing

Freshwater micrograzers are predominantly protozoans and rotifers, and seasonally include some juvenile macrograzers. These are known to feed on phytoplankton, bacteria, particulate organic matter and detritus (Garnett 1953). Evidence of micrograzer consumption of phytoplankton is beginning to accumulate as micrograzers are increasingly recognised as competitors with macrograzers for resources. Population growth of rotifers, has been reported to be suppressed by the presence of macrograzers (*e.g.* , cladocerans: Neill 1984, Gilbert and Stemberger 1985).

Suttle *et al.* (1986) isolated colourless microflagellates (6-14 μm in diameter) from lake water. These microflagellates frequently ingested entire diatom cells (*Synedra* sp.) up to six times their own diameter, digested the contents and then egested the empty frustule. Observations were made of similar flagellates free-swimming and attached to diatoms in the Great Lakes, suggesting that the laboratory observations were not artifacts. Grazing of this type may be widespread and its effects may contribute significantly to the species composition of natural phytoplankton assemblages.

Grazing effects

Most primary producers are influenced by grazing, and natural populations may be regarded as the residue of grazing (Ferguson-Wood 1967). The effects of grazing on primary producers may be considered in three categories: physical, chemical, and biological.

Physical effects result from consumption of part(s) of primary producers (*e.g.*, cells of an algal colony such as *Uroglena volvox*, leaves of a tree) or of whole organisms (*e.g.* , unicellular algae such as *Chlorella vulgaris* and non-colonial diatoms), and structural damage (*e.g.* , breaking of phytoplankton spines, trampling of higher plants). Physical effects tend to result from direct actions, with the exception of detrital production. Detritus in the water column absorbs significant amounts of light and thus reduces light available for photosynthesis and phytoplankton growth (Jewson and Taylor 1978). The bodies of algivorous zooplankton may absorb light and may similarily influence photosynthesis when present in sufficient numbers, *e.g.* , *Daphnia* spp. in enriched shallow ponds. Under usual conditions in aquatic environments zooplankton are probably not abundant enough to reduce the amount of light available for photosynthesis significantly.

Chemical effects typically result from indirect interactions between primary producers and grazers, and include nutrient enrichment via excretory and respiratory products (*e.g.* , an increase in the amount of carbon dioxide in the environment may lead to an increase in photosynthesis and plant growth). Growth inhibition of the primary producers may also occur via metabolic products from the grazers. Evidence of these effects tends to be secondary to evidence of physical

effects, but can occasionally be more drastic (*e.g.* , toxins released by members of the Cyanophyceae), and such effects are often mediated allelopathically as are biological effects.

Biological effects usually occur as a consequence of chemical and physical effects. They result from food selection or avoidance, and competition among primary producers for available resources (*e.g.* , space and nutrients). Life history strategies and modes of reproduction contribute to the ways in which species respond to grazing and the resulting inter- and intra-specific competition.

Allelopathy and grazing deterrents

The word allelopathy was originally proposed by Molisch (1937) to describe the influence of one plant on the physiology of others, and was derived from two greek words meaning reciprocal harm. More recently, allelopathy has been used to describe both inhibitory and stimulatory, reciprocal, biochemical reactions between all types of plants (Rice 1984), and between phytoplankton and algivorous zooplankton, in particular inhibitory reactions (*e.g.* , Ryther 1954, Ostrofsky *et al.* 1983). Allelopathy depends on biochemical compounds being added to the environment and may influence aquatic grazing interactions.

Rice (1984) reviewed allelopathy among phytoplankton and explored its role in phytoplankton succession. He stated that there is strong evidence for the production of phytoplankton inhibitors by other phytoplankton under culture conditions. Ryther (1954) reported that the filtering rate of *Daphnia magna* was inhibited by substances produced by *Chlorella vulgaris*, *Scenedesmus quadricauda* and *Navicula pelliculosa*. The inhibitory product of *C. vulgaris* seemed to be

identical to the antibiotic chlorellin described by Pratt *et al.* (1945).

Ostrofsky *et al.* (1983) reported that *Daphnia pulex* showed low fitness, in terms of survivorship and reproduction, in algal-free filtrates of log phase *Anabaena flos-áqua* than in control cultures. The authors suggested that such extracellular metabolites of phytoplankton serve an ecological function by deterring grazers from consuming them.

Investigating the production of such inhibitors under natural as opposed to laboratory conditions would be very difficult as the water contains materials produced by other plants and animals, in addition to any biochemicals produced by the phytoplankton. However, from results of laboratory studies Rice (1984) suggested that "fluctuations in numbers of phytoplankton and succession of species with time is controlled, at least in part, by allelopathic interactions".

Ecological implications of grazing

Although laboratory investigations have provided much information on aquatic grazing interactions, caution must be exercised when transferring laboratory data to the ecosystem (Allen 1977).

Jewson *et al.* (1981) found grazing to be one of the factors influencing the growth and decline of diatoms in Lough Neagh, Northern Ireland. These authors also reported that grazing by zooplankton and the sinking of dead phytoplankton cells were responsible for the major losses of phytoplankton from the euphotic zone.

Algivorous zooplankton may enhance primary production by regenerating nutrients such as phosphorus (in phosphates) and nitrogen (as ammonia) (Lehman

1980a, b). These are examples of chemical effects of grazers. Bacterial degradation of incompletely digested remains of egested algal cells supplies nutrients to "dissolved pools" from which they are rapidly sequestered by the phytoplankton (Lehman 1980b). The presence of grazers in an aquatic ecosystem will increase the movement of organic matter between trophic levels (Lehman 1980a). Growth of grazed phytoplankton species and their competitors may be enhanced by regenerated nutrients. Nutrient regeneration is extremely important when phytoplankton growth is nutrient limited. Recycling efficiency will be less than complete. Nutrients taken up by ungrazed phytoplankton species are less likely to be recycled *in situ* than those taken up by grazed phytoplankton. This accumulation of nutrients in ungrazed species within the phytoplankton assemblage may contribute towards the dominance of the larger phytoplankton species, such as *Peridinium* sp. and *Ceratium* sp., over smaller ones (Reynolds 1984).

MATERIALS AND METHODS

Study site

The study was conducted in Hogan's Pond (47°35'N, 52° 51'W), a lake with an area of 60.1 hectares (Davis 1972b), on the Avalon Peninsula of Newfoundland. This lake is 140 m above sea-level, has a maximum depth of 12 m and an average depth of 5 m, and has no permanent inlets, with most of the water supplied via springs (Davis 1972b).

Hogan's Pond is a rock-basin of glacial origin and is surrounded by wooded areas, patches of marsh, and private residences. The littoral areas are rocky, with very few aquatic vascular plants even in the shallow parts. The rocky bottom is covered by mud which is inhabited by a prolific benthic diatom population. The lake is polymictic due to the locally strong winds and the moderate depth of the lake (Davis 1976), except during the winter months of ice cover when inverse thermal stratification may occur. (See Yoxall 1981 for further hydrographical details).

Hogan's Pond was chosen for this study for several reasons: the phytoplankters were diverse, and occurred in association with algivorous zooplankton species (Davis 1972a, 1972b, and 1976; Woodhead and Tweed 1960); such an assemblage was suitable for an investigation of the effects of zooplankton grazing on phytoplankton. The lake is readily accessible (12.5 km by road) from St. John's, but is not exposed to urban eutrophication; although Hogan's Pond is not eutrophic, it is enriched relative to other Newfoundland and boreal lakes (Davis 1972a).

In situ chambers

Experiments were conducted using plexiglass chambers (Figure 1) containing filtered lake water. Chamber size was limited by the weight of water (about 14 kg) which could be lifted out of and lowered into the lake from a boat or canoe and to the standard sizes of plexiglass cylinders available for construction. Plexiglass cylinders (38.7 cm long, 19.6 cm inner diameter) were used as external walls. Chamber tops and bases were cut from plexiglass sheets (1.25 cm thick) with centering grooves to hold the internal plexiglass cylinders (13 cm inner diameter), which divided the chambers into inner and outer compartments. Sampling ports (1.2 cm in diameter) with screw caps in the tops of the chambers, allowed sampling of each compartment (Figure 1).

Two openings (6.5 cm x 30 cm) were cut in each inner cylinder and covered with 5 μm nylon monofilament bolting cloth or gauze glued at the edges (Figure 1) with Lepage^{TM} china-weld cement. These gauze-covered openings allowed small particles (less than 5 μm), including metabolites, nutrients and dissolved gases, to exchange between the two compartments; this facilitated examination of some of the chemical effects of macrograzing. Such exchange of material is dependent upon diffusion and lake water movement. Under controlled laboratory conditions in which diffusion was virtually the only movement, six drops of food colouring were added without stirring to the inner compartment. Water in both the outer and inner compartments developed the same colour intensity within two hours.

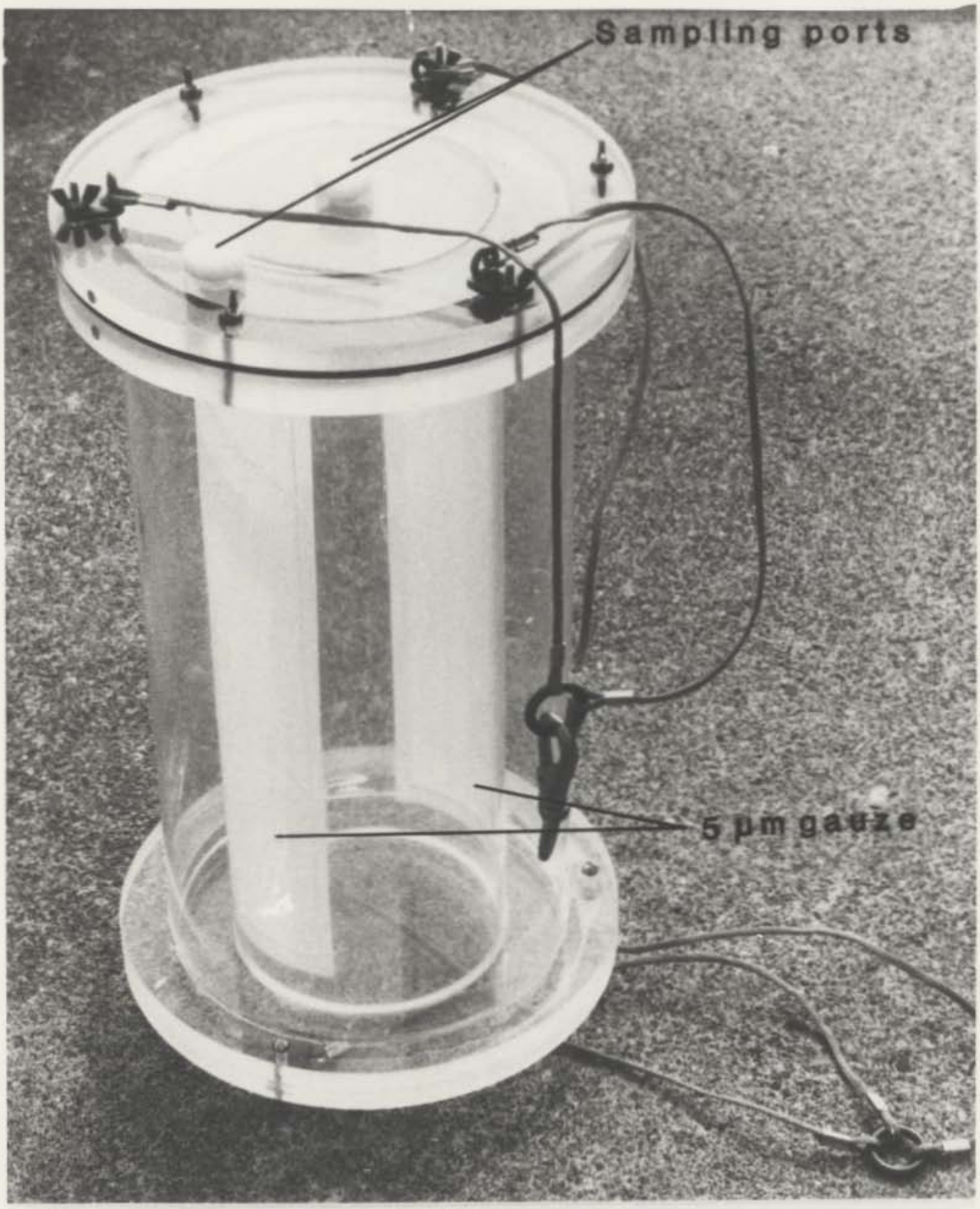


Figure 1: Grazing chamber.

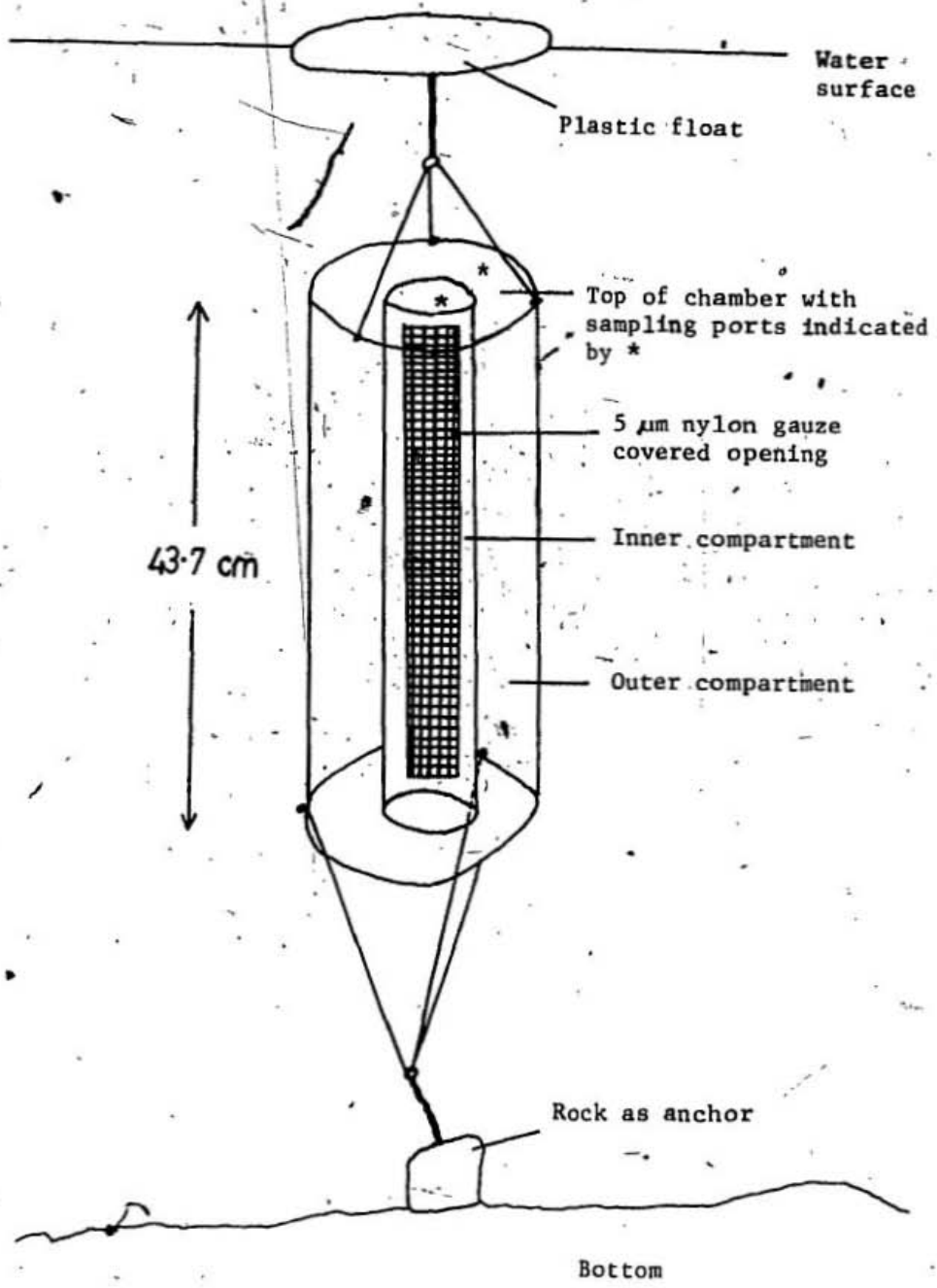


Figure 2: Diagram of grazing chamber suspended in lake.

A rubber gasket was placed between the top plate of the chamber and the reinforcement ring of plexiglass around the top of the outer cylinder on which the top plate was aligned. This gasket ensured that the chamber was water and gas tight when sealed. All materials used in the construction of the chambers were established as non-toxic to plankton (Dyer and Richardson 1962), prior to their use.

Deployment of chambers

Lake water was filtered through a 125 μm mesh net to remove the macrograzers with minimal effect on the remaining plankton (Porter 1973). The inner cylinder was lowered through the filtered water enclosed by the outer wall of the chamber, and sealed into the grooves with silicon grease. An air space of approximately 1 cm was left at the top of each chamber throughout the experiments.

