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Abstract

The response of phytoplankton to nutrient loading and planktivorous fish additions was investigated in large experimental enclosures installed in lac Croche at the Station de Biologie des Laurentides de l'Université de Montréal (74° 00' N, 45° 59' W). Eight enclosures, 8 m in diameter and 12 m deep (total volume of 6.0×10^5 L), were installed in the deep part of the lake. Eight other enclosures, 8 m in diameter and 4 m deep (total volume of 2.0×10^5 L), were located on a shallow ledge. The two separate depths resulted in contrasting mixing regimes; presence of thermal stratification in the deep enclosures, absence of thermal stratification in the shallow enclosures. Each set of 8 enclosures was arranged in a 2 X 2 factorial design in which two levels (presence and absence) of planktivorous fish (redbelly dace) and two levels (presence and absence) of weekly nutrient loading (N:P 13:1) were used.

During the summer period (July and August), phytoplankton biomass significantly increased with fertilization ($p=.001$) and the presence of fish ($p=.008$) in the deep, thermally stratified, enclosures. The presence of fish increased algal biomass, particularly under the fertilized conditions. In the shallow, thermally mixed enclosures, total phytoplankton biomass was significantly affected by fertilization ($p=.004$) but not by the presence of fish ($p=.486$).

In both the shallow and deep enclosures, the size distribution of algal biomass was affected by fertilization and the presence of fish. In the deep enclosures the contribution of small cells (2-10µm) to total biomass increased to 80-90 % in the presence of fish. In the shallow fertilized enclosures, larger cells were dominant with 60-90 % of total biomass composed of cells >20µm.

The taxonomic composition at both the species and the division levels differed in all treatments. In the deep stratified enclosures, both the addition of nutrient ($p<.001$) and fish ($p=.003$) favored a large increase in Chlorophyta biomass which was composed of 1 or 2 species. Pyrrhophytes increased slightly with the presence of fish ($p=.014$). In the shallow enclosures, nutrient additions significantly affected the division composition of total algal biomass, whereas presence of fish did not.

Algal diversity, measured with Margalef's index of diversity, was reduced by fertilization in both the deep ($p<.001$) and the shallow enclosures ($p=.002$). The presence of fish further decreased diversity in the fertilized enclosures, but increased diversity in the non-fertilized ones.

The presence of planktivorous fish influenced phytoplankton community structure by modulating total algal biomass, the distribution of biomass according to size classes and the overall taxonomic composition. The impacts of fish were more numerous in the deep than in the shallow enclosures. Thermal stratification may thus be an important factor influencing the impact of planktivorous fish on phytoplankton.

Résumé

L'influence des poissons planctivores et d'un apport hebdomadaire d'éléments nutritifs sur la structure de la communauté phytoplanctonique ont été l'objet d'une investigation à l'aide d'enclos installés à la Station de Biologie des Laurentides de l'Université de Montréal (74° 00' N, 45° 59' W). Une série de huit enclos de 8 m de diamètre et de 12 m de profondeur (volume total de 6.0×10^5 L) ont été installés dans la partie profonde du lac Croche. Huit autres enclos de 8 m de diamètre et 4 m de profondeur (volume total de 2.0×10^5 L) ont été installés dans la partie peu profonde du lac. Chacune des deux séries de huit enclos a été installée en fonction d'un plan d'analyse factorielle (2 X 2) avec deux niveaux (présence et absence) de poissons planctivores (méné à ventre rouge) et deux niveaux (présence et absence) de fertilisation (N:P 13:1).

Pendant la période estivale (juillet et août), la fertilisation ($p=.001$) et la présence de poissons planctivores ($p=.008$) ont favorisé un accroissement de la biomasse phytoplanctonique totale dans les enclos profonds. Dans les enclos peu profonds, la biomasse ne s'est accrue qu'avec la fertilisation ($p=.004$). La présence de poissons n'a pas significativement affecté la biomasse totale ($p=.486$).

Dans les enclos profonds et peu profonds, la distribution en spectre de taille des algues composant la biomasse totale a été

affectée par la fertilisation et la présence des poissons. La contribution des petites algues (2-10 µm de diamètre) à la biomasse phytoplanctonique totale s'est accrue dans les enclos profonds et peu profonds lorsqu'il y avait présence de poissons. Dans les enclos peu profonds, les algues plus grandes que 20 µm ont dominé les traitements fertilisés.

La composition taxonomique du phytoplancton s'est avérée différente pour chacun des traitements, et ce, tant au niveau des espèces qu'au niveau des divisions. Dans les enclos profonds, la biomasse des chlorophycées s'est significativement accrue avec la fertilisation (p<.001) et la présence de poissons (p<.003). Cet accroissement de la biomasse des chlorophycées est principalement dû à un ou deux taxons. En présence de poissons, la biomasse des Pyrrhophytes s'est accrue (p=.014). Dans les enclos peu profonds, seul l'ajout d'éléments nutritifs a significativement influencé la distribution de la biomasse totale selon les divisions taxonomiques.

La diversité phytoplanctonique, évaluée à l'aide de l'index de diversité de Margalef, a diminué avec la fertilisation dans les enclos profonds (p<.001) et peu profonds (p=.002). Dans les enclos fertilisés, la présence de poissons a, elle aussi, fait décroître la diversité phytoplanctonique tandis que dans les enclos non fertilisés, les poissons ont favorisé une augmentation de la diversité.

Les changements observés au niveau de la structure de la communauté phytoplanctonique (changements au niveau de la biomasse

phytoplanctonique totale, de la distribution en spectre de taille, de la composition taxonomique et de la diversité des algues) ont été, en partie, modulés par la présence de poissons planctivores. L'influence relative des poissons a été plus proéminente dans les enclos profonds. La stratification thermale est donc, potentiellement, un facteur primordial déterminant l'impact relatif des poissons et de la fertilisation sur la communauté phytoplanctonique.

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Chapter One

What Controls the Structure and Taxonomic Composition of Biological Communities?

1.1 An Old Problem

The structure of biological communities varies dramatically from one geographic area to another. Descriptions of this phenomenon can be retraced as far back as ancient Greece. Aristotle classified nature along a great chain or ladder of life: the *Scala Naturae*. According to the *Scala Naturae*, the components of nature were ranked in a perfect chain of life along a hierarchical scheme of development. Each component of nature strived to become a perfect form of life. Variability in nature was the consequence of the presence of unperfected and uncompleted forms transforming themselves towards perfection. It was not until the seventeenth century, that our current ideas focusing on the variability among biological communities were developed. The works of Lamarck (1809), Wallace (1878) and Darwin (1859) were key in the development of contemporary studies on the structure of biological communities.