The chambers were suspended from floats in 1.7 - 2.0 m of water (Figure 2), and anchored in position (Figure 3, page 16). The tops of the chambers were 0.7 m below the water surface. The phytoplankton and micrograzers were allowed to acclimatize for 24 hours before the macrograzers were introduced.

Macrograzers were collected with a 125 μm mesh vertical plankton tow 24 hours before each experiment. They were then identified and sorted. Pennak (1978) and Davis (1976) were used for the zooplankton identifications. The dominant macrograzer in the water column the day before each experiment was initiated was used as the macrograzer for that experiment, at a density of approximately four times that calculated for the lake water sampled. Adult

macrograzers, *Bosmina longispina* Leydig or *Diaptomus minutus* Lilljeborg, were added to the outer compartment of the "grazed" chamber (Table 1).

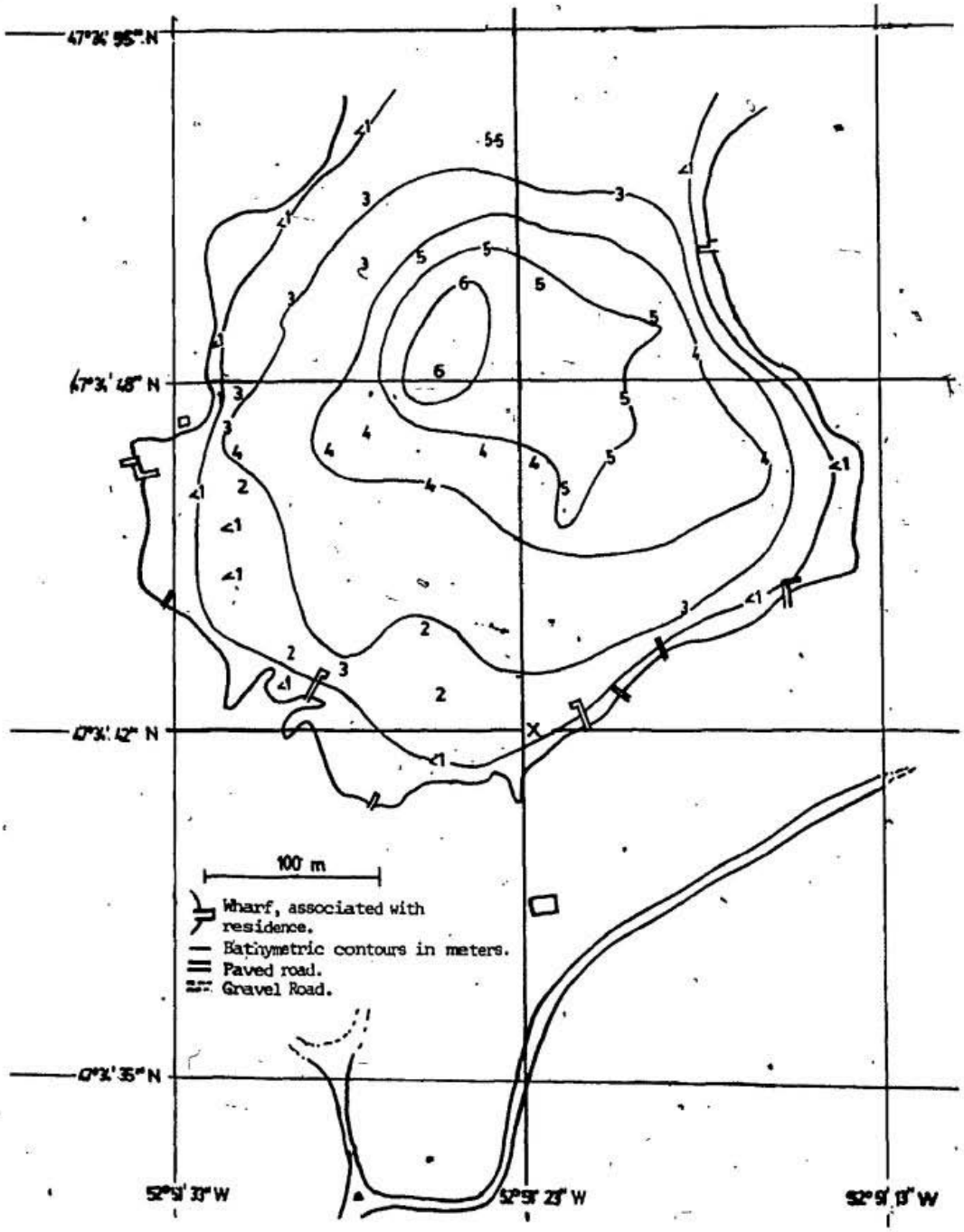
Table 1: Zooplankton species used in grazing experiments.

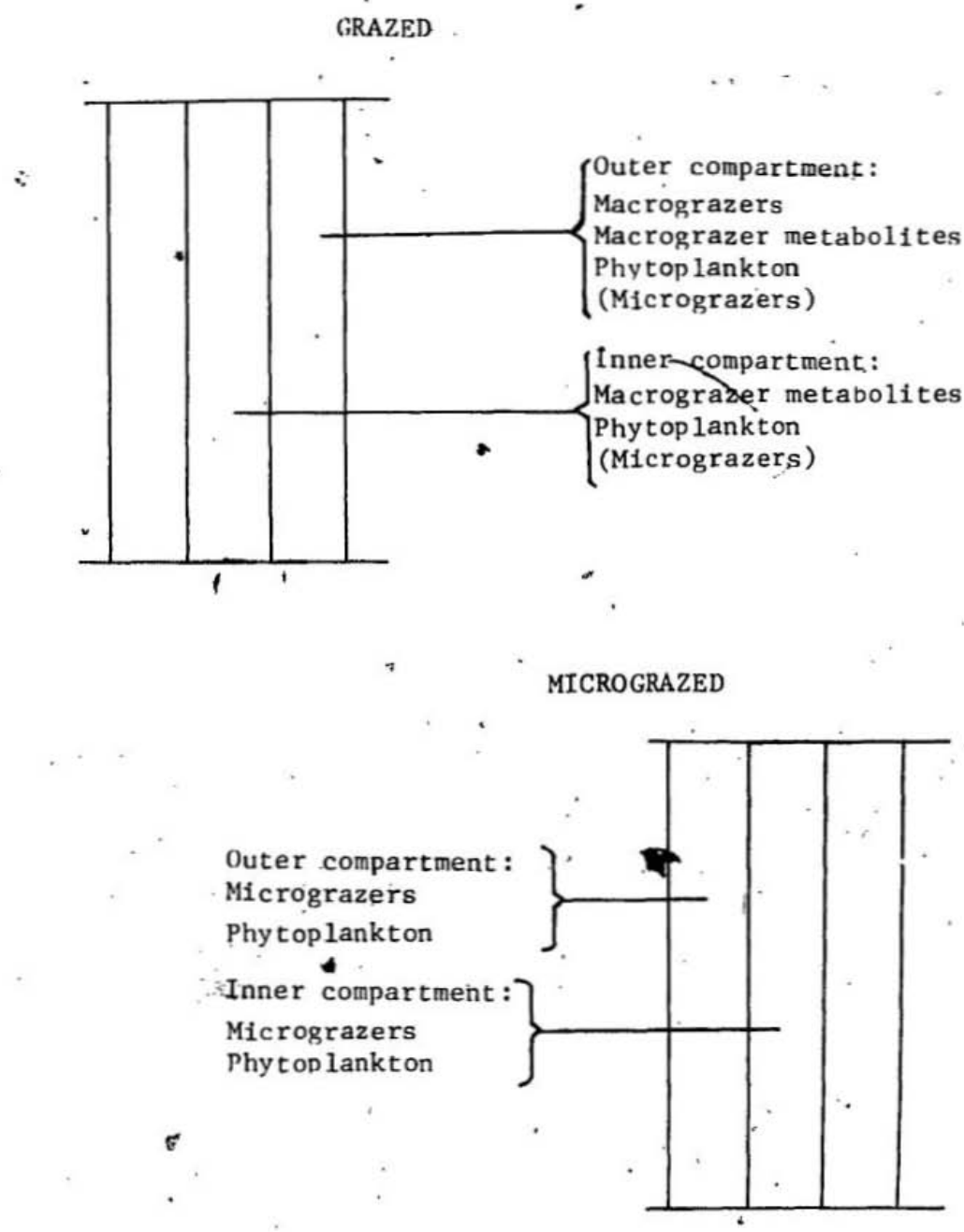
Experiment number	Zooplankton introduced	Number added	Density l^{-1}	Start date	Duration in days
1	*Diaptomus minutus*	40	6	25-5-85	13
2	*D. minutus*	80	11	25-6-85	13
3	*Bosmina longispina*	80	11	16-7-85	13

Prior to being added to the chambers, the zooplankton were kept for 24 hours in lake water from which particles 1.2 μm or larger (including phytoplankton) had been removed by filtration through Whatman GF/C filters. This was done to ensure that the zooplankton added to the grazed outer compartment were ready to feed at the beginning of each experiment.

Two different treatments were employed simultaneously (Figure 4), one with added macrograzers (grazed chamber) and the other without macrograzers (micrograzed). Micrograzers were parenthesized in Figure 4 since they were less dense in the grazed chamber, both inner and outer compartments (personal observation), than in the micrograzed chamber.

Figure 3: Southern region of Hogan's Pond. Experimental site indicated with an 'X' (taken from topological series 1N10-165, 1:25,000). Bathymetric contours in meters were taken from unpublished Bathymetric data courtesy of K. Cooper, Memorial University of Newfoundland.


47°3' 45" N
47°3' 42" N
47°3' 35" N
52°5' 33" W
52°5' 25" W
52°5' 13" W
100 m
Wharf, associated with residence.
Bathymetric contours in meters.
Paved road.
Gravel Road.



Outer compartment volume = 7.2 l

Inner compartment volume = 6.0 l

Figure 4: Initial contents of the chamber compartments.

Phytoplankton in the grazed inner compartment accessed metabolites, released by the macrograzers in the outer compartment, that passed through the 5 μm gauze. Phytoplankton in the grazed inner compartment were exposed to released macrograzer metabolites in the absence of the macrograzers. The water in the grazed inner compartment may be expected to be nutrient enriched relative to the lake water. The phytoplankton in the micrograzed chamber experienced grazing by rotifers, protozoans and possibly juvenile macrograzers not excluded by the 125 μm mesh.

Sampling procedure

The chambers were usually sampled between 1400 and 1430 h every other day during each experiment (Table 1), although sampling was occasionally delayed by up to one hour by strong winds. Prevailing weather conditions and cloud cover were noted, air and surface water temperatures, and Secchi depth were recorded.

Immediately prior to sampling the chambers, nine 40 ml glass vials were rinsed and filled with 125 μm filtered lake water. Eight of these were used to replace the volume of water removed during sampling and one was kept and preserved as a sample.

The temperature of the inner compartment of each chamber was recorded just after the chamber had been lifted into the boat. Samples were collected with a clean glass tube, 1.25 cm in diameter, which was gently lowered through the water column via the sampling ports, thus providing integrated samples with respect to depth in the compartments. Two integrated water samples each totalling 35 ml were placed in clean 40 ml vials. The remaining 5 ml volume in

each vial was taken up by preservative. Before the sampling port caps were replaced, two vials of 125 μm filtered water were added to each compartment; this maintained a constant volume in the compartments and introduced a small but fresh input of phytoplankton and micrograzers from the lake. Lake water samples of 250 ml were collected near the chambers at a depth of 1 m for comparison with chamber populations.

Preservation and enumeration of samples

Water samples containing phytoplankton were stored in darkness for about 1 - 1.5 hours, before they were preserved with 0.3 - 0.5 % glutaraldehyde and formaldehyde, which were added separately (Berlyn and Miksche 1976, Throndson 1978). Subsamples of 10 - 20 ml were micro-filtered onto 25 mm diameter, 0.45 μm pore size Millipore^{R} filters with marked grids. The filters were dried in a desiccator, trimmed, mounted on slides in immersion oil, and sealed under a coverslip (22 mm x 22 mm).

The mounted filters were examined with a Leitz dialux 22 compound microscope with a blue light filter at X 400 and X 100. Subsample volume examined was proportional to the area of filter onto which it was filtered. From this information the numbers of the different species of phytoplankton encountered were standardized as number per ml of sample. The standardized counts formed a continuous distribution as opposed to the raw counts which formed a discontinuous distribution. The X 400 count was disregarded for phytoplankton species counted at both magnifications since a larger sample area (area of filter with complete grid squares) was examined at X 100.

Colonial phytoplankters were recorded as the total number of cells and of colonies per ml. Filamentous desmids were dealt with as filament numbers in analysis, since the filaments did not break up easily and it is likely that the grazers encountered them as filaments. Reproductive stages and empty cells were recorded separately for species in which they could be distinguished.

Transformation of data

The means of the raw data were roughly proportional to their respective standard deviations, indicating that the variance may be stabilized by a log transformation of the data (Barnes 1952). The data also included zero values. Both of these features are commonly observed in plankton data, and the raw data were appropriately transformed: $x' = \log_{10}(x+1)$, where x was the standardized count ml^{-1}.

The mean (logmean), standard deviation, and variance of the transformed data (logvar) were calculated. In order to make the derived means comparable to values obtained by straight averaging, but not liable to large distortion by one or two extreme values, it was necessary to make small adjustments to them (Barnes 1952). The variance (logvar) multiplied by 1.15 was added to the mean of the transformed data (*i.e.*, the logmean), then 1.0 was subtracted from the antilog of this value. These adjustments have a sound mathematical basis (Bartlett, Department of Mathematics and Statistics, personal communication).

Experimental design and statistical analysis

The relationships between the samples and the experimental grazing treatments are shown in Table 2. The grazed inner compartment contained phytoplankton, macrograzer metabolites which were able to pass through the 5 μm gauze from the grazed outer compartment, and possibly a few micrograzers. The micrograzers were never as dense in either of the grazed compartments as in the lake water or the micrograzed chamber. The grazed outer compartment contained phytoplankton, macrograzers, their metabolites and again possibly a few micrograzers, although micrograzers tend to be suppressed by macrograzers. The micrograzed compartment contained phytoplankton and micrograzers.

Table 2: Relationships between samples and treatments.

Sample	Abbreviation	Treatment
Grazed inner compartment	GI	Macrograzer metabolites
Grazed outer compartment	GO	Macrograzed
Lake water	LW	Natural conditions
Micrograzed inner compartment	MI	Micrograzed
Micrograzed outer compartment	MO	Micrograzed

Standardization and log transformation of the phytoplankton count data ($x'=\log_{10}(x+1)$ normalized their frequency distributions. These standardized and transformed data were used in the statistical analysis. Seasonal differences were anticipated between the experiments, and therefore separate multiple analyses of variance (MANOVAs) were conducted for each experiment using the general linear

models (GLM) procedure in SAS (Ray 1982). Each MANOVA consisted of a series of two-way ANOVAs, one for each phytoplankton taxon. The phytoplankton taxa are presented in their taxonomic groups in Appendix A. Each two-way ANOVA had five levels of grazing treatment (GI, GO, LW, MI, MO) and usually six levels of date. The type I errors, in which one may reject the null hypothesis when in fact it is true, were unbiased by this analysis. Tables of analyses of variance may be seen in Appendix B.

The experiments were designed to allow comparisons between the grazing treatments that the phytoplankton were exposed to. The comparisons made were selected deductively and logically prior to the data analysis. For species with statistically significant ($P < 0.05$) F values, the following specific *a priori* treatment comparisons were made to examine the null hypotheses:

GI = LW	The grazed inner compartment and the lake water population densities do not differ.
GO = LW	The grazed outer compartment (macrograzed) and lake water population densities do not differ.
GI = GO	The grazed inner compartment and grazed outer compartment (macrograzed) population densities do not differ.
GI = MI	The grazed inner compartment and micrograzed inner compartment population densities do not differ.
GO = MO	The grazed outer compartment (macrograzed) and the micrograzed outer compartment population densities do not differ.
MI = MO	The micrograzed inner compartment and outer compartment population densities do not differ.
(MI = LW	The micrograzed inner compartment and lake water population densities do not differ).

(MO = LW The micrograzed outer compartment and lake water population densities do not differ).

Interactions between the inner and outer compartments of each micrograzed chamber via the 5 μm gauze were examined with the following hypothesis:

(MI+MO)/2 = LW The mean micrograzed chamber and the lake water population densities do not differ.

There were insufficient data for some species and so results of some of the treatment comparisons were non-estimable (Appendix B). This was due to inadequate sampling of the less common and rare species, a problem commonly encountered by limnologists. The grazed inner and micrograzed outer compartments, and the micrograzed inner and grazed outer compartments were deemed not comparable (Table 3), since these comparisons would be complicated by both compartment and chamber differences and they would not provide information relevant to macrograzing or micrograzing. The averaged grazed inner and outer compartment populations, (GI+GO)/2, and the lake water were deemed not comparable, since the populations of the two compartments of the grazed chamber represented the results of two distinct treatments, although the macrograzer metabolite treatment is dependent on the macrograzed treatment.

One objection to this analysis must be pointed out; the different cell or colony counts from each transect or grid square examined on each slide were standardized and log transformed individually. These may have been pseudoreplicates (Hurlbert 1984). However, unicellular and colonial phytoplankton, analysed as cells per ml and colonies per ml respectively, may be expected to have arrived independently on a particular area of the filter during

Table 3: Summary of the null hypotheses on which the *a priori* comparisons were based.

Grazed Outer compartment	Micrograzed Inner compartment	Micrograzed Outer compartment	Lake Water	Sample	Lake Water
GI=GO	GI=MI	Not comparable	GI=LW	Grazed Inner compartment	Not comparable
	Not comparable	GO=MO	GO=LW	Grazed Outer compartment	
		MI=MO	MI=LW	Micrograzed Inner compartment	(MI+MO)/2 = LW
			MO=LW	Micrograzed Outer compartment	

Key:
GI : grazed inner compartment
GO : grazed outer compartment
LW : lake water
MI : micrograzed inner compartment
MO : micrograzed outer compartment

filtration of the water samples. Thus the standardized phytoplankton numbers were considered to be independent of each other. Edge effects were eliminated in every case as the filters were trimmed.

Population densities of phytoplankton were plotted against date. Although inherent variation was fairly high, close inspection revealed trends in the general

direction of the graphs with respect to experimental treatments which were confirmed by the MANOVAs (Appendix B). The complexity of the experimental design made a time series analysis inadvisable (Bartlett, personal communication).

The specificity and *a priori* nature of the comparisons made them more sensitive than, or at least as robust as, Scheffé's pairwise treatment comparisons (Thatcher 1987). The specific comparisons involved nine comparisons (Table 3), compared to twenty pairwise comparisons using Scheffé's method, for each taxon. Unequal sample sizes were accomodated within both analyses.

The null hypotheses did not anticipate the direction of their associated grazing effects, (*e.g.* , the grazed inner population densities will be larger than the grazed outer population densities). This approach seems reasonable since the magnitude and direction of such effects depend on various factors, such as the other phytoplankton within the assemblage, the grazers, nutrient availability and the light environment, which are all influenced by season. The tests in the analysis were two-tailed for this reason. In instances where the null hypothesis was rejected, the larger of the two corrected means (Page 20) of phytoplankton densities was identified by inspection.

RESULTS.

Phytoplankton from the chambers and the lake water had adequate levels of light and temperature (Appendix C) for good phytoplankton growth. There was no evidence of chytrid infection of any cells, or of phytoplankton sinking within the chambers; sinking from the euphotic zone did not occur since the chambers were suspended within the euphotic zone. The results of the *a priori* comparisons were therefore attributable to grazing treatments.

The hypotheses examined in the comparisons may be divided into three categories: physical effects of macrograzers, chemical effects of macrograzers, and micrograzer effects respectively. Grazing effects were manifested in depression, augmentation or unaffected phytoplankton densities between samples.

The chi-square (X^2) test was used to examine the hypothesis that the number of taxa augmented in a comparison did not differ significantly from the number of taxa depressed in the same comparison. A broad overview of the direction of grazing effects in each comparison in terms of total numbers of phytoplankton taxa, with the exception of those which were non-estimable, is given in Table 4. If the differences between treatments were due to random variation, the number of phytoplankton taxa augmented by a particular treatment would be expected to be equal to the number depressed. The associated grazing effect may be considered highly significant when this hypothesis is rejected, and small when accepted. Three of the seven Chi-square tests performed were significant, one within each category of grazing effect.

Table 4: Summary of comparison results: total numbers of phytoplankton taxa augmented, depressed, or unaffected relative to the other sample in the comparison.

	Comparison results	Number of taxa	x^2	
Physical effects	GO<LW	8		
	GO=LW	42	2.6667	n.s.
	GO>LW	16		
	GI<GO	8		
	GI=GO	46	1.1905	n.s.
	GI>GO	13		
	GO<MO	18		
	GO=MO	53	8.9091	**
	GO>MO	4		
Chemical effects	GI<LW	7		
	GI=LW	36	7.0000	**
	GI>LW	21		
	GI=GO	see above		
	GI<MI	18		
	GI=MI	33	1.2000	n.s.
	GI>MI	12		
Micrograzer effects	MI<MO	11		
	MI=MO	46	0.0000	n.s.
	MI>MO	11		
	(MI+MO)/2 < LW	2		
	(MI+MO)/2 = LW	38	18.6154	**
	(MI+MO)/2 > LW	24		
	GI=MI	see above		

Key:- GI : grazed inner, GO : grazed outer, MI : micrograzed inner, MO : micrograzed outer compartments and LW : lake water, n.s. : not significant, ** : significant at 0.01, * : significant at 0.05.

A significant number of taxa were less dense in the grazed outer compartment than in the micrograzed outer compartment (Table 4), and a significant number of taxa were more dense in the grazed inner compartment than in the lake water. It should be noted that equal numbers of taxa were less dense in the micrograzed inner than in the micrograzed outer compartment and *vice versa*; however, when the averaged micrograzed compartment densities were compared a larger number of taxa were found to be more dense in the micrograzed chamber than in the lake water.

The data are presented by algal group in Tables 5, 6 and 7. (Twenty per cent of these chi-square tests performed were significant).

Table 5: Numbers of taxa augmented, depressed, or unaffected by physical effects of macrograzers relative to the other treatment in the comparison.

	Zygnemaphyceae (desmids)	Chlorophyceae and microflagellates	Bacillariophyceae (diatoms)	Chrysophyceae	Cyanophyceae
GO<LW	1	2	2	2	2
GO=LW	12	8	10	7	6
GO>LW	1	9	1	0	5
X^2	0.000 n.s.	4.455 *	0.333 n.s.	2.000 n.s.	2.667 n.s.
GI<GO	2	3	1	1	1
GI=GO	8	18	8	3	8
GI>GO	4	0	4	3	2
X^2	0.667 n.s.	3.000 n.s.	1.800 n.s.	1.000 n.s.	0.333 n.s.
GO<MO	5	4	4	1	4
GO=MO	12	14	10	9	8
GO>MO	0	3	0	1	0
X^2	5.000 *	0.143 n.s.	4.000 *	0.000 n.s.	4.000 *

Key:- GI : grazed inner, GO : grazed outer, MO : micrograzed outer compartments and LW : lake water;
* : significant at 0.05, n.s. not significant.
If the differences between treatments were due to random variation, the number phytoplankton taxa augmented by a particular treatment would be expected to be equal to the number depressed. Where this hypothesis is rejected the associated grazing effect may be considered highly significant and where the hypothesis was accepted the associated grazing effect may be considered small.

Table 6: Numbers of taxa augmented, depressed, or unaffected by chemical effects of macrograzer metabolite relative to the other treatment in the comparison.

	Zygnemaphyceae (desmids)	Chlorophyceae and microflagellates	Bacillariophyceae (diatoms)	Chrysophyceae	Cyanophyceae
GI<LW	1	3	0	1	2
GI=LW	9	10	6	4	7
GI>LW	5	7	4	2	3
X^2	2.667 n.s.	1.600 n.s.	4.000 *	0.333 n.s.	0.200 n.s.
GI<GO	2	3	1	1	1
GI=GO	8	18	8	3	8
GI>GO	4	0	4	3	2
X^2	0.667 n.s.	3.000 n.s.	1.800 n.s.	1.000 n.s.	0.333 n.s.
GI<MI	1	10	4	0	3
GI=MI	11	0	7	4	5
GI>MI	1	4	0	3	4
X^2	1.000 n.s.	2.571 n.s.	4.000 *	3.000 n.s.	0.143 n.s.

Key:- GI : grazed inner, GO : grazed outer, MI : micrograzed inner compartments and LW : lake water;
* : significant at 0.05, n.s. not significant.
If the differences between treatments were due to random variation, the number phytoplankton taxa augmented by a particular treatment would be expected to be equal to the number depressed. Where this hypothesis is rejected the associated grazing effect may be considered highly significantand where the hypothesis was accepted the associated grazing effect may be considered small.

Table 7: Numbers of taxa augmented, depressed, or unaffected by micrograzer effects relative to the other treatment in the comparison.

	Zygnemaphyceae (desmids)	Chlorophyceae and microflagellates	Bacillariophyceae (diatoms)	Chrysophyceae	Cyanophyceae
MI<MO	4	3	0	2	2
MI=MO	7	14	10	6	9
MI>MO	3	3	4	0	1
X^2	0.143 n.s.	0.000 n.s.	4.000 *	2.000 n.s.	0.333 n.s.
(MI+MO)/2 < LW	0	2	0	0	0
(MI+MO)/2 = LW	7	13	7	6	5
(MI+MO)/2 > LW	7	4	7	0	6
X^2	7.000 *	0.571 n.s.	3.500 n.s.	0.000 n.s.	6.000 *

Key:- MI : micrograzed inner, MO : micrograzed outer compartments and LW : lake water;
* : significant at 0.05, n.s. not significant.
If the differences between treatments were due to random variation, the number phytoplankton taxa augmented by a particular treatment would be expected to be equal to the number depressed. Where this hypothesis is rejected the associated grazing effect may be considered highly significantand where the hypothesis was accepted the associated grazing effect may be considered small.

The results of the comparisons were examined, in terms of individual taxa, under the following headings: physical effects of macrograzing, chemical effects of macrograzing and micrograzer effects. Non-estimable results were omitted from the detailed tables that follow, since non-estimable results merely indicate the absence or presence in very small numbers of individual taxa. *Ceratium hirundinella* was dealt with separately from the other phytoplankton because of its unexpected occurrence in the chambers.

Physical effects of macrograzers

Comparisons of macrograzed (physical effects) and lake water phytoplankton densities. Null hypothesis: GO=LW.

In experiment 2, densities of *Arthrodesmus* spp., *A. triangularis* var. *rotundatus* in particular, were greater in the grazed outer compartments than in the lake water (Table 8). In experiment 2, 80 *Diaptomus minutus* (c.f. 40 in experiment 1) had initially been added. The densities of other desmid taxa in experiment 2, and of most desmids in experiments 1 and 3, did not differ between the grazed outer compartments and the lake water. Only *Spondylosium planum* in experiment 3 were less abundant in the grazed outer compartment than in the lake water (Table 8).

In both experiments 1 and 2, several taxa of the Chlorophyceae were more dense in the grazed outer compartments than in the lake water (Table 8). In experiment 3, in which *Bosmina longispina* was the macrograzer, *Chlorella vulgaris* and *Quadrigula lacustris* were less dense in the grazed outer than in the lake water (Table 8).

Microflagellates were more dense in the grazed outer compartment than in

the lake water in experiment 2; however, in experiments 1 and 3 the densities did not differ significantly (Table 8).

Most of the diatom taxa densities did not differ between the grazed outer compartments and the lake water (Table 9). Exceptions comprised *Synedra* sp. in experiment 2, which was more dense in the grazed outer compartment than in the lake water, and *Tabellaria fenestrata* var. *lacustris* in experiment 3, for which the reverse was true (Table 9).

Members of the Chrysophyceae tended not to differ in density between the grazed outer compartments and lake water (Table 9). Exceptions included *Dinobryon bavaricum* empty cells in experiment 3, and *Uroglena volvox* in experiment 1, which were less abundant in the grazed outer compartments than the lake water.

Densities of taxa of the Cyanophyceae in the grazed outer compartment were either greater than or not significantly different from those in the lake water. Cyanophycean taxa in experiment 2 did not differ significantly in densities between the grazed outer compartment and the lake water (Table 9).

Table 8: Macrograzed and lake water mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	=		**	+	=	
Arthrodesmus convergens	=					
Arthrodesmus incus			=			
Arthrodesmus subulatus	=					
Arthrodesmus triangularis	=		**	+		
A. triangularis juveniles			=			
Mesotaenium sp.	=		=		=	
Staurodesmus sp.						
Spondylosium planum			=		**	−
Teilingia granulata	=		=		=	
Chlorophyceae						
Ankistrodesmus spp.	=		**	+		
Chlamydomonas globosa			=			
Chlorella ellipsoidea	*	+	**	+	=	
Chlorella vulgaris cells	**	+	**	+	**	−
C. vulgaris autospores	**	+	**	+	=	
Enteromorpha intestinalis						
Quadrigula lacustris			=		=	
Selenastrum minutum	**	+			*	−
Cryptophyceae						
Microflagellates	=		**	+	=	

= : no significant difference between GO and LW, null hypothesis H_0: GO=LW accepted;
* : $p < 0.05$, ** : $p < 0.01$ null hypothesis rejected;
+ : GO > LW, − : GO < LW.

Table 9: Macrograzed and lake water mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1	Expt. 2	Expt. 3
Bacillariophyceae (diatoms)			
Asterionella formosa cells			=
A. formosa colonies			=
Synedra sp.	=	** +	=
Tabellaria fenestrata cells		=	** −
T. fenestrata colonies		=	* −
T. fenestrata empty frustules	=		=
T. fenestrata colonies with empty frustules	=		=
Chrysophyceae			
Dinobryon bavaricum cells	=		
D. bavaricum colonies	=		
D. bavaricum empty loricas			** −
Dinobryon sertularia cells			=
D. sertularia empty loricas			=
Syncrypta volvox			=
"Ribbed" chrysophyte		=	
Uroglena volvox cells	** −	=	
Cyanophyceae			
Chroococcus turgidus colonies	** +	=	* +
Coelosphaerium kuetzingianum		=	
Gloeocapsa punctata colonies		=	** +
Gloeothece linearis	=		** −
Microcystis aeruginosa cells	** +	=	
M. aeruginosa colonies	** +		

= : no significant difference between GO and LW, null hypothesis H_0: GO=LW accepted;

* : $p < 0.05$, ** : $p < 0.01$ null hypothesis rejected;

+ : GO > LW, − : GO < LW.

Comparisons of the physical effects and chemical effects of macrograzers on phytoplankton densities. Null hypothesis: GI=GO.

The comparisons of the grazed inner and grazed outer compartments show differences between phytoplankton responses to physical and chemical effects of macrograzers, while the grazed outer compartment and lake water, and grazed inner compartment and lake water comparisons which follow may show trends due to both grazing and containment effects.

With the exception of *Teilingia granulata* in experiments 1 and 2, desmid densities of grazed inner compartments were either larger than or did not differ from those in the grazed outer compartments (Table 10). The chlorophycean taxa did not differ significantly in density between the grazed inner and grazed outer compartments with one exception, *Ankistrodesmus* spp., which was less dense in the grazed inner than in the grazed outer compartments in experiments 1 and 3 (Table 10).

Microflagellate densities did not differ significantly between the grazed inner and grazed outer compartments in experiments 2 and 3. However, densities in the grazed inner compartments were less than in the grazed outer compartments in experiment 1 (Table 10).

In experiment 3 the grazed inner compartment densities of *Tabellaria fenestrata* var. *lacustris* were greater than those of the grazed outer compartment (Table 11). In experiment 1, *Synedra* sp. was less abundant in the grazed inner compartment than the grazed outer compartment.

Among the chrysophycean taxa, empty cells of both *Dinobryon bavaricum*, in experiment 2, and *Dinobryon sertularia* in experiment 3, were more numerous

in the grazed inner compartments than in the grazed outer compartments. *Uroglena volvox* cells were less abundant in the grazed outer compartments than in the grazed inner compartments in experiment 1, the reverse was true in experiment 3, and the densities did not differ significantly in experiment 2 (Table 11).

Microcystis aeruginosa were more dense in the grazed inner compartments than in the grazed outer compartments, in experiments 1 and 2; the reverse was found in experiment 3. The other cyanophycean taxa did not differ significantly between the grazed inner and grazed outer compartments (Table 11).

Table 10: Physical and chemical effects of macrograzers on mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	=		**	+		
Arthrodesmus convergens						
Arthrodesmus incus			*	+		
Arthrodesmus subulatus	=		=			
Arthrodesmus triangularis	=		*	+	*	+
A. triangularis juveniles			=			
Mesotaenium sp.	=		=			
Staurodesmus sp.	=					
Spondylosium planum			=			
Teilingia granulata	*	–	**	–	**	+
Chlorophyceae						
Ankistrodesmus spp.	**	–	=		*	–
Chlamydomonas globosa			=			
Chlorella ellipsoidea	=		=		=	
Chlorella vulgaris cells	=		=		=	
C. vulgaris autospores	=		=		=	
Enteromorpha intestinalis	=					
Quadrigula lacustris	=				=	
Selenastrum minutum	=				=	
Cryptophyceae						
Microflagellates	*	–	=		=	

= : no significant difference between GI and GO,
null hypothesis H_0: GI = GO accepted;
* : $p < 0.05$, ** : $p < 0.01$, null hypothesis rejected;
+ : GI > GO, – : GI < GO.