Darwin's theory of natural selection stimulated the most interest because of the large amount of supporting data he gathered over a wide geographic range. His theory contrasted with Creationist ideas and explained, at least on an evolutionary scale, the temporal and spatial variations in species composition, abundance and diversity (Darwin 1859). Empirical evidence derived from both natural and agricultural situations supported the theory of natural selection. For example, the high species diversity he described among the Galapagos finches is often used as a striking illustration of natural selection. Paradoxically, the lack of predictability and the difficulty in testing concepts such as " survival of the fittest " limit the usefulness of Darwin's theory. Nevertheless, the theory of natural selection became the most influential scientific work of the early 1900's. It laid the foundations for one of the fundamental goals of ecology: the prediction of community structure.

The study of community structure has become an important field in contemporary biology. Various approaches have been developed to identify and describe the factors influencing community structure in both terrestrial and aquatic environments. Theoretical approaches have led to the elaboration of mechanisms by which general processes, such as competition and predation, can influence community structure. Specific predictions of these mechanisms have been tested either empirically, through the identification of general patterns or experimentally through, manipulations of specific parameters.

1.2 Various Approaches to the Study of Community Structure

1.2.1 Competition as the Factor Structuring Communities

Darwin emphasized the importance of the struggle for survival. Daily, weekly and seasonal variations in species abundance, composition and diversity were associated with the outcome of competition between species sharing a given limited resource. Lotka

(1925) and Volterra (1926) mathematically described the relationship between species sharing a resource. Their models suggested that only the most competitive of two species sharing a resource would survive. Gause's (1934) *Paramecium* and Crombie's (1947) *Tribolium* experiments were set up to test the outcome of competition. These experiments and many others (e.g., Park 1954; Harper 1961) did not support the Lotka and Volterra prediction of the survival of only the fittest organism. Only under simple and controlled experimental conditions did one species eliminate the others.

The limitations of Lotka and Volterra equations in natural systems has been imputed to phenomena such as emigration and the difficulty in finding prey as they get scarce. Lotka and Volterra models have, nonetheless, interesting implications (Pianka 1981). For example, Gause's principle of competitive exclusion states that no two species may occupy and rely exclusively on the same resource. However, demonstration of the competitive exclusion principle, and determining the impact of competition in natural systems is difficult. No two species seem to rely entirely on the same given resource. When two species use the same resource, subtle temporal or physical differences ensure that competition is reduced. The term niche, although defined differently by many authors, has become associated with this partitioning of resources (Pianka 1981). On the basis of his observations of the feeding habits of warblers, MacArthur (1958) provided experimental support and promoted the idea of species niches within communities. Niches may therefore be conceived as the end result of a partitioning of resources in order to reduce competition among species. The differences between the structure of biological communities can thus be considered as the outcome of competition for a limiting or key resource.

1.2.2 Predation as the Factor Structuring Communities

Predation is also considered to be a factor influencing the structure and taxonomic composition of terrestrial and aquatic communities (e.g., Hairston et al. 1960; Oksanen et al. 1981). Paine (1966) provided experimental support for this view when he observed changes in an inter-tidal community after removal of the main predator. The removal of the starfish *Pisaster* initiated a decrease in the biological diversity of the New England inter-tidal shore. Paine stated that inter-specific competition changed due to the removal of the predator. The absence of the top predator favored the domination of the bivalve *Mytilus*, otherwise controlled by *Pisaster.* Paine hypothesized that predation modifies the intensity of competition, in this case for space, and favors an increase in species diversity. Species abundance, composition and diversity may thus be viewed as the outcome of the interaction between predation and competition. For Paine, predation is the main process influencing the structure of biological communities. Predation controls competitors to levels where different competing species can coexist.

1.2.3 Competition vs. Predation: Is There a Consensus?

Experimental evidence indicates that both competition and predation can affect the structure and taxonomic composition of biological communities. Crashes of the moose population due to overgrazing on Isle Royale (Lake Superior) represent one example of the influence of competition on populations. The subsequent introduction of wolves on Isle Royale led to a stabilization of the moose population (Levine & Miller 1991). Therefore, predation can be considered as a process which maintains the abundance of competitors to levels where competitors can coexist (Paine 1966). Due to the difficulty of quantifying and discerning the specific influence of competition and predation, very few studies have tested the impact of both processes. The influences of competition and predation on community structure are thus best examined together through the elaboration of factorial design experiments.

1.2.4 Patterns in the Structure and Taxonomic Composition of Communities

Various patterns and gradients in the structure of terrestrial and aquatic biological communities have been identified using empirical and correlative approaches. Patterns in the composition, abundance and diversity of species have been associated with many environmental parameters: latitude (Brown & Gibson 1983), altitude, island size and location (MacArthur & Wilson 1963), nutrient status (Tilman 1982), physical stability of the environment (Sanders 1968), and evapotranspiration (Currie & Paquin 1987). Abundance, composition and diversity patterns have also been correlated with biological parameters. For example, community structure has been related to total biomass (Tilman 1982) and species connectance (Briand 1983).

Although the empirical studies have not lead to a unifying principle, they nonetheless indicate that the factors explaining variations in community structure are highly dependent on the scale of investigation (Stiling 1992). For example, 76 % of the variations in the number of tree species observed at a given latitude and longitude can be explained by realized annual evapotranspiration (Currie & Paquin 1987). On a regional scale, however, evapotranspiration does not account for tree richness variability. Therefore, explanation of diversity or of any other parameter describing biological community structure at a global scale does not necessarily explain regional scale variability. The study of aquatic systems provides another example of the importance of the scale of investigation. Lake productivity is best predicted by variables related to energy availability on a global scale (Brylinsky & Mann 1973), whereas on a local scale, (in a narrow range of latitude), nutrient availability is the best productivity predictor (Schindler 1978).

An ideal experimental environment for the study of the factors affecting community structure should thus have clear cut boundaries and a manageable size because of the scale effect. Organisms of short generation time are another desirable environmental feature due to time constraints on experimental studies. With respect to these characteristics, aquatic environments are ideal test systems. The present study was designed to determine the relative impact of changes in resource availability (nitrogen and phosphorus), and of predation, through changes in food web components (presence of planktivorous fish), on phytoplankton community structure.