Table 11: Physical and chemical effects of macrograzers on mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae and the Cyanophyceae.

Taxa	Expt. 1		Expt. 2	Expt. 3	
Bacillariophyceae (diatoms)					
Asterionella formosa cells			=	=	
A. formosa colonies				=	
Synedra sp.	**	−	=	=	
Tabellaria fenstrata cells			=	**	+
T. fenestrata colonies			=	**	+
T. fenestrata empty frustules	=			**	+
T. fenestrata colonies with empty frustules	=			**	+
Chrysophyceae					
Dinobryon bavaricum cells					
D. bavaricum colonies					
D. bavaricum empty loricas	**	+			
Dinobryon sertularia cells				=	
D. sertularia empty loricas				**	+
Syncrypta volvox	=				
"Ribbed" chrysophyte					
Uroglena volvox cells	**	−	=	**	+
Cyanophyceae					
Chroococcus turgidus colonies	=		=	=	
Coelosphaerium kuetzingianum			=		
Gloeocapsa punctata colonies			=	=	
Gloeothece linearis	=				
Microcystis aeruginosa cells	**	+	=		
M. aeruginosa colonies	**	+		*	−

= : no significant difference between GI and GO,
null hypothesis H_0: GI=GO accepted;
* : $p < 0.05$, ** : $p < 0.01$, null hypothesis rejected;
+ : GI > GO, − : GI < GO.

Comparisons of macrograzed and micrograzed phytoplankton densities. Null hypothesis: GO=MO.

Population densities of desmid taxa in the grazed outer compartment were either less than or did not differ significantly from those of the micrograzed outer compartment (Table 12). Most taxa of the Chlorophyceae did not differ significantly between the outer compartments. Notable exceptions included *Ankistrodesmus* spp. in experiments 1 and 3, and *Enteromorpha intestinalis* in experiment 1, in which densities were larger in the grazed outer compartments than in the micrograzed outer compartments; the reverse was true for *Chlorella vulgaris* in experiments 1 and 3, and *Quadrigula lacustris* in experiment 1 (Table 12).

Microflagellates (which consisted of *Cryptomonas* sp. and *Rhodomonas ovalis*) were either less abundant in the grazed outer compartment than in the macrograzed outer compartment, as in experiment 3, or did not differ significantly between the outer compartments (Table 12).

With the exception of *Tabellaria fenestrata* var. *lacustris* in experiment 3, in which densities were less in the grazed outer compartments than the micrograzed outer compartments (Table 13), the diatom taxa did not differ significantly between outer compartments.

The chrysophycean population densities did not differ significantly between the grazed and micrograzed outer compartments, with two exceptions both in experiment 1: *Uroglena volvox* were more dense in the grazed outer compartment than in the micrograzed outer compartment, and the reverse was found for *Dinobryon bavaricum* empty loricas (Table 13).

With the exception of *Microcystis aeruginosa* in experiments 1 and 2, which were less abundant in the grazed than the micrograzed outer compartments the cyanophycean taxa did not differ significantly between the outer compartments (Table 13).

Table 12: Macrograzed and micrograzed mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1	Expt. 2	Expt. 3
Zygnemaphyceae (desmids)			
Arthrodesmus spp.	=	* −	=
Arthrodesmus convergens	* −		
Arthrodesmus incus		* −	
Arthrodesmus subulatus	=	=	
Arthrodesmus triangularis	=	=	=
A. triangularis juveniles		=	
Mesotaenium sp.	=	** −	=
Staurodesmus sp.	=		
Spondylosium planum		* −	=
Teilingia granulata	=	** −	=
Chlorophyceae			
Ankistrodesmus spp.	** +	=	* +
Chlamydomonas globosa		=	
Chlorella ellipsoidea	=	=	=
Chlorella vulgaris cells	* −	=	** −
C. vulgaris autospores	=	=	=
Enteromorpha intestinalis	* +		
Quadrigula lacustris	** −		=
Selenastrum minutum	=		=
Cryptophyceae			
Microflagellates	=	=	* −

= : no significant difference between GO and MO, therefore null hypothesis H_0: GO=MO accepted;
* : $p < 0.05$, ** : $p < 0.01$, null hypothesis rejected;
+ : GO > MO, − : GO < MO.

Table 13: Macrograzed and micrograzed mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1	Expt. 2	Expt. 3
Bacillariophyceae (diatoms)			
Asterionella formosa cells		=	=
A. formosa colonies			=
Synedra sp.	=	=	=
Tabellaria fenstrata cells		=	** –
T. fenestrata colonies		=	** –
T. fenestrata empty frustules	=		** –
T. fenestrata colonies with empty frustules	=		** –
Chrysophyceae			
Dinobryon bavaricum cells			
D. bavaricum colonies			
D. bavaricum empty loricas	** –		
Dinobryon sertularia cells	=		=
D. sertularia empty loricas			=
Syncrypta volvox	=		
"Ribbed" chrysophyte	=	=	=
Uroglena volvox cells	** +	=	=
Cyanophyceae			
Chroococcus turgidus colonies	=	=	=
Coelosphaerium kuetzingianum		=	
Gloeocapsa punctata colonies		=	=
Gloeothece linearis	=		=
Microcystis aeruginosa cells	** –	* –	
M. aeruginosa colonies	** –	** –	

= : no significant difference between GO and MO,
null hypothesis H_0: GO=MO accepted;
* : $p < 0.05$, ** : $p < 0.01$, null hypothesis rejected;
+ : GO > MO, – : GO < MO.

Chemical effects of macrograzers

Comparisons of phytoplankton densities under chemical effects of macrograzers and lake water conditions. Null hypothesis: GI=LW.

Desmid densities in the grazed inner compartments were either greater than or not significantly different from those of the lake water (Table 14) with one exception. The exception was in experiment 1, in which filaments of *Teilingia granulata* were less dense in the grazed inner compartment than in the lake water (Table 14).

Several of the chlorophycean taxa were more dense in the grazed inner compartments than in the lake water in experiments 1 and 2 (Table 14). In experiment 3, the densities of most taxa did not differ between the grazed inner compartment and the lake water; *Chlorella vulgaris* and its autospores were exceptions. The microflagellate densities did not differ significantly in experiments 1 and 3 (Table 14), in contrast to experiment 2, in which the microflagellates were more dense in the grazed inner compartment than in the lake water (Table 14).

Diatom densities in the grazed inner compartments were either greater than, as in experiments 2 and 3, or did not differ from, those of the lake water (Table 15). Significant results were sparse for the chrysophycean taxa (Table 15). *Dinobryon sertularia* cells and empty loricas were more dense in the grazed inner compartment than in the lake water (Table 15). In experiment 1, *Chroococcus turgidus* and *Microcystis aeruginosa* were more dense in the grazed inner compartment than in the lake water (Table 15). The reverse was true for *Coelosphaerium kuetzingianum* and *Gloeothece linearis* in experiment 3. Several of the other cyanophycean taxa densities did not differ between the grazed inner

compartments and the lake water (Table 15).

Table 14: Grazed inner compartment and lake water mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	*	+	**	+	=	
Arthrodesmus convergens						
Arthrodesmus incus			=			
Arthrodesmus subulatus	=		**	+		
Arthrodesmus triangularis	=		**	+	=	
A. triangularis juveniles			*	+		
Mesotaenium sp.	=		=		=	
Staurodesmus sp.						
Spondylosium planum			=		=	
Teilingia granulata	*	−	**	+	**	+
Chlorophyceae						
Ankistrodesmus spp.	=		**	+		
Chlamydomonas globosa			=			
Chlorella ellipsoidea	=		**	+	=	
Chlorella vulgaris cells	*	+	**	+	**	−
C. vulgaris autospores	**	+	**	−	*	−
Enteromorpha intestinalis						
Quadrigula lacustris	=				=	
Selenastrum minutum	**	+	=		=	
Cryptophyceae						
Microflagellates	=		**	+	=	

= : no significant difference between GI and LW,
null hypothesis H_0: GI=LW accepted;
* : $p < 0.05$; ** : $p < 0.01$ null hypothesis rejected;
+ : GI > LW, − : GI < LW.

Table 15: Grazed inner compartment and lake water mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1	Expt. 2	Expt. 3
Bacillariophyceae (diatoms)			
Asterionella formosa cells		=	
A. formosa colonies			
Synedra sp.	=	** +	
Tabellaria fenestrata cells		=	
T. fenestrata colonies		* +	** +
T. fenestrata empty frustules	=		* +
T. fenestrata colonies with empty frustules	=		=
Chrysophyceae			
Dinobryon bavaricum cells			
D. bavaricum colonies			
D. bavaricum empty loricas	=		
Dinobryon sertularia cells			** +
D. sertularia empty loricas			** +
Syncrypta volvox			
"Ribbed" chrysophyte			** −
Uroglena volvox cells	=	=	=
Cyanophyceae			
Chroococcus turgidus colonies	** +	=	=
Coelosphaerium kuetzingianum		* −	
Gloeocapsa punctata colonies		=	=
Gloeothece linearis	=		** −
Microcystis aeruginosa cells	** +		=
M. aeruginosa colonies	** +		=

= : no significant difference between GI and LW,
null hypothesis H_0: GI=LW accepted;
* : $p < 0.05$, ** : $p < 0.01$ null hypothesis rejected;
+ : GI > LW, − : GI < LW.

Comparisons of metabolite enriched and micrograzed phytoplankton densities. Null hypothesis: GI=MI.

Densities of *Arthrodesmus* spp. in experiment 3 and, *Mesotaenium* sp. in experiment 2 were greater in the grazed inner compartments than in the micrograzed inner compartments (Table 16). The reverse was true for *Arthrodesmus* spp. in experiment 1. The remaining desmid taxa did not differ between the inner compartments (Table 16).

The chlorophycean taxa showed various responses in the inner compartment comparisons, *e.g.* , *Chlorella vulgaris* cells were less numerous in the grazed inner compartments than in the micrograzed inner compartments in experiments 1 and 2; the reverse was true for *C.vulgaris* autospores in experiment 2. *C. vulgaris* and *C. ellipsoidea* densities did not differ significantly between the inner compartments in experiment 1 (Table 16). The microflagellates were less dense in the grazed inner compartments than in the micrograzed inner compartments in experiment 1 and 3; the reverse was true for experiment 2 (Table 16).

With the exception of *Tabellaria fenestrata* var. *lacustris* in experiment 3, which was less abundant in the grazed than in the micrograzed inner compartments, the diatom densities did not differ significantly (Table 17). Compare these results with those for this species in Table 11 where the grazed inner compartment densities were greater than in the micrograzed inner compartment. The densities of the chrysophycean taxa were either greater in the grazed inner compartments than in the micrograzed inner compartments or they did not differ significantly (Table 17). Various responses were revealed among the taxa of the Cyanophyceae by the inner compartment comparisons (Table 17).

Table 16: Effects of macrograzer metabolites and micrograzing on mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	**	−	=		*	+
Arthrodesmus convergens						
Arthrodesmus incus			=			
Arthrodesmus subulatus	=		=			
Arthrodesmus triangularis			=		=	
A. triangularis juveniles			=			
Mesotaenium sp.	=		*	+	=	
Staurodesmus sp.						
Spondylosium planum					=	
Teilingia granulata	=		**	−	=	
Chlorophyceae						
Ankistrodesmus spp.	*	−	*	+		
Chlamydomonas globosa					=	
Chlorella ellipsoidea	=		**	−	*	−
Chlorella vulgaris cells	=		**	−	**	−
C. vulgaris autospores	=		**	+	=	
Enteromorpha intestinalis	**	−				
Quadrigula lacustris	*	−			=	
Selenastrum minutum	**	+			*	−
Cryptophyceae						
Microflagellates	**	−	**	+	*	−

= : no significant difference between GI and MI,
null hypothesis H_0: GI=MI accepted;
* : $p < 0.05$, ** : $p < 0.01$, null hypothesis rejected;
+: GI > MI, − : GI < MI.

Table 17: Effects of macrograzer metabolites and micrograzing on mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Bacillariophyceae (diatoms)						
Asterionella formosa cells						
A. formosa colonies						
Synedra sp.	=		=		=	
Tabellaria fenstrata cells			=		**	−
T. fenestrata colonies			=		**	−
T. fenestrata empty frustules	=				**	−
T. fenestrata colonies with empty frustules	=				**	−
Chrysophyceae						
Dinobryon bavaricum cells						
D. bavaricum colonies						
D. bavaricum empty loricas	=					
Dinobryon sertularia cells			**	+		
D. sertularia empty loricas			**	+		
Syncrypta volvox						
"Ribbed" chrysophyte			=			
Uroglena volvox cells	=		**	+	=	
Cyanophyceae						
Chroococcus turgidus colonies	*	−	=		=	
Coelosphaerium kuetzingianum			=			
Gloeocapsa punctata colonies			*	−	**	−
Gloeothece linearis	=				=	
Microcystis aeruginosa cells	*	+	**	+		
M. aeruginosa colonies	*	+	**	+		

= : no significant difference between GI and MI,
null hypothesis H_0: GI=MI accepted;
* : $p < 0.05$, ** : $p < 0.01$, null hypothesis rejected;
+ : GI > MI, − : GI < MI.

Micrograzer effects

The micrograzer assemblages differed in species composition and relative abundances between the micrograzed inner and outer compartments (Table 18).

Table 18: Micrograzer average densities (number l^{-1}) in the micrograzed inner and outer compartments.

	Expt. 1		Expt.2		Expt. 3	
	MI	MO	MI	MO	MI	MO
Bosmina longispina juveniles			290	101		20
Kellicottia longispina			114	101	500	61
Keratella cochlearis	160	143	328	400	200	141
Copepod naup[illegible]		160	101	224	500	
Small rotifer				163		

The data in Table 18 reflects the patchy nature of the distribution of micrograzers and may explain the differences between phytoplankton population densities in the micrograzed inner and outer compartments (Tables 19 and 20).

Comparisons of micrograzed inner and outer compartment phytoplankton densities. Null hypothesis: MI = MO.

Several of the desmid taxa did not differ significantly between the micrograzed compartments (Table 19), six taxa were exceptions. Many of the chlorophycean taxa also did not differ significantly between the micrograzed compartments (Table 19). Exceptions included *Ankistrodesmus* spp. and *Enteromorpha intestinalis* in experiment 1, and *Chlorella vulgaris* in experiment 2, all of which were more abundant in the micrograzed inner compartments than in the micrograzed outer compartments. The reverse was true for *Chlorella*

ellipsoidea in experiments 2 and 3, and *C. vulgaris* autospores in experiment 2. Only one result was available for the microflagellates; in experiment 1, the microflagellates did not differ significantly in density between the micrograzed compartments (Table 19).

With the exception of *Tabellaria fenestrata* in experiment 3, the densities of the diatoms did not differ significantly between the micrograzed compartments (Table 20). Several of the chrysophycean densities also did not differ significantly, although results were sparse (Table 20).

Densities of the cyanophycean taxa in experiment 2 did not differ significantly between the micrograzed compartments; this was also the case for a few taxa in experiments 1 and 3. In experiment 3, *Gloeocapsa punctata* was more abundant in the micrograzed inner compartment than in the outer compartment, the reverse was true for *Gloeotheçe linearis* and *Microcystis aeruginosa* in experiment 1 (Table 20).

Table 19: Micrograzed inner and outer compartment mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	**	+	=		=	
Arthrodesmus convergens	*	−				
Arthrodesmus incus			=			
Arthrodesmus subulatus	**	+	=			
Arthrodesmus triangularis			*	−	=	
A. triangularis juveniles			=			
Mesotaenium sp.	=		**	−	=	
Staurodesmus sp.						
Spondylosium planum					=	
Teilingia granulata	*	−	**	+	**	+
Chlorophyceae						
Ankistrodesmus spp.	**	+	=		=	
Chlamydomonas globosa			=			
Chlorella ellipsoidea	=		**	−	**	−
Chlorella vulgaris cells	=		**	+	=	
C. vulgaris autospores	=		**	−	=	
Enteromorpha intestinalis	**	+				
Quadrigula lacustris	=				=	
Selenastrum minutum	=		=		=	
Cryptophyceae						
Microflagellates	=					

= : no significant difference between MI and MO,
null hypothesis H_0: MI = MO accepted;
* : $p < 0.05$, ** : $p < 0.01$;
+ : MI > MO, − : MI < MO.