1.3 The Study of the Structure and Taxonomic Composition of Aquatic Communities.

Geographically and ecologically, lakes are study systems that present clear cut boundaries. They have the advantage of being entities with well-described seasonal patterns in temperature and chemical characteristics. Lakes of similar latitude and morphometry usually present similar physical conditions (Wetzel 1983) thus, they allow for the development of general models. From a biological point of view, the plankton of lakes is particularly well suited for the study of the variations in abundance and diversity of communities. The cosmopolitan nature, short generation time, and relatively small size of plankton species all contribute to the suitability of aquatic environments as study systems.

1.3.1 Theoretical Approaches to the Study of Aquatic Communities

Hutchinson (1961) was one of the first to formally address the problem of plankton community structure. The " paradox of the plankton " refers to the apparent contradiction between the competitive exclusion theory and the high diversity of phytoplankton species. The competitive exclusion theory states that in restricted habitats species compete for the same resource. As a result, only a few species should simultaneously inhabit a restricted area such as the water column. However, in small volumes of water tens to hundreds of phytoplankton species can be observed.

This " paradox of the plankton " has been explained in terms of the instability or non-equilibrium of the habitat. If the habitat is not in equilibrium or steady state, one of the basic conditions of competitive exclusion is not reached. As a consequence of the changing conditions, no one species will be able to out-compete the others. An alternative explanation for the paradox is that many species can coexist because each species has different limiting constraints. Thus, species are never in direct competition (Tilman 1982). When limiting constraints cease, fewer species will co-exist because of fewer species specific constraints. When many limiting constraints exist, more species will be able to co-exist due to increased specific limitations. For example, nutrients are frequently considered as limiting in lakes. Several studies suggest that lakes with high nutrient availability have fewer coexisting species and exhibit low species diversity (Reynolds 1984).

1.3.2 Qualitative Approaches to the Study of Aquatic Communities or " What Controls the Composition of Phytoplankton Assemblages ? "

Reynolds (1984) developed a qualitative predictive matrix which provides an indication of the dominant algal species based on lake water column stability and nutrient availability. Although no quantitative predictions can be drawn from the hypothetical matrix, the matrix does point out the deterministic influence of both water column stability and nutrient availability on the phytoplankton community structure.

By examining a large number of lakes Harris (1986) tried to correlate Cyanobacteria summer blooms with the ecological variables identified in Reynolds hypothetical matrix. Water column stability (M) was measured as the ratio of the estimated thermocline depth to the mean depth of the lake. Thus M values lower than 1 represented stable conditions and M values higher than 1 represented strong vertical mixing. Nutrient availability was evaluated as the total nitrogen : total phosphorus (TN : TP) ratio. The species composition of algal blooms in 435 US EPA study lakes was plotted against the stratification parameter M and the TN : TP ratio. In these plots the influence of both the physical (M) and the chemical (TN : TP) factors on the occurrence of particular species became apparent. For example, *Anabaena* blooms were restricted to a narrow range of low N : P ratios but were not influenced by M values. On the other hand, N : P ratios had little influence on the occurrence of *Microcystis* which was restricted to lakes with small values of M (Harris 1986).

Other laboratory and experimental studies have found that there is no clear indication that N : P ratios are an important factor determining dominance by specific taxa (Pick & Lean 1987). Accurate prediction of overall composition of algal assemblages is not possible even though TP levels will predict quite well the relative contribution to total biomass of Cyanobacteria (Smith 1985; Harris 1986) or of Chrysophyta (Sandgren 1988). Factors other than N : P ratios may be important in regulating the community structure of phytoplankton assemblages.

1.3.3 Quantitative Approaches to the Study Aquatic Communities or " What controls the abundance of Phytoplankton? "

Nutrient regimes have long been suspected to be the key factor controlling phytoplankton abundance, composition and diversity in lakes. Unfortunately, most of the historical accounts concerning phytoplankton are descriptive taxonomic studies. Pearsall (1932), and Rawson (1955) were among the first to investigate phytoplankton abundance with respect to lake nutrient status.

Sakamoto (1966) developed predictive relationships for summer chlorophyll-*a* concentrations from either spring total phosphorus or total nitrogen. In temperate lakes, the level of chlorophyll-*a* represents an indirect measure of phytoplankton biomass. The spring total phosphorus-summer chlorophyll-*a* relationship gained wide acceptance when Dillon and Rigler (1974) obtained a similar relationship for North American lakes.

On the basis of the developed regression equations, regulations on nutrient loading to lakes have been implemented. Many lakes have responded positively to the reduction of nutrient loading, others have not. Aquatic ecologists have since been attempting to refine the phosphorus-chlorophyll relationship. For example, Prairie et al. (1989) suggested that the phosphorus-chlorophyll relationship was better described by a sigmoid model rather than the previous linear models. However, the precision of the model using phosphorus as the sole predictor of plankton biomass remains fairly weak. Predictions can vary as much as 1 to 3 orders of magnitude from the measured mean (Mazumder et al. 1992). Total phosphorus is thus an important determinant of algal biomass, but it is certainly not the only one.

Hrbacek et al. (1961) reported that the plankton community of two ponds differed mainly because of contrasting fish stocking. Alterations in the physical and chemical characteristics of water as well as changes in the phytoplankton community structure were attributed to the presence of planktivorous fish.

Since Hrbacek's work, several hypotheses have been proposed to explain the potential influence of fish and planktivory on phytoplankton (e.g., Brooks & Dodson 1965). The cascading trophic interaction hypothesis states that, at a constant nutrient loading, predatory influences are transmitted (cascade down) to the lower trophic levels and produce observable changes in the biomass and in the overall phytoplankton community structure (Carpenter et al.

1985). " Biomanipulation " (Shapiro et al. 1975) the manipulation of food web components in order to control phytoplankton growth in lakes, has become a potential lake management tool (e.g., Moss 1990; Shapiro 1990). The biomanipulation hypothesis states that an increase in piscivore fish abundance reduces planktivore fish abundance which, in turn, enhances the relative abundance of large zooplankton (herbivores). As a consequence, total phytoplankton biomass drops due to increased herbivory.

A variety of laboratory, enclosure and small pond experiments have been undertaken to quantify these effects. Some have manipulated nutrient loading (summarized in Reynolds 1984), others fish densities (e.g., Lazzaro et al. 1992) and finally others have manipulated both factors (Mazumder et al. 1988). Unfortunately, confounding results have been obtained (summarized in DeMelo et al. 1992 and Carpenter & Kitchell 1992).

In order to predict the specific influence of both resource availability (Bottom-up factors) and predators (Top-Down factors) on the major components of freshwater systems McQueen et al. (1986), proposed the Bottom-up:Top-down (BU : TD) theory. According to the BU:TD theory, the maximum potential biomass of each trophic level is determined by nutrient availability (BU influences). Therefore, phytoplankton biomass is most strongly linked to nutrient availability. Measured phytoplankton biomass will differ from potential biomass (dictated by BU factors) due to the influence of TD factors (McQueen et al. 1986).

Top-Down influences are hypothesized to be strong at the top of the food web and to weaken, by a factor of two, with each lower trophic level (McQueen et al. 1986). Specific quantification of BU and TD influences cannot be clearly established since BU and TD effects change with the trophic status of lakes. In lakes with high nutrient concentrations (eutrophic lakes) the model predicts little or no influence of fish on the phytoplankton. In oligotrophic systems an important planktivorous fish population could result in a significant zooplankton - phytoplankton interaction due to reduced nutrient buffering or weak BU influences (low nutrient availability).

The effects of mean depth and associated mixing patterns on the TD influences have not been evaluated. However several studies have suggested that hydrodynamics characteristics may be an abiotic factor with a profound influence on aquatic food chains (e.g., Cushing 1989).

The present study evaluates the influences of food web structure and major abiotic factors on phytoplankton community structure. The response of phytoplankton to nutrient enrichment and planktivorous fish predation is investigated in two sets of large enclosures installed in an oligotrophic system at two separate mean depths, which result in contrasting mixing regimes. Phytoplankton community structure is assessed by measuring total biomass, average size distribution, taxonomic composition and diversity.

Chapter Two

Methods

2.1 Study Site

Lac Croche (74° 00' N, 45° 59' W) is a small dystrophic soft-water lake located at the Station de Biologie des Laurentides, Université de Montréal (70 km north of the city of Montréal). The total volume of water, 4.1×10^5 m^3, is distributed among two major basins with a total of 1.09 km of shoreline. The shoreline is covered by leather leaf, shrubs and *Betula* sp. Water enters the lake predominately through spring runoff streams, while a single outlet in the south-eastern section of the east basin drains the lake. Lac Croche has a spring total phosphorus (TP) level of 5 $\mu g \cdot L^{-1}$. The lake maximum depth is of 11.5 m. The epilimnion is typically 3 m deep with a summer temperature range of 20 to 25° C. Hypolimnetic temperatures range from 5° to 6° C. Other morphometric and physical characteristics of lac Croche can be found in Lafond et al. (1990).

2.2 Experimental Design

2.21 The Enclosures

In order to test for the effects of nutrient loading, presence of planktivorous fish and thermal stratification, 2 sets of 8 nylon reinforced polyethylene experimental enclosures were installed in lac Croche. Eight enclosures, each 8 m in diameter and 4 m deep (total volume of 2.0×10^5 L), were installed in the littoral zone of the lake (Fig. 1). Eight other enclosures, 8 m in diameter and 12 m deep (total volume of 6.0 X 10^5 L), were located in the deepest part of the western basin of lac Croche. Each enclosure was equipped with an 8 inch polyurethane floating collar attached to a 2" X 4" cedar wood support frame. A weighted chain, embedded in the bottom of each enclosure wall, ensured both the settlement of the enclosure wall in the sediments, and the complete separation of the water column inside the enclosure from the surrounding lake water. The enclosures were open to the lake sediments. In such large enclosures, the edge effets are minimal and there is no defined edge zone with respect to phytoplankton density or biomass (Stephenson et al 1984)

2.22 The Design

Both the deep and the shallow enclosures, were arranged in a 2X2 factorial design where the presence of planktivorous fish and the addition of nutrients were the selected independent factors. Four experimental conditions resulted from the selection of two levels (presence and absence) of each two manipulated factors (nutrients and fish). The four experimental conditions were thus: the addition of nutrients (N), the addition of nutrients and the addition of fish (NF), no treatment or control (C) and the addition of fish (F). Each experimental condition was replicated twice in the shallow and twice in the deep zone of lac Croche. Duplicate treatments were placed side by side for pratical reasons even though this arrangement is not statistically optimal. Previous experiments with similar enclosures showed that the intra treatment variability was not significantly affected by the spatial arrangement of the enclosures (Lean pers. comm.).