Table 20: Micrograzed inner and outer compartment mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1	Expt. 2	Expt. 3
Bacillariophyceae (diatoms)			
Asterionella formosa cells		=	=
A. formosa colonies			=
Synedra sp.	=	=	=
Tabellaria fenestrata cells		=	** +
T. fenestrata colonies		=	** +
T. fenestrata empty frustules	=		** +
T. fenestrata colonies with empty frustules	=		** +
Chrysophyceae			
Dinobryon bavaricum cells			
D. bavaricum colonies	=		
D. bavaricum empty loricas	*		
Dinobryon sertularia cells			=
D. sertularia empty loricas			=
Syncrypta volvox			
"Ribbed" chrysophyte			=
Uroglena volvox cells	=	** −	=
Cyanophyceae			
Chroococcus turgidus colonies	=	=	=
Coelosphaerium kuetzingianum		=	
Gloeocapsa punctata colonies		=	** +
Gloeothece linearis	* −		=
Microcystis aeruginosa cells	=	=	
M. aeruginosa colonies	** −	=	

=: no significant difference between MI and MO,
null hypothesis H_0: MI = MO accepted;
* : $p < 0.05$, ** : $p < 0.01$;
+ : MI > MO, − : MI < MO.

The few significant differences between the phytoplankton population densities in the micrograzed inner and outer compartments do not indicate serious containment effects, rather they show the effects of the different micrograzer assemblages. For this reason the micrograzed inner compartment and lake water, and the micrograzed outer compartment and lake water, comparisons were not examined in any detail; tables of the results of these comparisons were placed in Appendix D. Instead the interactions between the micrograzed compartments were considered.

Interaction between the micrograzed compartments.
Null hypothesis: (MI + MO) / 2 = LW.

Interactions between the micrograzed inner and micrograzed outer compartments were anticipated, since material exchanged through the 5 μm gauze. The averaged densities of phytoplankton taxa in the micrograzed inner and outer compartments, (MI + MO) / 2, will be referred to as the density of the micrograzed chamber.

In experiment 1, the desmid densities did not differ significantly between the micrograzed chamber and the lake water (Table 21). In experiment 2, the micrograzed chamber densities were greater than those of the lake water for most desmid taxa. This was also true of *Mesotaenium* sp. and *Teilingia granulata* in experiment 3, while the remaining desmid taxa in experiment 3 did not differ significantly between the micrograzed chamber and the lake water (Table 21).

In experiment 1, *Chlamydomonas globosa* and *Chlorella vulgaris* were more abundant in the micrograzed chamber than in the lake water. In experiment 2, *Chlorella vulgaris* autospores and *Quadrigula lacustris* were less abundant in the

micrograzed chamber than in the lake water (Table 21). The remaining chlorophycean taxa did not differ significantly in density between the micrograzed chamber and the lake water. The microflagellates either did not differ significantly or were more abundant in the lake water than in the micrograzed chamber (Table 21).

Tabellaria fenestrata var *lacustris* in experiments 2 and 3 , and *Synedra* sp. in experiment 2 were more dense in the micrograzed chamber than in the lake water (Table 22). The remaining diatom taxa and the chrysophycean taxa did not differ significantly between the micrograzed chamber and lake water (Table 22). The cyanophycean taxa were either more dense in the micrograzed chamber than the lake water, *e.g.* , *Microcystis aeruginosa*, or did not differ significantly (Table 22).

Table 21: Micrograzed chamber, (MI + MO)/2, and lake water mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	=		**	+	=	
Arthrodesmus convergens	=					
Arthrodesmus incus			=			
Arthrodesmus subulatus	=		*	+		
Arthrodesmus triangularis			**	+	=	
A. triangularis juveniles			**	+		
Mesotaenium sp.	=		**	+	*	+
Staurodesmus sp.						
Spondylosium planum					=	
Teilingia granulata	=		**	+	**	+
Chlorophyceae						
Ankistrodesmus spp.	=		=			
Chlamydomonas globosa			=			
Chlorella ellipsoidea	*	+	=		=	
Chlorella vulgaris cells	=		=		**	+
C. vulgaris autospores	*	+	**	−	=	
Enteromorpha intestinalis						
Quadrigula lacustris	=		**	−		
Selenastrum minutum	=				=	
Cryptophyceae						
Microflagellates	=		=		*	+

= : no significant difference between (MI + MO)/2 and LW,
null hypothesis H_0: (MI + MO)/2 = LW accepted;
* : $p < 0.05$, ** : $p < 0.01$;
+ : (MI + MO)/2 > LW, − : (MI + MO)/2 < LW.

Table 22: Micrograzed chamber, (MI + MO)/2, and lake water mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1	Expt. 2	Expt. 3
Bacillariophyceae (diatoms)			
Asterionella formosa cells	=	=	=
A. formosa colonies			=
Synedra sp.	=	** +	=
Tabellaria fenestrata cells		* +	* +
T. fenestrata colonies		** +	** +
T. fenestrata empty frustules	=		** +
T. fenestrata colonies with empty frustules	=		** +
Chrysophyceae			
Dinobryon bavaricum cells			
D. bavaricum colonies			
D. bavaricum empty loricas	=		
Dinobryon sertularia cells			=
D. sertularia empty loricas			=
Syncrypta volvox			
"Ribbed" chrysophyte			
Uroglena volvox cells	=	=	=
Cyanophyceae			
Chroococcus turgidus colonies	=	=	* +
Coelosphaerium kuetzingianum		=	
Gloeocapsa punctata colonies		* +	=
Gloeothece linearis	=		
Microcystis aeruginosa cells	** +	** +	
M. aeruginosa colonies	** +	** +	

= : no significant difference between (MI + MO)/2 and LW, null hypothesis H_0: (MI + MO)/2 = LW accepted;

* : $p < 0.05$, ** : $p < 0.01$;

+ : (MI + MO)/2 > LW, − : (MI + MO)/2 < LW.

Grazing effects on *Ceratium hirundinella*

Ceratium hirundinella was the only dinophycean species that showed significant results in the comparisons. These data are presented in Table 23, separately from the main tables since full-sized *C. hirundinella* were too large to pass through the 125 μm net. Full-sized *C. hirundinella* were not recorded from the chambers until several days after the experiments were started.

Table 23: Results of comparisons for *Ceratium hirundinella* in experiment 3, with *Bosmina longispina* as macrograzer.

Probability associated with null hypothesis	Result of comparison by inspection
	GO = MO
	GI = MI
	GI = GO
**	GO < LW
	GI = LW
**	(GI + GO) /2 < LW
	MI = MO
*	(MI + MO) /2 < LW

= : no significant difference in densities of compared populations,
* : $p < 0.05$, ** : $p < 0.01$.

C. hirundinella was less abundant in the grazed outer compartment than in the lake water (Table 23). *C. hirundinella* was also less dense in the grazed chamber, (GI + GO) /2, and in the micrograzed chamber, (MI + MO) /2, than in the lake water.

DISCUSSION

The present study examined the physical and chemical effects of macrograzers separately, rather than emphasizing only the macrograzed taxa as many authors have in studies of *in situ*, species-specific effects of grazing (*e.g.*, Porter 1972, 1973; Weers and Zaret 1975; Lehman and Sandgren 1985). The current study emphasized the different results of chemical and physical effects of macrograzers on phytoplankton, and also showed that micrograzers can have significant effects on phytoplankton assemblages. With a few exceptions, *e.g.*, Skogstad *et al.* (1987); Lampert *et al.* (1986), micrograzing effects on phytoplankton have been largely dismissed in the grazing literature as negligible. These studies and the present one demonstrate significant micrograzing effects at the level of algal group and species, particularily in the absence of macrograzers. Differences in results from the three experiments of the present study were most likely related to seasonal differences; the dominant macrograzer and the micrograzer populations were among these seasonal variables.

Physical effects of macrograzers

Depression of phytoplankton densities is a very evident physical effect of macrograzers in general. In the present study, densities of some desmid species were depressed in the presence of macrograzers, *e.g.*, *Arthrodesmus convergens*, *Arthrodesmus incus*, *Mesotaenium* sp., *Spondylosium planum*, and *Teilingia granulata*. This is the first ecological study to demonstrate such a grazing effect on desmids. In a series of laboratory experiments Brook (1981) observed that *Cosmarium contratum*, *C. reniforme* and *Closterium peracerosum* can all be ingested and in turn digested by the macrograzer *Daphnia magna*; all that

remained in the cultures after 3 or 4 days were empty cells.

Results of the present study are antithetical to those of Porter (1972) who reported no detectable grazing effect on the total number of desmid cells. Porter's study was conducted in a body of water in which desmids were not abundant; in contrast, desmids were the dominant phytoplankton in Hogan's Pond. Although desmids tend to be the dominant freshwater phytoplankton in areas with acidic bedrock, (*e.g.* , Newfoundland) the effects of grazing on desmids has not previously been studied in waters in which they were abundant.

Most of the Chlorophyceae and microflagellate densities were unaffected or augmented by the physical effects of macrograzers. The chlorophycean taxa encountered were typically small. The majority of the smaller Chlorophyceae are capable of cell division in about two days or less (Happey-Wood 1985). Such rapid rates of potential population increase may explain why these taxa showed little evidence of depression, and a few were augmented in response to the physical effects of macrograzers. They may have been able to maintain their respective population sizes in spite of the effects of grazing. Knisely and Geller (1986) reported that zooplankters grazed more efficiently on phytoflagellates such as *Rhodomonas* and *Cryptomonas* than on Chlorococcales (an order in the Chlorophyceae). These authors assessed effective food concentration relative to *Rhodomonas minuta*, as a reference species for optimal food.

In the current study diatom densities were generally unaffected or depressed by the presence of macrograzers. *Tabellaria fenestrata* var. *lacustris* was depressed in the presence of the macrograzer *Bosmina longispina*, as was the number of empty frustules. *B. longispina* may have reduced the number of cells

which became senescent and subsequently empty. *Synedra* sp. was depressed in the presence of high densities of macrograzing *Diaptomus minutus*.

Densities of members of the Chrysophyceae were unaffected by macrograzing with two exceptions: *Uroglena volvox* was augmented in the presence of macrograzers, this may have been the result of reduced competition from macrograzer species. The empty loricas of *Dinobryon bavaricum* were depressed by macrograzing. Grazing by *Diaptomus minutus* may have reduced the number of individuals able to encyst or produce swarmers, thus reducing the number of empty loricas within the assemblage.

Several members of the Cyanophyceae were unaffected or depressed by physical effects of macrograzers in this study. *Microcystis aeruginosa* densities were depressed by grazing *Diaptomus minutus*. *Chroococcus turgidus* and *Gloeocapsa punctata* were augmented by macrograzing *Bosmina longispina*. *Chroococcus turgidus* and *Gloeocapsa punctata* form small colonies of 2 and 4 - 8 cells respectively; they were probably not grazed because they were 'distasteful' as are several of the Cyanophyceae (Ostrofsky *et al.* 1983), rather than because the cells were too large. Results of the current study concur with those of Weers and Zaret (1975) and Porter (1972) for the Cyanophyceae. Arnold (1971) reported that ingestion, assimilation, survivorship and reproduction of *Daphnia pulex* feeding on the Cyanophyceae were lower than in those feeding on the Chlorophyceae. Therefore it seems likely that macrograzers would select against grazing on the Cyanophyceae within natural phytoplankton assemblages when other more suitable food items were available.

Physical effects of macrograzers on *Ceratium hirundinella*

Full-sized *Ceratium hirundinella* were too large to pass through the 125 μm net. This fact and the delayed occurrence in the chambers indicate that the source in the chambers must have been a smaller life history stage. Gymnodinoid swarmers, which escape from germinating cysts and then develop into the "preceratium" phase in which the typical shape and elaborate system of plates are gradually acquired (Fritsch 1948), were probably the source of *C. hirundinella* in the chambers. Results of the present study suggest that the swarmer stage may have been macrograzed by *Bosmina longispina* and depressed the density of consequent adult population of *C. hirundinella* in the grazed outer compartment. It is also evident that as a result of containment *C. hirundinella* did not reach densities as high as those in the lake water. This suggests that the chambers were suboptimal environments for *C. hirundinella*, although, *C. hirundinella* adults were initially excluded by the 125 μm mesh net. Swarmers of *C. hirundinella* seem to be a vulnerable life history stage in the presence of *B. longispina*.

Chemical effects of macrograzers

Chemical effects of the macrograzers were most clearly shown in the detailed analysis of responses of individual species. The current study provided some evidence of augmentation of densities among specific desmid taxa, in particular the larger *Arthrodesmus* spp. (*A. subulatus* and *A. triangularis*) and also *Teilingia granulata*. A few individual taxa of the Chlorophyceae (*Selenastrum minutum*, *Ankistrodesmus* spp., *Chlorella vulgaris* autospores, and microflagellates) also showed augmentation of densities in the presence of macrograzer metabolites.

Most of the diatom densities were either unaffected or augmented by

macrograzer metabolites. Densities of *Tabellaria fenestrata* and *Synedra* sp. were augmented by *Bosmina longispina* metabolites.

Densities of two of the Chrysophyceae (*Uroglena volvox*, *Dinobryon sertularia* cells and empty loricas) were augmented by the macrograzer metabolites. In this case, the empty loricas may have resulted from the production of swarmers without previous division (Fritsch 1948). Reproduction may have been enhanced and so *D. sertularia* densities increased. Lehman and Sandgren (1985) stated that some of the discrepancy they encountered between their enclosure and lake water samples might be explained by increased rates of cyst production by enclosed populations, or alternatively by recruitment of excysting cells into the lake plankton.

Uroglena volvox, as well as *Tabellaria fenestrata* var. *lacustris* and *Synedra* sp. densities were augmented by *Bosmina longispina* metabolites. This is considerably fewer taxa than were augmented by metabolites from *Diaptomus minutus*. *D. minutus* may damage more algal cells, which are then lost from the assemblage of live cells, during feeding than *B. longispina*. Degradation of metabolites prior to release may be less advanced in *B. longispina* than in *D. minutus*, and so metabolites released by *B. longispina* may not be as readily available as nutrients to the other phytoplankton. There may be some basic biochemical difference in the nature of the metabolites released by the two macrograzers. Differences in glutamate dehydrogenase activity among marine zooplankton were reported by King *et al.* (1987). They found that glutamate dehydrogenase activity of microzooplankton (35 - 153 μm) was considerably lower than for the macrozooplankton (> 153 μm), suggesting that microzooplankton

made only a small contribution (1 - 11 %) of the total ammonium regenerated in the Gulf of Maine.

The density of *Microcystis aeruginosa* (Cyanophyceae) was augmented by *Diaptomus minutus* metabolites. Although *Microcystis aeruginosa* never reached bloom densities during the experiments, perhaps under natural conditions macrograzer metabolites may occasionally contribute to environmental conditions suitable for the initiation of blooms.

The chemical effects of macrograzers on phytoplankton should be studied in conjunction with chemical analysis of water samples for quantification of carbon dioxide and the important inorganic phytoplankton nutrients, and with qualitative and quantitative biochemical analysis of organic molecules (*e.g.*, amino acids) in the water samples. Such a study would be expensive, due to the precision required to detect the small quantities of the chemicals involved; nevertheless, it would be worthwhile even if it were only done for a few of the dissolved macrograzer metabolites.

Chemical effects of macrograzers make a significant contribution to organic matter in the water which may then be used by the phytoplankton assemblage. Lampert (1978), for example, reported that up to 17 % of the algal carbon ingested was initially lost as dissolved organic carbon (D.O.C.) from algae damaged during feeding. Additional D.O.C. was produced by secretion from *Daphnia* and by leaching from their faeces. Jörgensen (1987) suggested that degradation of phytoplankton cells can be a major contributor of dissolved free amino acids in natural waters. Small releases of dissolved organic matter and dissolved free amino acids such as referred to above, *i.e.*, the chemical effects of macrograzers,

may be important to phytoplankton under conditions of nutrient limitation.

Micrograzing

The desmid densities were augmented in the presence of micrograzers during the current study. This suggests that they were not significantly micrograzed. Micrograzers were very specific in their effects on the Chlorophyceae, to the extent of having opposite effects on *Chlorella vulgaris* autospores and *C. vulgaris* cells. Micrograzer effects resulted either directly through their grazing activities or indirectly via interspecific phytoplankton competition (*i.e.*, a biological effect). The micrograzers showed patchy distributions which is likely to have important implications in terms of their grazing effects in the lake.

Generally the diatoms were augmented in the presence of micrograzers, however, *Tabellaria fenestrata* var. *lacustris* densities were depressed. Suttle *et al.* (1986) reported that heterotrophic biflagellates [which may be considered micrograzers] were frequently observed to feed on much larger (40 - 84 μm long) pennate diatoms by engulfing the entire cell, digesting the contents and egesting the empty frustule. There was no evidence of similar occurrences in the present study.

Specific effects of the different micrograzers on phytoplankton suggested by the present study may be consequences of micrograzer food selection such as shown by Skogstad *et al.* (1987), who reported that diatoms were excellent food for only one of the five ciliates they studied. The chrysophycean taxa were little affected by micrograzing in the present study. Most of these taxa were comparatively large, flagellated cells, and were unlikely to be suitable as food items for the

micrograzers. Densities of several of the cyanophycean taxa were augmented by micrograzing, while others were unaffected. This suggests that the Cyanophyceae were not micrograzed in spite of their small cell size; they were probably avoided by both micrograzers and macrograzers for similar reasons.