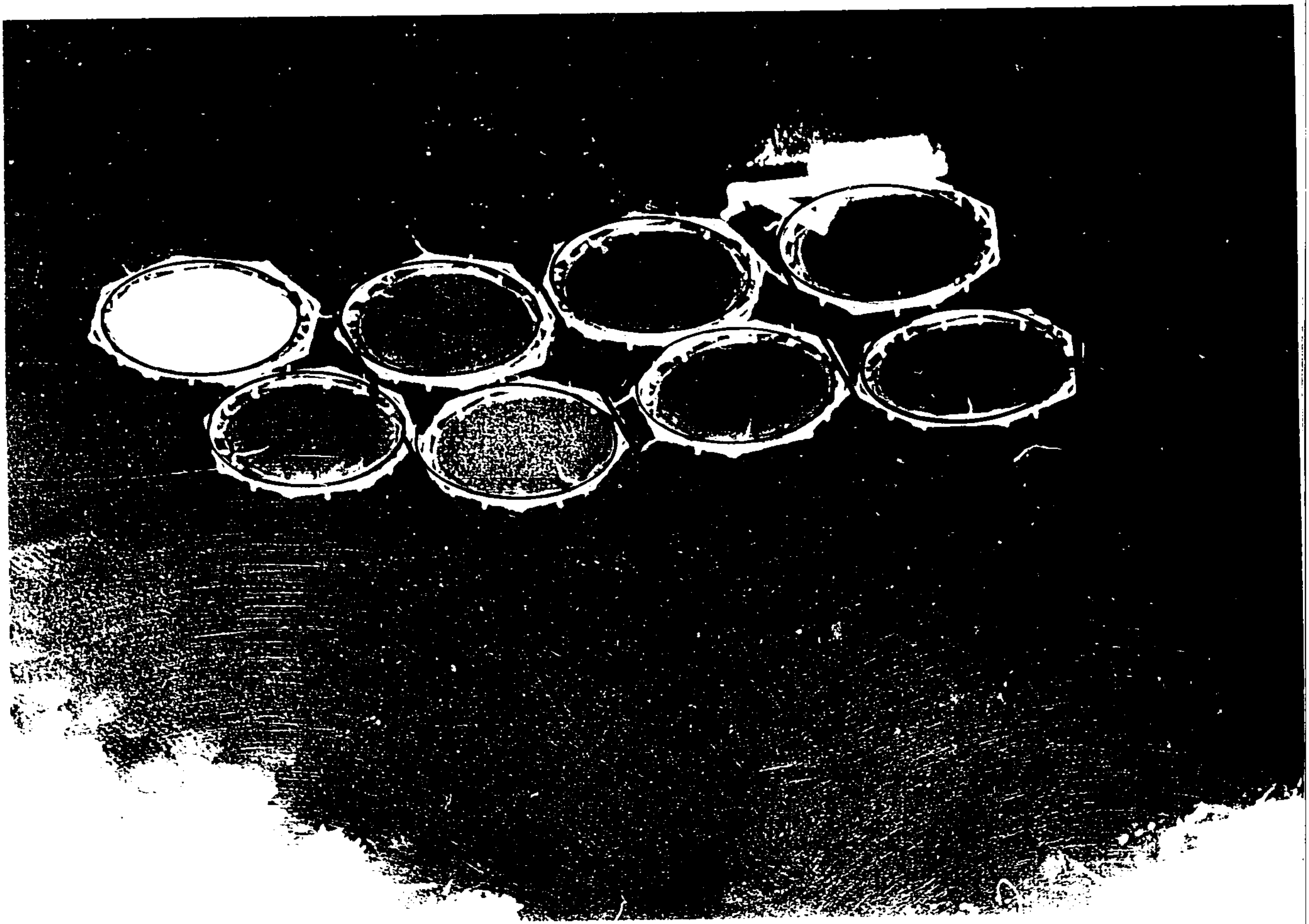
The treatments requiring nutrient addition (N and NF treatments) received weekly loading of $NaNO_3$ and $H_3PO_4^{3-}$ at a 13:1 N:P ratio (47.97 mg N m^{-2} d^{-1} and 3.69 mg P m^{-2} d^{-1}). The fertilization rate corresponds to the loading of a typical temperate eutrophic system (Mazumder et al. 1988). Nutrient additions were identical in the shallow and the deep enclosures because the volume of the epilimnion; the layer in which phytoplankton assimilate nutrients for growth, is the same in both cases. Enclosures were first fertilized on June 19 1991.

At the start, fish were removed from the enclosures using nets and traps. The enclosures with fish (F and NF treatments) were stocked with redbelly dace (*Chrosomus eos* Cope), an autochtonous species of lac Croche. The selected fish stocking was 5 $g \cdot m^2$ or about 160-170 minnows of 6-8 cm of length (~2.6 g / fish). Fish fences (0.6 m high) were built around each enclosure to prevent fish from jumping in or out of the enclosures. Fish traps were installed in the fishless enclosures to ensure that the fishless treatments were free of fish. Enclosures of similar dimensions have been reported to sustain normal growth of planktivorous fish populations for a summer (Post & McQueen 1987).

Figure 1. Aerial photograph of the eight shallow enclosures arranged in a 2 X 2 factorial design in lac Croche. The deep enclosures were arranged in the same fashion.

C= Control or no treatment enclosures, F= enclosures with Fish,

N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.



2.3 Sampling Procedure

Integrated epilimnetic water samples (0-3m) were collected every other week from July to October 1991. The samples were collected from the center of each enclosure between 8:00 and 10:30 AM. A total volume of 16 liters of water was collected by rapidly lowering a 5 meter Plexiglas tube of 6.5 cm of diameter to a depth of 3 m. Once the tube reached the depth of 3 m, both tube extremities, the one at 3 m depth and the one at surface, were tightly closed and sealed by rubber balls. The samples were stored in 20 liter opaque polyethylene containers.

Of the collected 16 liter sample, a minimum of 250 ml of water was preserved in Lugol's iodine solution. The Lugol's preserved samples were used for phytoplankton enumeration. The rest of the collected water was fractionated for water chemistry, primary production and bacterial analysis, as part of a larger study on factors regulating aquatic ecosystems.

2.4 Taxonomic Enumeration

2.41 Enumeration Method

Taxonomic identification and enumeration of the Lugol's preserved samples were made using a Wild Leitz M-40 inverted microscope following the Utermöhl technique (Utermöhl 1958).

Aliquots were sedimented overnight (8 hrs minimum) in 26 mm diameter sedimentation chambers. For each sample, a minimum of 350-400 phytoplankton cells, colonies and fragments were counted along randomly selected transects to ensure a ±10% counting precision (Lund et al. 1958). The length of each transect equaled the chamber's diameter. Cell counts and dimensions were recorded on a computerized counter (Hamilton 1990) to facilitate the calculations of the parameters describing phytoplankton community structure. Cells less than 5 µm were identified and enumerated at 600X magnification while the cells of 5-15 µm in diameter and those greater than 15 µm were counted at 300 and 150 X respectively. Picoplankton are difficult to enumerate using this technique and were enumerated by fluorescence microscopy in a separate study (Pick unpublished).

2.42 Dependent Variables

The estimations of total algal biomass, size and division distribution, as well as diversity were derived from the enumerations. Algal biomass was derived from estimations of the volume of each individual algal cell. One of eight preselected geometric shapes (sphere, cone, double cone, ellipsoid parallelepiped, half parallelepiped and rod) was assigned to each species (Hamilton 1990). The dimensions were measured on 3-10 individuals per species. The summation of the individual cell volumes, the total biovolume, was converted to fresh weight assuming a specific gravity of 1 (Utermöhl 1958).

Taxa were assigned to specific size classes based on the mean of their longest dimension. Accordingly, total biomass was partitioned into three size classes. The ultra plankton (2-10 µm), the nanoplankton (10-20 µm) and the micro and net plankton (>20 µm).

Total biomass was further separated into seven main taxonomic divisions (Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanobacteria, Euglenophyta and Pyrrhophyta).

Algal diversity was calculated using Margalef's (1958) index of diversity.

$$d_S = (s-1)/\log N$$

where: s is the number of species
N is the number of individuals.

This index is commonly used in phytoplankton ecology (Reynolds 1984).

2.43 Taxonomic References

For most of the algal divisions, taxonomic identification followed the nomenclature and taxonomy suggested by Prescott (1973). However, since Prescott's work is not complete, additional authors were consulted, in particular Huber-Pestallozzi (1941), Komarek & Fott (1983), Starmach (1985), Contant and Duthie (1978), and Bourrelly (1985; 1968; 1966). The phytoplankton photograph collection of the Canadian Museum of Nature was also used as reference material.