Allelopathy

Some of the experimental observations may have been the consequence of allelopathic interactions, however such interactions among phytoplankton were not examined in the present study. The experimental chambers used in the study would lend themselves to an investigation of allelopathic interactions between phytoplankton monocultures, deployed in one of the compartments, and intact phytoplankton assemblages.

Implications for phytoplankton ecology

Aquatic grazing has not previously been investigated in terms of separate physical and chemical effects simultaneously in a single study. Harper (1977) pointed out that, while the influence of grazing on terrestrial plants was in part due to defoliation, trampling and the deposition of dung and urine were also important. In the aquatic environment the different effects of grazers are usually indistinguishable; under carefully arranged experimental conditions as in this study, they may be separated.

This study demonstrated that macrograzers can have significant physical and chemical effects on phytoplankton assemblages, although chemical effects are less readily detected than physical effects. This may be due to a time lag in the availability of macrograzer metabolites to phytoplankton. Physical and chemical

effects often produced distinctly different responses from individual phytoplankton taxa. Physical effects of macrograzers involve consumption of whole phytoplankton cells or colonies, or parts thereof, while chemical effects may involve augmentation of phytoplankton densities or possible inhibition of phytoplankton growth. Thus physical and chemical effects of macrograzers on phytoplankton assemblages would be expected to be different. Further study of the physical and chemical effects of macrograzers on desmids within natural phytoplankton assemblages dominated by desmids would be worthwhile.

Various micrograzing effects on phytoplankton assemblages were demonstrated in this study. The ecological impact of micrograzers may be much greater than is currently appreciated. It is hard to assess their impact in a natural setting, since the numbers of micrograzers tend to be suppressed in the presence of macrograzers, especially in enclosure studies. Examination of the effects of micrograzer monocultures on phytoplankton assemblages would elucidate the potential impact of specific micrograzers.

Results of the current study lend some support to the suggestion by Gliwicz (1975) that grazing may keep phytoplankton (*e.g.* , Chlorophyceae) in the exponential growth phase by removing potentially senescent cells and regenerating organic and inorganic nutrients. Grazing is very important in determining the relative contributions of different phytoplankton species within assemblages, as displayed by the present study. Hutchinson (1961) discussed "the paradox of the plankton", and suggested that predation should permit some diversification of both predator and prey within a habitat. Grazing may be considered as a form of predation, with plants as the prey items. The results of the present study show

that many phytoplankton taxa within assemblages are influenced by the physical effects of macrograzers, the chemical effects of macrograzer metabolites and micrograzer effects. The extent to which the individual phytoplankton taxa are influenced by grazing effects depends on many factors, including season and initial phytoplankton densities. Thus micrograzing and macrograzing effects contribute considerably to the heterogeneity of the planktonic environment, and to an explanation of "the paradox of the plankton".

REFERENCES

Allen, T.F.H. 1977. Scale in microscopic algal ecology: a neglected dimension. *Phycologia* **16**: 253-257.

Arnold, D.E. 1971. Ingestion, assimilation, survival, and reproduction by *Daphnia pulex* fed seven species of blue-green algae. *Limnol. Oceanogr.* **16**: 906-920.

Barnes, H. 1952. The use of transformations in marine biological statistics. *J. Cons. Perm. Int. Explor. Mer* **18**: 61-71.

Bergquist, A.M., S.R. Carpenter and J.C. Latino. 1985. Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. *Limnol. Oceanogr.* **30**: 1037-1045.

Berlyn, G.P. and J.P. Miksche. 1976. *Botanical Microtechnique and Cytochemistry*. The Iowa State University Press. Ames, Iowa.

Berman, M.S. and S. Richman. 1974. The feeding behaviour of *Daphnia pulex* from Lake Winnebago, Wisconsin. *Limnol. Oceanogr.* **19**: 105-109.

Bloem, J. and J. Vijverberg. 1984. Some observations on the diet and food selection of *Daphnia hyalina* (Cladocera) in an eutrophic lake. *Hydrobiol. Bull.* **18**: 39-45.

Bourrelly, P. 1966. *Les Algues d'eau douce. Les Algues vertes*. Editions N. Boubée et C^{ie}. (First published in 1957). Paris.

Bourrelly, P. 1968. *Les Algues d'eau douce. Les Algues jaunes et brunes*. Editions N. Boubée et C^{ie}. (First published in 1957). Paris.

Boyer, C.S. 1927. *Synopsis of North American Diatomaceae*. Part 1. Proc. Acad. Nat. Sci. Philadelphia. **LXXVIII** 1926 supplement.

Brook, A.J. 1981. *The Biology of the Desmids*. Blackwell Scientific Publications. Oxford.

Burns, C.W. 1968. The relationship between body size of filter feeding cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* **13**: 675-678.

Burns, C.W. and R.H. Rigler. 1967. Comparison of filtering rates of *Daphnia rosea* in lake water and in suspensions of yeast. *Limnol. Oceanogr.* **12**:

492-502.

Carvalho, G.R. and R.N. Hughes. 1983. The effect of food availability, female culture-density and photoperiod on ephippia production in *Daphnia magna* (Strauss). *Freshwat. Biol.* 13: 37-46.

Davis, C.C. 1972a. Plankton dynamics in a Newfoundland lake. *Verh. Internat. Verein: Limnol.* 18: 278-283.

Davis, C.C. 1972b. Plankton succession in a Newfoundland lake. *Int. Revue ges. Hydrobiol.* 57: 367-395.

Davis, C.C. 1976. Simultaneous quantitative comparison of planktic Crustacea in two Newfoundland boreal lakes. *Int. Revue ges. Hydrobiol.* 61: 807-823.

DeMott, W.R. 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnol. Oceanogr.* 27: 518-527.

Drouet, F. 1959. Myxophyceae. *In*: (H.B. Ward and G.C. Whipple). W.T. Edmondson (editor). *Freshwater Biology*. 2nd edition. John Wiley and Sons, Inc. Chapter 5 Pp. 95-115. (First published in 1918).

Dyer, D.L. and D.E. Richardson. 1962. Materials of construction in algal culture. *Appl. Microbiol.* 10: 129-132.

Earle, J.C., H.C. Duthie and D.A. Scruton. 1987. Factors influencing the distribution of phytoplankton in 97 headwater lakes in insular Newfoundland. *Can. J. Fish. Aquat. Sci.* 44: 639-649.

Ferguson, A.J.D., J.M. Thompson and C.S. Reynolds. 1982. Structure and dynamics of zooplankton communities maintained in closed systems, with special reference to the algal food supply. *J. Plankt. Res.* 4: 523-543.

Ferguson-Wood, E.J.F. 1967. *Microbiology of Oceans and Estuaries*. Elsevier Oceanography series 3. Elsevier Publishing Co. Amsterdam.

Förster, K. 1970. Beitrag zur Desmidieenflora von Süd-Holstein und der Hansestadt Hamburg. *Nova Hedwig.* 20: 253-411.

Frank, P.W. 1957. Coactions in laboratory populations of two spp. of *Daphnia*. *Ecology* 38: 510-519.

Fritsch, 1948. *The Structure and Reproduction of the Algae*. Volume 1. Cambridge University Press. Cambridge.

Garnett, W.J. 1953. *Freshwater Microscopy.* Constable and Company, Ltd. London.

Gauld, D.T. 1950. A fish cultivation experiment in an arm of a sea-loch. III. The plankton of Kyle Scotnish. *Proc. Roy. Soc. Edinburgh,* Section B **LXIV** Part 1 (Number 3): 36-64.

Gilbert, J. and R.S. Stemberger. 1985. Control of *Keratella* populations by interference competition from *Daphnia*. *Limnol. Oceanogr.* **30**: 180-188.

Gliwicz, Z.M. 1975. Effect of zooplankton grazing on photosynthetic activity and composition of phytoplankton. *Verh. Internat. Verein. Limnol.* **19**: 1490-1497.

Gophen, M., B.Z. Cavari and T. Berman. 1974. Zooplankton feeding on differentially labelled algae and bacteria. *Nature* **247**: 393-394.

Happey-Wood, C.M. 1985. Growth characteristics of micro-green algae. *Verh. Internat. Verein. Limnol.* **22**: 2855-2860.

Harper, J.L. 1977. *Population Biology of Plants.* Academic Press. London.

Hebert, P.D. 1978. The population biology of *Daphnia*. *Biol. Rev.* **53**: 387-426.

Horton, P.A., M. Rowan, K.E. Webster and R.H. Peters. 1979. Browsing and grazing by cladoceran filter feeders. *Can. J. Zool.* **57**: 206-212.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. mongr.* **54**: 187-211.

Hustedt, F. 1923. *Süsswasser-Diatomeen Deutschlands.* Geschäftsstelle des Mikrokosmos: Franckh'sche Verlagshandlung, Stuttgart.

Hutchinson, G.E. 1961. The paradox of the plankton. *Am. Naturalist* **95**: 137-145.

Jewson, D.H. and J.A. Taylor. 1978. The influence of turbidity on net phytoplankton photosynthesis in some Irish lakes. *Freshwat. Biol.* **8**: 575-584.

Jewson, D.H., B.H. Rippey and W.K. Gilmore. 1981. Loss rates from sedimentation, parasitism, and grazing during the growth, nutrient limitation, and dormancy of a diatom crop. *Limnol. Oceanogr.* **26**: 1045-1057.

Jörgensen, N.O.G. 1987. Free amino-acids in lakes: concentrations and assimilation rates in relation to phytoplankton and bacterial production. *Limnol. Oceanogr.* **32**: 97-111.

Kersting, K. and W. van der Leeuw. 1976. The use of the Coulter counter for measuring the feeding rates of *Daphnia magna*. *Hydrobiol.* **49**: 233-237.

King, F.D., T.L. Cucci and D.W. Townsend. 1987. Microzooplankton and macrozooplankton glutamate dehydrogenase as indices of the relative contributions of these fractions to ammonium regeneration in the Gulf of Maine. *J. Plankt. Res.* **9**: 277-289.

Knisely, K. and W. Geller. 1986. Selective feeding of four zooplankton species on natural lake phytoplankton. *Oecologia* (Berlin) **69**: 86-94.

Kristiansen, J. 1959. *Flagellates from some Danish lakes and ponds*. Ejnar Munksgaard, Copenhagen.

Lampert, W. 1974. A method for determining food selection by Zooplankton. *Limnol. Oceanogr.* **19**: 995-997.

Lampert, W. 1978. Release of dissolved organic carbon by grazing zooplankton. *Limnol. Oceanogr.* **23**: 831-834.

Lampert, W., W. Flecker, H. Rai, and B.E. Taylor. 1986. Phytoplankton control by grazing zooplankton: A study of the spring clear water phase. *Limnol. Oceanogr.* **31**: 478-490.

Lehman, J.T. 1980a. Nutrient recycling as an interface between algae and grazers in communities. Pp. 251-263. *In*: W.C. Kerfoot (editor) *Evolution and Ecology of Zooplankton Communities*. University Press of New England. Hanover.

Lehman, J.T. 1980b. Release and cycling of nutrients between planktonic algae and herbivores. *Limnol. Oceanogr.* **25**: 620-632.

Lehman, J.T. and C.D. Sandgren. 1985. Species-specific rates of growth and grazing loss among freshwater algae. *Limnol, Oceanogr.* **30**: 34-46.

McMahon, J.W. and R.H. Rigler. 1965. Feeding rate of *Daphnia magna* Strauss in different foods labelled with radioactive phosphorus. *Limnol. Oceanogr.* **10**: 105-114.

Meister, Fr. 1912. *Die Kieselalgen der Schweiz*. Druck und Verlag von K.J. Wyss. Bern.

Molisch, H. 1937. *Der Einfluss einer Planze auf die andere Allelopathie.* Verlag von Gustav Fischer in Jena.

Neill, W.E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. *Oecologia* **61**: 175-181.

Omori, M. and T. Ikeda. 1984. Feeding. Chapter 7. *In*: *Methods in Marine Zooplankton Ecology.* John Wiley & Sons, Inc. New York.

Ostrofsky, M.L., F.G. Jacobs and J. Rowan. 1983. Evidence for the production of extracellular herbivore deterrents by *Anabaena flos-aquae. Freshwat. Biol.* **13**: 501-506.

Patrick, R. and C.W. Reimer. 1966. *The Diatoms of the United States, Exclusive of Alaska and Hawaii.* Monogr. Acad. Nat. Sci. Philadelphia. Number 13.

Pennak, R.W. 1978. *Freshwater Invertebrates of the United States.* 2nd Edition. John Wiley and Sons, New York.

Porter, K.G. 1972. A method for the *in-situ* study of zooplankton grazing effects on algal species composition and standing crop. *Limnol. Oceanogr.* **17**: 913-917.

Porter, K.G. 1973. Selective grazing and differential digestion of algae by zooplankton. *Nature* **244**: 179-180.

Porter, K.G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. *Science* **192**: 1332-1334.

Porter, K.G., J. Gerritsen and J.D. Orcutt Jr. 1982. The effect of food concentrations on swimming patterns, feeding behaviours, ingestion, assimilation, and respiration by *Daphnia. Limnol. Oceanogr.* **27**: 935-949.

Pratt, R.J., J.F. Oneto and J. Pratt. 1945. Studies on *Chlorella vulgaris.* X. Influence of the age of the culture on the accumulation of chlorellin. *Amer. J. Bot.* **32**: 405-408.

Prescott, G.W. 1962. *Algae of the Western Great Lakes area.* W.C. Brown Co. Publishers, Dubuque, Iowa. (First published in 1951).

Prescott, G.W. 1979. *How to know the freshwater algae.* 3rd Edition. W.C. Brown Co. Publishers, Dubuque, Iowa. (First published in 1954).

Price, H.J. and G.A. Paffenhöfer. 1986. Effects of concentration on the feeding of

a marine copepod in algal monocultures and mixtures. *J. Plankton Res.* **8**: 119-128.

Ray, A.A.(editor) 1982. *SAS User's Guide: Statistics.* SAS Institute Inc. Cary, North Carolina.

Reynolds, C.S. 1984. *The Ecology of Freshwater Phytoplankton.* Cambridge University Press. Cambridge.

Rice, E.L. 1984. *Allelopathy.* 2nd edition. Academic Press, Inc. Florida.

Richman, S. and S.I. Dodson. 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. *Limnol. Oceanogr.* **28**: 948-956.

Rigler, F.H. 1975. Nutrient kinetics and the new typology. II. Lakes. 2. Chemical Limnology. *Verh. Internat. Verein. Limnol.* **19**: 197-210.

Round, F.E. 1984. *The Ecology of the Algae.* Cambridge University Press. First published 1981.

Ryther, J.H. 1954. Inhibitory effects of phytoplankton on the feeding of *Daphnia magna* with reference to growth, reproduction and survival. *Ecology* **35**: 522-533.

Skogstad, A., L. Granskog and D. Klaveness. 1987. Growth of freshwater ciliates offered planktonic algae as food. *J. Plankton Res.* **9**: 503-513.

Slobodkin, L.B. 1954. Population dynamics in *Daphnia obtusa* Kurz. *Ecol. Monogr.* **24**: 69-88.

Smith, G.M. 1950. *The Fresh-water Algae of the United States.* McGraw-Hill Book Company, Inc. New York.

Smith, G.M. 1977. *Phytoplankton of the inland lakes of Wisconsin.* Bibliotheca Phycologica. Herausgegeben von J. Cramer. Band 30. Madison. (First published in 1924).

Suttle, C.A., A.M. Chan, W.D. Taylor. and P.J. Harrison. 1986. Grazing of planktonic diatoms by microflagellates. *J. Plankt. Res.* **8**: 393-398.

Taub, F.B. and A.M. Dollar. 1968. The nutritional inadequacy of *Chlorella* and *Chlamydomonas* as foods for *Daphnia pulex*. *Limnol. Oceanogr.* **13**: 607-617.

Teiling, E. 1948. *Staurodesmus, genus novum. Botaniska Notiser* 1:49-83.

Thatcher, S.J. 1987. Some effects of grazing on enclosed freshwater phytoplankton populations in a small Newfoundland lake. *Br. Phycol. J.* Abstract *in press.*

Thompson, J.M., A.J.D. Ferguson and C.S. Reynolds. 1982. Natural filtration rates of zooplankton in a closed system: the derivation of a community grazing index. *J. Plankt. Res.* 4: 545-560.

Throndson, J. 1978. Preservation and storage. Pp.69-74. *In*: A. Sournia (editor) *Phytoplankton Manual.* The UNESCO Press, Paris.

Weers, E.T. and T.M. Zaret. 1975. Grazing effects on nanoplankton in Gatum Lake, Panama. *Verh. Internat. Verein. Limnol.* 19: 1480-1483.

Woodhead, N. and R.D. Tweed. 1960. Additions to the algal flora of Newfoundland. 1. New and interesting algae in the Avalon Peninsula and Central Newfoundland. *Hydrobiol.* 15: 309-362.

Yoxall, W. H. 1981. The surface waters and associated landforms of the island of Newfoundland. Pp. 154-188. *In*: Macpherson, A.G. and J.B. Macpherson, editors. *The Natural Environment of Newfoundland, Past and Present.* Memorial University Printing Services. St. John's.

Appendix A: Identification and classification of phytoplankton

The overall classification used follows that of Smith (1950). Phytoplankton encountered and identified were from five phyla (with reference to keys parenthesized): Chlorophyta (Prescott 1962, 1979; Smith 1977), Chrysophyta (Kristiansen 1959), Cryptophyta (includes Bacillariophyceae) (Boyer 1927; Hustedt 1923; Meister 1912; Patrick and Reimer 1966), Cyanophyta (Drouet 1959; Prescott 1962; 1979) and Pyrrhophyta (Prescott 1962, 1979) (Table 24).

Table 24: Phytoplankton classification

CHLOROPHYTA
- Chlorophyceae
  - Chlorococcales
    - Oocystaceae
      - *Ankistrodesmus* spp. Corda
      - *Chlorella ellipsoidea* Gerneck
      - *Chlorella vulgaris* Beyerinck
      - *Kirchneriella contorta* (Schmidle) Bohlin
      - *Quadrigula lacustris* (Chod.) G.M. Smith
      - *Selenastrum minutum* (Nägeli) Collins
      - *Selenastrum westii* G.M. Smith
    - Micractiniaceae
      - *Acanthosphaera zachariasi* Lemmermann
      - *Golenkinia paucispina* West and West
      - *Golenkinia radiata* (Chod.) Wille
  - Tetrasporales
    - Coccomyxaceae
      - *Elakatothrix gelatinosa* Wille
    - Scenedesmaceae
      - *Crucigenia tetrapedia* (Kirch.) West and West
      - *Scenedesmus bijuga* (Turp.) Lagerheim
  - Ulvales
    - Ulvaceae
      - *Enteromorpha intestinalis* (L.) Grev.

Volvocales
Chlamydomonadaceae
Chlamydomonas globosa Snow

CHLOROPHYTA
Zygnemaphyceae
Zygnematales
Desmidiaceae
Arthrodesmus convergens Ehrenberg
Arthrodesmus incus (De Brébisson) Hassell
Arthrodesmus Ralfsii W. West
Arthrodesmus subulatus Kützing
Arthrodesmus triangularis var. *rotundatus* (Raciborski) *comb. nov.*
Closterium sp. Nitzsch
Cosmarium reniforme (Ralfs) Arch.
Euastrum sp. Ehrenberg (emend. Ralfs)
Micrasterias sp. Agardh
Spondylosium planum (Wolle)
Staurastrum paradoxum Meyen
Staurodesmus spp. Teiling
Teilingia granulata (Roy et Biss) Bourelly
Mesotaeniaceae
Gonatozygon pilosum Wolle
Mesotaenium sp. Nägeli
Zygnemataceae
Spirogyra sp. Link

CRYPTOPHYTA
Cryptophyceae
Cryptomonadales
Cryptochrysidaceae
Rhodomonas ovalis Nygaard
Cryptomonadaceae
Cryptomonas sp. Ehrenberg

CHRYSOPHYTA
Bacillariophyceae
Centrales
Coscinodiscaceae
Cyclotella bodanica Kützing
Melosira varians Agardh

Pennales
Cymbellaceae
Cymbella sp. Agardh
Gomphonema spp. Agardh
Eunotiaceae
Eunotia spp. Ehrenberg
Fragilariaceae
Asterionella formosa var. *formosa* Hass.
Asterionella formosa var. *gracillima* (Hantz.) Grun
Diatoma sp. Bory *nom. cons. non.* Loureiro
Semiorbis hemicyclus Ehrenberg Patrick *comb. nov.* var. *hemicyclus*
Synedra spp. Ehrenberg
Tabellaria fenestrata var. *lacustris* Meister
Tabellaria flocculosa var. *flocculosa* (Roth) Kützing
Naviculaceae
Frustulia rhomboides (Ehrenberg) Cleve
Navicula spp. Bory
Pinnularia sp. Ehrenberg *nom. cons.*
Stauroneis sp. Ehrenberg
Nitzschiaceae
Nitzschia spp. Grun
Surirellaceae
Cymatopleura solea var. *regula* Grun.
Surirella sp. Turpin (probably *Surirella ovalis* Bréb.)

CHRYSOPHYTA
Chrysophyceae
Chrysomonadales
Syncryptaceae
Syncrypta volvox Ehrenberg
Ochromonadales
Dinobryaceae
Dinobryon bavaricum Imhof
Dinobryon sertularia Ehrenberg
Ochromonadaceae
Uroglena volvox Ehrenberg

CYANOPHYTA
Cyanophyceae
Chroococcales
Chroococcaceae
Aphanothece stagnina (Spreng.)
(*Aphanothece braun* in Rabenhorst)
Chroococcus minutus (Kützing) Nägeli

Chroococcus turgidus (Kützing) Nägeli
Coelosphaerium kuetzingianum Nägeli
Gloeocapsa punctata Nägeli
Gloeothece linearis Nägeli
Gloeothece rupestris (Lyng.) Barnet *in* Wittrock and Nordstedt
Microcystis aeruginosa Kützing
Merismopedia tenuissima Lemmerman

Oscillatoriales
Nostocaceae
Anabaena oscillarioides Bory
Nostoc sp. Vaucher (chain form)
Oscillatoriaceae
Lyngbya taylorii Drouet and Strickland *in* Strickland
Oscillatoria sp. Vaucher

PYRRHOPHYTA
Dinophyceae
Peridinales
Ceratiaceae
Ceratium hirundinella (O.F. Müll) Dujardin

MISCELLANEOUS PHYTOPLANKTON
microfilaments
ribbed autospore

Notes on phytoplankton identifications

Arthrodesmus Ehrenberg

Teiling (1948) erected the genus *Staurodesmus* to include the genus *Arthrodesmus* and those forms of *Staurastrum* typified by the possession of a single spine, or papillea at each angle, of each semicell. The references used to identify the desmids found in the present study (Bourrelly, 1966; Prescott 1962, 1979; Smith 1977) still use the genus *Arthrodesmus* and so its' use has been maintained in this study.

Chroococcus turgidus

Specimens of *Chroococcus turgidus* from Hogan's Pond were small (cell

lengths about 3.75 μm and cell widths 2.5 - 2.75 μm compared with sizes mentioned by Prescott (1962). Prescott (1962) regarded *Chroococcus giganteus* as a variety maximum of *C. turgidus*. The *C. turgidus* specimens from Hogan's Pond may be considered variety minima.

"Ribbed" chrysophyte

This taxon was initially identified as a "ribbed autospore" because of the similarity the specimens showed in cellular organisation with *Chlorella vulgaris* autospores. Professor F.R. Round (University of Bristol, personal communication) and Dr. C.M. Happey-Wood (University College of North Wales, personal communication) suggested that the specimens might belong to the Chrysophyceae. Reference to Bourrelly (1968), which deals with this group thoroughly, neither confirmed nor refuted this suggestion.

Syncrypta volvox

Individual cells of this colonial chrysophycean from Hogan's Pond were usually 4 - 6 μm in length and each equipped with two flagella. Colonies were about 14 μm in diameter. Cells of the genus *Syncrypta* have smooth membranes in contrast to members of the genus *Synura* which have short spines or apiculations formed by scales on the membrane. These two genera are sometimes difficult to distinguish.

Teilingia granulata

Reference was made to Förster (1970) in the identification of *Teilingia granulata*, which provided a more detailed illustration than the north american texts.

Appendix B: MANOVA results

Table 25: MANOVA results for taxa in experiment 1.

Source of variation:	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Anabaena oscillarioides	5	0.27	n.s.		-	
A. oscillarioides filaments	5	0.25	n.s.		-	
Ankistrodesmus spp.	9	2.14	*	4	3.83	**
Arthrodesmus convergens	5	4.71	**		-	
Arthrodesmus incus	8	1.08	n.s.		-	
Arthrodesmus ralfsii	10	1.85	n.s.	4	2.26	n.s.
A. ralfsii empty	4	1.92	n.s.		-	
A. ralfsii juveniles	5	1.58	n.s.		-	
Arthrodesmus subulatus	8	2.82	**	4	2.96	*
Arthrodesmus triangularis	5	3.48	*		-	
Arthrodesmus spp.	10	5.41	**	4	8.77	**
Asterionella formosa	10	1.33	n.s.	4	1.59	n.s.
A. formosa colonies	10	1.25	n.s.	4	1.40	n.s.
Chlamydomonas globosa	9	0.68	n.s.	4	0.98	n.s.
Chlorella ellipsoidea	10	4.05	**	4	1.70	n.s.
Chlorella vulgaris	10	4.38	**	4	2.62	*

Key: d.f. degrees of freedom, F F-value, sign. statistical significance, ** significant at 0.01 probability, * significant at 0.05 probability, n.s. not significant, - non-estimable.
Cells are the morphological unit used unless otherwise indicated.

Table 25:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Chlorella vulgaris autospores	10	3.01	**	4	2.65	*
Chroococcus turgidus colonies	10	9.75	**	4	3.72	**
Closterium sp.	5	1.53	n.s.		-	
Cyclotella bodanica	6	0.62	n.s.		-	
Cymbella sp.	6	0.72	n.s.		-	
Diatoma sp.	6	0.61	n.s.		-	
Dinobryon bavaricum	5	4.02	**		-	
D. bavaricum colonies	5	4.07	**		-	
D. bavaricum empty cells	7	16.19	**	4	20.20	**
Dinobryon sertularia	5	4.78	**		-	
D. sertularia colonies	5	4.00	**		-	
D. sertularia empty cells	7	1.00	n.s.		-	
Elakatothrix gelatinosa	4	2.28	n.s.		-	
Enteromorpha intestinalis	6	9.77	**		-	
Eunotia spp.	4	2.45	n.s.		-	
Filamentous chlorophycean	8	40.13	**	4	62.37	**
Frustulia rhomboides	5	0.33	n.s.		-	
Green microflagellates	8	3.03	**	4	4.65	**

Table 25:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Gloeocapsa punctata colonies	8	1.02	n.s.		-	
Gloeothece linearis	8	5.91	**	4	1.53	n.s.
Golenkinid radiata	4	0.71	n.s.		-	
Gomphonema spp.	4	0.48	n.s.		-	
Lyngbya taylorii	4	0.62	n.s.		-	
Mesotaenium sp.	10	2.51	**	4	0.35	n.s.
Micrasterias sp.	1	0.33	n.s.		-	
Microcystis aeruginosa	9	23.15	**	4	36.92	**
M. aeruginosa colonies	9	27.82	**	4	52.68	**
Navicula spp.	10	1.31	n.s.	4	0.21	n.s.
Nitzschia spp.	6	1.46	n.s.		-	
Quadrigula lacustris	8	2.32	*	4	2.81	*
"Ribbed" chrysophycean	4	3.37	*		-	
Scenedesmus bijuga	5	1.23	n.s.		-	
S. bijuga colonies	5	1.15	n.s.		-	
Selenastrum minutum	8	3.71	**	4	5.47	**
Selenastrum westii	8	0.79	n.s.	4	0.69	n.s.
Spondylosium planum	9	0.66	n.s.	4	0.58	n.s.

Table 25:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Spondylosium planum filaments	9	0.63	n.s.	4	0.56	n.s.
Staurodesmus sp.	5	10.19	**		-	
Stauroneis sp.	4	1.00	n.s.		-	
Synedra spp.	10	10.72	**	4	2.16	*
Syncrypta volvox	5	2.71	*		-	
Tabellaria fenestrata	10	1.50	n.s.	4	1.25	n.s.
T. fenestrata colonies	10	1.19	n.s.	4	1.16	n.s.
T. fenestrata empty cells	10	1.99	*	4	0.20	n.s.
T. femestrata empty colonies	10	3.22	**	4	0.28	n.s.
Tabellaria flocculosa	6	0.56	n.s.		-	
T. flocculosa colonies	6	0.51	n.s.		-	
Teilingia granulata	8	2.63	*	4	2.95	*
T. granulata filaments	8	2.11	n.s.	4	2.48	n.s.
U. volvox	10	2.16	*	4	3.88	**

Table 26: MANOVA results for taxa in experiment 2.

Source of variation:	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Anabaena oscillarioides	7	0.76	n.s.	4	0.48	n.s.
A. oscillarioides filaments	7	2.00	n.s.	4	1.48	n.s.
Ankistrodesmus spp.	9	4.33	**	4	4.61	**
Arthrodesmus incus	8	3.55	**	4	1.68	n.s.
A. incus empty cells	5	1.05	n.s.	4	0.92	n.s.
Arthrodesmus subulatus	8	3.61	**	4	3.03	*
A. subulatus juveniles	4	1.28	n.s.		-	
Arthrodesmus triangularis	9	15.29	**	4	11.80	**
A. triangularis empty cells	8	0.51	n.s.	4	0.70	n.s.
A. triangularis juveniles	8	4.03	**	4	4.05	**
Arthrodesmus spp.	9	18.02	**	4	21.69	**
Asterionella formosa	8	2.51	*	4	1.73	n.s.
Ceratium hirundinella	6	0.88	n.s.	4	0.54	n.s.
Chlamydomonas globosa	8	2.23	*	4	1.73	n.s.
Chlorella ellipsoidea	9	11.42	**	4	12.71	**
Chlorella vulgaris	9	15. 09	**	4	11.14	**

Key: d.f. degrees of freedom, F F-value, sign. statistical significance, ** significant at 0.01 probability, * significant at 0.05 probability, n.s. not significant, - non-estimable.
Cells are the morphological unit used unless otherwise indicated.

Table 26 :

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Chlorella vulgaris autospores	9	14.99	**	4	23.46	**
Chroococcus minutus	5	7.77	**		-	
Chroococcus turgidus colonies	9	4.69	**	4	0.82	n.s.
Coelosphaerium kuetzingianum	8	6.27	**	4	1.85	n.s.
Dinobryon sertularia	8	1.05	n.s.	4	0.67	n.s.
D. sertularia empty cells	4	0.76	n.s.		-	
Elakatothrix gelatinosa	4	1.04	n.s.		-	
Enteromorpha intestinalis	6	1.87	n.s.	4	2.63	n.s.
Eunotia spp.	4	0.50	n.s.		-	
Filamentous chlorophycean	4	2.29	n.s.		-	
Frustulia rhomboides	4	3.67			-	
Green microflagellates	9	9.00	**	4	13.64	**
Gloeocapsa punctata colonies	9	1.86	n.s.	4	2.36	n.s.
Glaeothece linearis	4	9.07	**		-	
Golenkinia radiata	4	2.29	n.s.		-	
Gomphonema spp.	6	0.62	n.s.		-	
Lyngbya taylorii	4	4.81	**		-	
Mesotaenium sp.	7	12.77	**	4	19.99	**

Table 26 :

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Microcystis aeruginosa	9	8.68	**	4	4.84	**
M. aeruginosa colonies	9	10.46	**	4	7.52	**
Navicula spp.	8	0.95	n.s.	4	0.27	n.s.
Nitzschia spp.	4	0.93	n.s.		-	
Nostoc sp.	4	21.75	**		-	
Nostoc sp. chains	4	22.37	**		-	
Quadrigula lacustris	9	1.60	n.s.	4	1.12	n.s.
"Ribbed" chrysophycean	5	21.19	**		-	
Scenedesmus bijuga	5	0.59	n.s.		-	
S. bijuga colonies	5	0.59	n.s.		-	
Selenastrum minutum	5	10.91	**		-	
Semiorbis hemicyclus	4	0.81	n.s.		-	
Spondylosium planum	8	4.17	**		-	
S. planum filaments	8	4.19	**		-	
Staurodesmus sp.	4	6.18	**		-	
Synedra spp.	9	23.52	**	4	41.96	**
Tabellaria fenestrata	8	2.81	**	4	2.55	*
T. fenestrata	8	3.44	**	4	3.68	**

Table 26:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Tabellaria fenestrata empty cells	8	0.47	n.s.	4	0.80	n.s.
Tabellaria flocculosa	7	0.53	n.s.	4	0.63	n.s.
T. flocculosa colonies	7	0.60	n.s.		-	
T. flocculosa empty cells	*	0.85	n.s.		-	
Teilingia granulata	9	7.95	**	4	7.14	**
T. granulata filaments	9	11.32	**	4	10.32	**
Uroglena volvox	6	2.75	*	4	3.61	*

Table 27:- MANOVA results for taxa in experiment 3.