2.5 Statistical Analyses

Statistical analyses were performed with version 5.1 of the SYSTAT statistical package (Wilkinson 1989). The influences of nutrients, fish, and their interaction were evaluated with a repeated measure analysis of variance (ANOVAR). ANOVAR was selected over a series of univariate ANOVAS because the measurements of the response variables are interdependent through time. Repeated measure analysis of variance allows the use of dependent variables which are not independent in time.

In order to conduct the ANOVAR, a SYSTAT Multivariate General Model was built with two grouping elements and a time trial factor. Each grouping factor (fish and nutrients) had two levels (presence and absence). The time trial factor was composed of five sampling dates for the deep enclosures, and of four sampling dates for the shallow enclosures. The selected sampling dates for the statistical analysis correspond to the summer sampling periods (July and August). The time interval between each sampling date is constant throughout the summer period. A separate ANOVAR was conducted on each dependent variable. Deep and shallow enclosures were considered as two independent experiments and were analyzed separately. The 2X2 factorial design was chosen over a 3X2 factorial to reduce the number interactions terms and increase the number of degrees of freedom.

Repeated measures analysis of variance conducts both univariate and multivariate analyses. Univariate results are separated in two sections: the between-subject and the within-subject effects. The main effects, effects of nutrients, fish and their interaction, are reported in the between-subject section of the ANOVAR table for each of the analyzed parameters. These effects are evaluated by comparing the treatment responses averaged over all sampling intervals (McQueen et al. 1992). The error term is based on the number of experimental enclosures.

The other univariate procedure, the within-subject analysis evaluates temporal effects. The tested null hypothesis is thus whether the response of the dependent variable to the manipulated factors is the same over time. In other words the within-subject analysis checks whether the slope of the best-fitting straight line through the measurements over time is the same for the two treatments with a manipulated factor (Gurevitch & Chester 1986). The within-subject results are reported in the within-subject section of the ANOVAR tables. Error terms associated with the within-subject analyses are derived from the number of repeated measures.

Three tests (Wilk's Lambda, the Pillai's Trace and the Hotelling-Lawley Trace) were computed to evaluate the multivariate statistic. Although there is little difference in the three, the Pillai's Trace is considered to be the most robust of the three (Chatfield and Collins 1980) and was thus selected throughout the study. The multivariate statistics are, as in the univariate within-subject, testing for time (trial) effects. When univariate and multivariate analyses differ in their conclusions, the univariate procedures are the most powerful for small sample sizes when there is no departure from the underlying assumptions (LaTour & Miniard 1983).

Before conducting the statistical analyses, biomass and diversity data were log-transformed whereas the partitioning of biomass according to size class and taxonomic division were arcsine transformed. The distribution of biomass according to size class and taxonomic division were arc-sin transformed because they were proportions. The transformations were performed in order to reduce deviations from homogeneity of variance and normality assumptions. A third and critical assumption of the univariate section of the ANOVAR, assumes that the covariance across all pairs of cells are equivalent. This restrictive requirement, called compound symmetry in Wilkinson (1989), covariance symmetry in Potvin et al. (1990), or sphericity of covariance matrix in Winer (1971), is specific to the univariate ANOVAR analyses. Departures from the assumption of compound symmetry are critical and have deleterious effects on the ANOVAR. Compound symmetry can be evaluated by the Huynh-Feldt epsilon and the Mauchly's criterion (SAS 1988). Correction measures (e.g., Greenhouse and Geisser correction) have been developed for deviant data (SAS 1988) since the assumption of compound symmetry rarely holds for real data (Wilkinson 1989). A few mathematical exceptions to the compound symmetry assumption do, however, occur (Wilkinson 1989). For example, when all within-subjects factors have only two levels, as in this study, symmetry of treatment variance is irrelevant because there is only a single difference in treatment variance for each significance test (LaTour & Miniard 1983). Therefore the assumption of compound symmetry was not applicable to this study. Since data met the univariate underlying assumptions, univariate ANOVAR analyses can be interpreted directly without regard to the multivariate analyses.

Chapter Three

Results

3.1 Total Algal Biomass

3.11 Total Biomass in the Deep Enclosures

The ANOVAR between-subject analysis showed that the mean phytoplankton biomass was significantly affected by both fertilization (p=0.001) and the presence of fish (p=0.008) in the deep enclosures during the summer period of July and August (Table 1). Biomass increased with fertilization and with the presence of fish (Fig. 2). After the first sampling date and throughout the entire summer period, algal biomass was highest in the fertilized treatment with fish (NF treatment) and lowest in the control enclosures. Analysis of variance applied on each sampling date separately reveals that algal biomass was significantly affected by the presence of fish on all sampling dates with the exception of the first and the last (Fig. 2). These non-significant time periods correspond to the beginning of the experiment and to fall turnover (October).

The ANOVAR within-subject analysis and the multivariate analysis gave different results in their analyses of the pattern or trend response for total biomass. Since in small sample size experiments, the univariate procedure is more powerful, the null hypothesis of no interaction of trial is rejected. The temporal comparisons showed that the trend for total biomass differed between the fertilized and non-fertilized enclosures (p=0.002), and between the fish and fishless enclosures (p=0.007). Contrast analysis indicated that the difference in both cases was between the quadratic comparison (p=0.024 for the C vs. N and p= 0.041 for the N vs. NF comparisons).

Figure 2. Total epilimnetic phytoplankton biomass in the deep enclosures during the summer and fall. Error bars represent the standard deviation of the mean of the duplicate enclosures.
C= Control or no treatment enclosures, F= enclosures with Fish,
N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

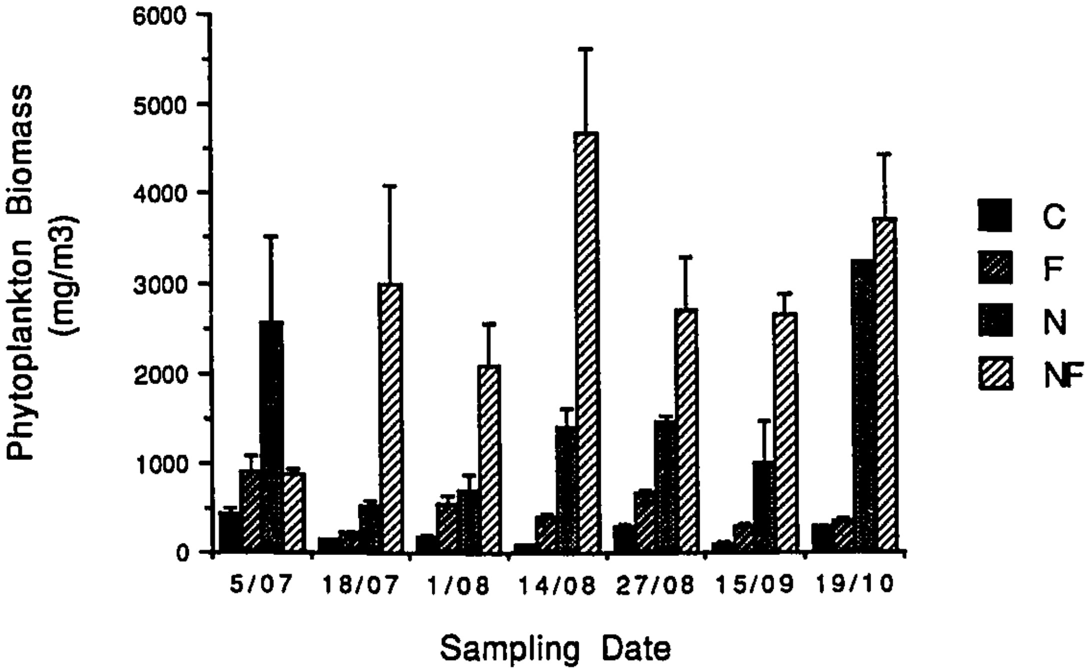

Phytoplankton Biomass
(mg/m3)
6000
5000
4000
3000
2000
1000
0
5/07
18/07
1/08
14/08
27/08
15/09
19/10
Sampling Date
C
F
N
NF

Table 1. Nutrient and fish effects on total algal biomass in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	27.233	1	27.233	102.407	0.001
Fish	6.638	1	6.638	24.961	0.008
Nutrients X Fish	0.289	1	0.289	1.087	0.356
Subj w/groups	1.064	4	0.266		
Within Subjects					
Trials	2.937	4	0.734	5.809	0.004
Nutrients X Trials	3.614	4	0.904	7.150	0.002
Fish X Trials	2.622	4	0.655	5.187	0.007
Nutrient X Fish X Trial	1.828	4	0.457	3.617	0.028
Trial X Subj w/groups	2.022	16	0.126		

Multivariate Results:

Source	Multiv. F	df	P
Trials	7.488	4,1	0.267
Nutrients X Trials	7.064	4,1	0.274
Fish X Trials	2.505	4,1	0.438
Nutrient X Fish X Trials	0.993	4,1	0.028

3.12 Total Biomass in the Shallow Enclosures

In the shallow enclosures, the ANOVAR between-subject analysis revealed that fertilization significantly affected (p=0.004) the mean phytoplankton biomass during the summer period while the presence of planktivorous fish did not (p=0.486)(Table 2). Total algal biomass increased with fertilization (Fig. 3).

Both the univariate within subject and the multivariate test for an interaction of time revealed no temporal effect (Table 2). Therefore there were no differences in the pattern of response of total biomass over time for the fertilized and the non fertilized enclosures (univariate p=0.624) and for the fish and no fish enclosures (univariate p=0.930).

Figure 3. Total epilimnetic phytoplankton biomass in the shallow enclosures during the summer. Error bars represent the standard deviation of the mean of the duplicate enclosures.

C= Control or no treatment enclosures, F= enclosures with Fish, N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

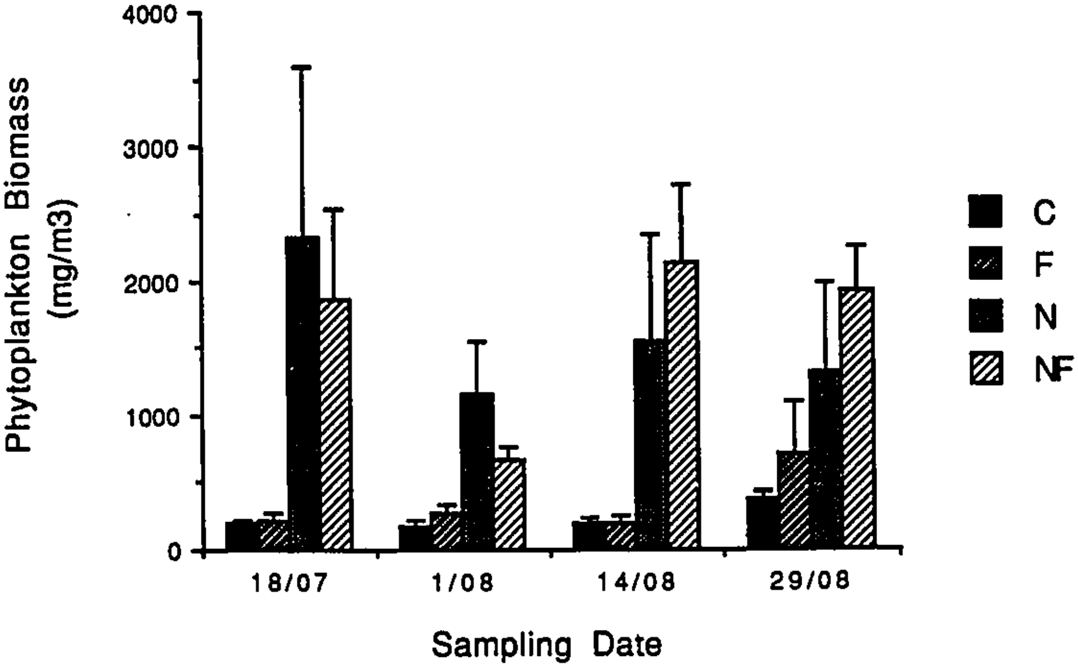

4000
3000
2000
1000
0
Phytoplankton Biomass
(mg/m3)
18/07
1/08
14/08
29/08
Sampling Date
C
F
N
NF

Table 2. Nutrient and fish effects on total algal biomass in the shallow enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	21.397	1	21.397	35.108	0.004
Fish	0.358	1	0.358	0.587	0.486
Nutrients X Fish	0.006	1	0.006	0.010	0.925
Subj w/groups	2.438	4	0.609		
Within Subjects					
Trials	1.227	3	0.409	0.582	0.638
Nutrients X Trials	1.277	3	0.426	0.606	0.624
Fish X Trials	0.310	3	0.103	0.147	0.930
Nutrient X Fish X Trial	0.696	3	0.232	0.330	0.804
Trial X Subj w/groups	8.433	12	0.703		