Source of variation:	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Anabaena oscillarioides	9	0.69	n.s.	4	0.15	n.s.
A. oscillarioides filaments	9	0.68	n.s.	4	0.31	n.s.
Ankistrodesmus spp.	2	0.27	n.s.		-	
Aphanothece stagnina	4	9.18	**		-	
Arthrodesmus incus	7	0.21	n.s.	4	0.16	n.s.
Arthrodesmus subulatus	7	0.82	n.s.		-	
Arthrodesmus triangularis	9	1.95	n.s.	4	1.59	n.s.
A. triangularis empty cells	9	1.83	n.s.	4	2.84	*
A. triangularis juveniles	4	0.41	n.s.		-	
Arthrodesmus spp.	9	1.97	*	4	1.98	n.s.
Asterionella formosa	8	1.85	n.s.	4	1.41	n.s.
A. formosa colonies	8	2.34	*	4	1.82	n.s.
Ceratium hirundinella	9	5.53	**	4	4.18	**
Chlamydomonas globosa	7	0.45	n.s.		-	
Chlorella ellipsoidea	9	4.31	**	4	2.40	n.s.

Key: d.f. degrees of freedom, F F-value, sign. statistical significance, ** significant at 0.01 probability, * significant at 0.05 probability, n.s. not significant, - non-estimable.
Cells are the morphological unit used unless otherwise indicated.

Table 27:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Chlorella vulgaris	9	11.29	**	4	18.06	**
C. vulgaris autospores	9	2.01	*	4	1.63	n.s.
Chroococcus turgidus colonies	9	3.98	**	4	2.39	n.s.
Crucigenia tetrapedia	7	0.33	n.s.		-	
Cyclotella bodanica	9	0.95	n.s.	4	0.67	n.s.
Cymbella sp.	5	0.13	n.s.		-	
Diatoma sp.	2	0.02	n.s.		-	
Dinobryon bavaricum	4	0.68	n.s.		-	
D. bavaricum empty cells	3	0.05	n.s.		-	
Dinobryon sertularia	8	2.91	**	4	3.57	*
D. sertularia empty cells	8	4.24	**	4	4.43	**
Elakatothrix gelatinosa	9	1.80	n.s.	4	0.76	n.s.
Filamentous chlorophyceae	9	7.73	**	4	8.55	**
Frustulia rhomboides	1	0.09	n.s.		-	
Green microflagellates	9	8.37	**	4	2.78	*
Gloeocapsa punctata colonies	9	6.32	**	4	9.46	**
Gloeothece linearis	8	4.11	**	4	6.17	**
Gloeothece rupestris	1	0.20	n.s.		-	

Table 27:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Golenkinia paucispina	7	0.81	n.s.	4	0.27	n.s.
Golenkinia radiata	6	0.61	n.s.		-	
Gomphonema spp.	1	0.76	n.s.		-	
Merismopedia tenuissima	8	1.22	n.s.	4	2.06	n.s.
M. tenuissima colonies	8	1.36	n.s.	4	2.08	n.s.
Mesotaenium sp.	7	2.87	*	4	3.82	*
Microcystis aeruginosa	8	1.15	n.s.	4	1.93	n.s.
M. aeruginosa	8	1.17	n.s.		-	
Navicula spp.	9	1.66	n.s.	4	2.60	*
Nitzschia spp.	4	2.75	n.s.		-	
Nostoc sp.	1	0.60	n.s.		-	
Nostoc sp. chains	1	0.59	n.s.		-	
Pinnularia sp.	1	0.40	n.s.		-	
Quadrigula lacustris	9	4.73	**	4	2.30	*
"Ribbed" chrysophycean	7	10.25	**		-	
Scenedesmus bijuga colonies	7	1.05	n.s.	4	0.98	n.s.
Selenastrum minutum	8	5.23	**	4	2.52	*
Spondylosium planum	8	2.95	**	4	1.84	n.s.

Table 27:

Continued...

	Grazing treatment by date			Comparisons overall		
	d.f.	F	sign.	d.f.	F	sign.
Spondylosium planum filaments	8	3.57	**	4	4.20	**
Synedra spp.	9	2.58	**	4	0.25	n.s.
Tabellaria fenestrata	9	11.08	**	4	12.18	**
T. fenestrata colonies	9	18.36	**	4	26.17	**
T. fenestrata empty cells	9	10.69	**	4	16.66	**
T. fenestrata empty colonies	9	12.98	**	4	17.89	**
Tabellaria flocculosa	9	0.53	n.s.	4	0.33	n.s.
T. flocculosa colonies	9	0.57	n.s.	4	0.13	n.s.
T. flocculosa empty cells	9	1.04	n.s.	4	1.02	n.s.
T. flocculosa empty colonies	9	0.52	n.s.	4	0.42	n.s.
Teilingia granulata	9	5.77	**	4	11.13	**
T. granulata filaments	9	5.09	**	4	8.70	**
U. volvox	9	3.47	**	4	2.82	*

Table 28: Percentage of significant F values for MANOVAs with respect to each experiment.

	Experiment 1 — Number		Experiment 2 Number		Experiment 3 Number	
Cases:	68	100 %	59	100 %	65	100 %
Cases with significant F values for treatment by date:	31	46 %	34	58 %	29	45 %
Cases with significant F values for comparisons overall:	15	22 %	18	31 %	22	34 %
Taxa:	49	100 %	42	100 %	45	100 %
Taxa with significant F values for treatment by date:	24	49 %	26	62 %	20	44 %
Taxa with significant F values for comparisons overall:	12	25 %	12	29 %	15	33 %

Cases included the different morphological and life history stages of each taxon separately in this analysis; taxa in this analysis constituted only taxonomically distinct entities, *e.g.* , *Chlorella vulgaris* cells and autospores were considered as two cases, but only one taxon in the analysis.

The probability of all the comparisons overall for each case was determined after the individual comparisons had been made. The percentages of significant F values shown in (Table 28) are well above the 5 % level and therefore the MANOVAs can be considered statistically acceptable with respect to each experiment. The complexity and quantity of data involved prevented these results from being obtained more directly, *i.e.* , within the MANOVAs.

Appendix C: Light and temperature data

Secchi disc depth provided an indication of the depth of light penetration and therefore the depth of the euphotic zone, which is typically estimated as 3 times the Secchi depth (Round 1984). The euphotic zone extended beyond the bottom depth of most of Hogan's Pond throughout the experiments (Table 29).

Table 29: Secchi readings and cloud cover during the experiments.

Experiment	Date	Secchi depth (m)	Depth of euphotic zone (m)	Cloud cover in eighths
1	27-05-85	3.50	10.50	-
	28-05-85	1.75	5.25	7
	29-05-85	3.75	11.25	5
	30-05-85	-	-	3
	31-05-85	4.50	13.50	2
	03-06-85	3.75	11.25	4
	06-06-85	2.10	6.30	6
2	25-06-85	-	-	0
	27-06-85	5.00	15.00	--
	29-06-85	3.50	10.50	4
	01-07-85	6.00	18.00	5
	03-07-85	3.50	10.50	3
	05-07-85	6.40	19.20	1
3	15-07-85	4.50	13.50	-
	16-07-85	3.50	10.50	7.5
	18-07-85	4.50	13.50	8
	20-07-85	4.10	12.30	7
	22-07-85	3.75	11.25	5
	24-07-85	4.25	12.75	3
	26-07-85	2.50	7.50	5
	28-07-85	-	-	<1

The phytoplankton in the chambers and from the lake water samples were

well within the euphotic zone. Cloud cover provides an inverse estimate of the amount of sunlight reaching the site. Cloud cover was very variable throughout the experiments, although it should be noted that no very cloudy day was recorded during experiment 2 (Table 29).

The first experiment was conducted shortly after ice break-up which occurred between 22nd April and 6th May; the lake became ice free soon after the latter date. Temperatures were not significantly variable during the experiments (Table 30 and Figure 5).

Table 30: Temperature ranges (°C) during each experiment.

Experiment	Air	Surface water	Inner compartment water
1	11.0 - 15.8	9.0 - 14.5	11.0 - 14.0
2	14.0 - 28.0	15.0 - 20.0	14.0 - 18.5
3	17.5 - 26.0	19.5 - 20.5	19.5 - 21.0

Isolated peaks, particularly for air temperatures (Figure 5), reflect the dynamic nature of the local climate. Air temperature showed a marked increase on 3rd July which was followed by an increase in water temperatures. Water temperatures were less variable than air temperatures during experiments 2 and 3.

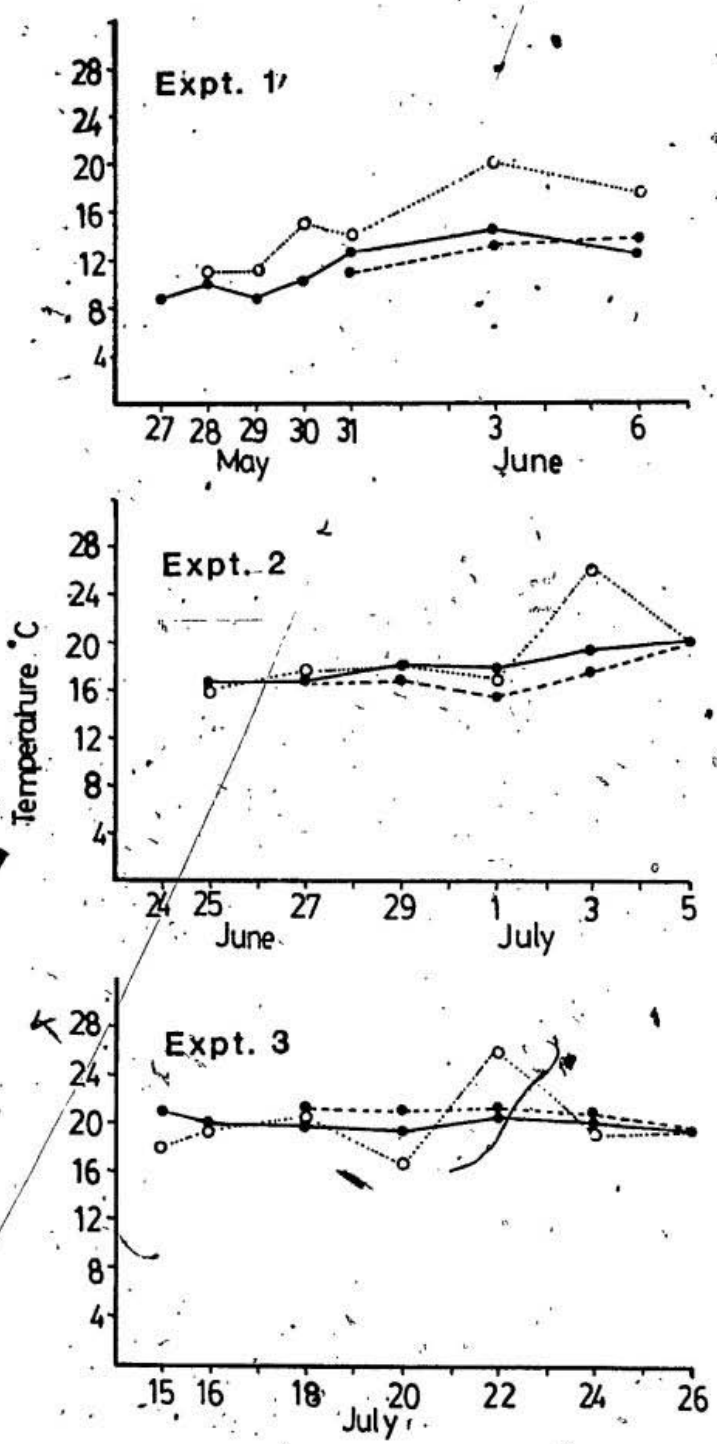


Figure 5:
Graphs of air (o---o), surface water (•—•) and inner compartment water (•---•) temperatures ± 0·25°C during the three experiments.

Appendix D: Comparisons of micrograzed and lake water phytoplankton densities

Table 31: Micrograzed inner compartment and lake water mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae species.

Taxa	Expt. 1.		Expt. 2		Expt. 3	
Zygnemaphyceae (desmids)						
Arthrodesmus spp.	=		**	+	*	−
Arthrodesmus convergens	=					
Arthrodesmus incus			=			
Arthrodesmus subulatus	=		**	+		
Arthrodesmus triangularis			**	+	=	
A. triangularis juveniles			*	+		
Mesotaenium sp.	=		=		**	+
Staurodesmus sp.						
Spondylosium planum					=	
Teilingia granulata	=		=		**	+
Chlorophyceae						
Ankistrodesmus spp.	=		=		=	
Chlamydomonas globosa			=			
Chlorella ellipsoidea	*	+	=		*	+
Chlorella vulgaris cells	=		=		**	+
C. vulgaris autospores	**	+	**	+	=	
Enteromorpha intestinalis	*	+	=		=	
Quadrigula lacustris	=				**	−
Selenastrum minutum	=				**	+
Cryptophyceae						
Microflagellates	=		=		*	−

=: no significant difference between MI and LW,
null hypothesis H_0: MI = LW accepted;
*: $p < 0.05$, **: $p < 0.01$;
+: MI > LW, −: MI < LW.

Table 32: Micrograzed inner compartment and lake water mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae species.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Bacillariophyceae (diatoms)						
Asterionella formosa cells			*	+	=	
A. formosa colonies					*	+
Synedra sp.					=	
Tabellaria fenestrata cells			**	+	**	+
T. fenestrata colonies			**	+	**	+
T. fenestrata empty frustules	=				**	+
T. fenestrata colonies with empty frustules	=				**	+
Chrysophyceae						
Dinobryon bavaricum cells						
D. bavaricum colonies						
D. bavaricum empty loricas	=					
Dinobryon sertularia cells					=	
D. sertularia empty loricas					=	
Syncrypta volvox						
"Ribbed" chrysophyte					=	
Uroglena volvox cells	=				=	
Cyanophyceae						
Chroococcus turgidus colonies	=		=		*	+
Coelosphaerium kuetzingianum			=			
Gloeocapsa punctata colonies			*	+	=	
Gloeothece linearis	=					
Microcystis aeruginosa cells	**	+	=			
M. aeruginosa colonies	**	+	**	+		

= : no significant difference between MI and LW,
null hypothesis H_0: MI = LW accepted; * : $p < 0.05$,
** : $p < 0.01$; + : MI > LW, - : MI < LW.

Table 33: Micrograzed outer compartment and lake water mean densities compared for the individual taxa of the Zygnemaphyceae (desmids), the Chlorophyceae and the Cryptophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3
Zygnemaphyceae (desmids)					
Arthrodesmus spp.	**	−	**	+	=
Arthrodesmus convergens	=				
Arthrodesmus incus			=		
Arthrodesmus subulatus	=		*	+	
Arthrodesmus triangularis	=		**	+	=
A. triangularis juveniles			**	+	
Mesotaenium sp.	=		**	+	=
Staurodesmus sp.					
Spondylosium planum			=		=
Teilingia granulata	=		**	+	=
Chlorophyceae					
Ankistrodesmus spp.	=		=		=
Chlamydomonas globosa			=		
Chlorella ellipsoidea	=		**	+	=
Chlorella vulgaris cells	=		**	+	=
C. vulgaris autospores	=		**	−	=
Enteromorpha intestinalis					
Quadrigula lacustris	=				=
Selenastrum minutum	=				=
Cryptophyceae					
Microflagellates	=		**	+	=

$=$: no significant difference between MO and LW,
null hypothesis H_0: MO = LW accepted;
* : $p < 0.05$, ** : $p < 0.01$;
+ : MO > LW, - : MO < LW.

Table 34: Micrograzed outer compartment and lake water mean densities compared for the individual taxa of the Bacillariophyceae (diatoms), the Chrysophyceae, and the Cyanophyceae.

Taxa	Expt. 1		Expt. 2		Expt. 3	
Bacillariophyceae (diatoms)						
Asterionella formosa cells			=		=	
A. formosa colonies					=	
Synedra sp.	=		**	+	=	
Tabellaria fenestrata cells			*	+	=	
T. fenestrata colonies			*	+		
T. fenestrata empty frustules	=				*	+
T. fenestrata colonies with empty frustules	=				**	+
Chrysophyceae						
Dinobryon bavaricum cells	=					
D. bavaricum colonies						
D. bavaricum empty loricas	=					
Dinobryon sertularia cells					=	
D. sertularia empty loricas					=	
Syncrypta volvox						
"Ribbed" chrysophyte			=			
Uroglena volvox cells	=		=		=	
Cyanophyceae						
Chroococcus turgidus colonies	=		=		=	
Coelosphaerium kuetzingianum			=			
Gloeocapsa punctata colonies			=		=	
Gloeothece linearis	=				**	-
Microcystis aeruginosa cells	**	+	*	+		-
M. aeruginosa colonies	**	+	**	+		

= : no significant difference between MO and LW,
null hypothesis H_0: MO = LW accepted;
* : $p < 0.05$, ** : $p < 0.01$;
+ : MO > LW, - : MO < LW.