Multivariate Results:

Source	Multiv. F	df	P
Trials	0.598	3,2	0.675
Nutrients X Trials	4.246	3,2	0.196
Fish X Trials	0.341	3,2	0.803
Nutrient X Fish X Trials	1.539	3,2	0.417

3.2 Size Distribution of Biomass

3.21 Size Distribution of Biomass in the Deep Enclosures

In the fertilized enclosures, the relative proportion of small cells (2-10 µm) increased up to 60 to 90 percent of total algal biomass with the presence of fish (NF treatment). In contrast, in the fertilized treatments free of fish (N treatments), the 10-20 µm cells were the dominant fraction (Fig. 4). In figure 4, the size distribution of phytoplankton for the deep enclosures is given for the summer period. Replicate enclosures are shown in adjacent panels in order to stress the similarity of the phytoplankton size distribution for each given treatment.

Statistically, the between-subject ANOVAR revealed that both nutrients and fish affected cell size distribution. The relative proportion of the 2-10 µm cells increased (Fig. 4) with the presence of fish (p=0.005). The relative contribution of the 10-20 µm group to total algal biomass, was affected by fertilization (p=0.013) and by presence of fish (p=0.009). Finally, the percentage of cells greater than 20 µm was not affected by fertilization (p=0.052), nor by fish (p=0.596)(Table 5).

The ANOVAR within-subject analysis found three significant differences in the time trend patterns for the phytoplankton size distribution. These were for the 2-10 µm cells between both high and low fertilized enclosure (N & C treatment), ($p<0.001$) and between high and low fish enclosures (NF & N treatment), ($p<0.001$)(Table 3). The third significant difference in time trend was found between the fish and fishless enclosures for the 10-20 µm cells distribution ($p=0.012$)(Table 4).

Figure 4. Size distribution of phytoplankton biomass in the deep enclosures during the summer. Replicate enclosures for each treatment are shown side by side.
C= Control or no treatment enclosures, F= enclosures with Fish,
N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

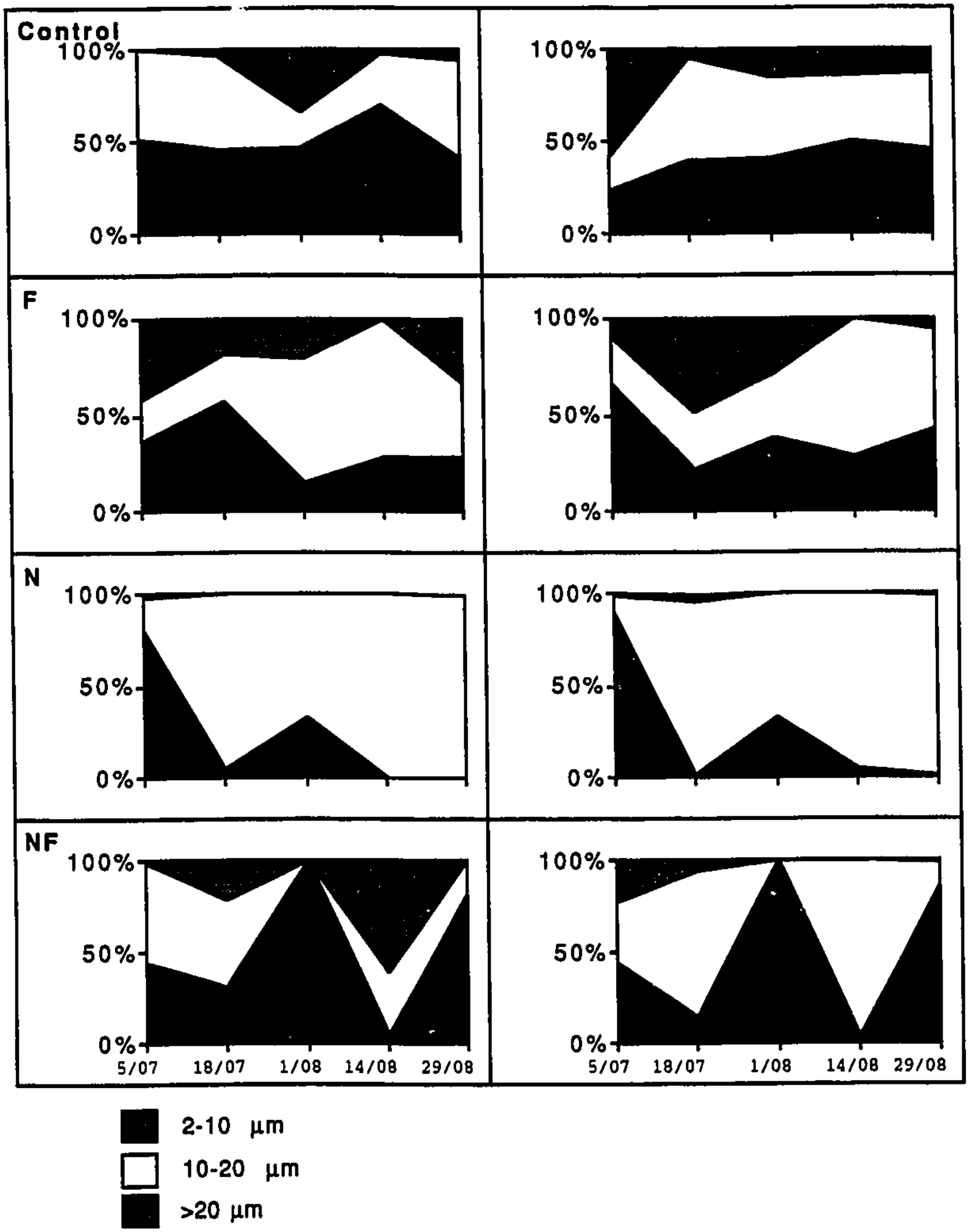

Control
F
N
NF
100%
50%
0%
5/07
18/07
1/08
14/08
29/08
2-10 µm
10-20 µm
>20 µm

Table 3. Nutrient and fish effects on the proportion of 2-10 µm algal cells in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.036	1	0.036	2.447	0.193
Fish	0.474	1	0.474	32.546	0.005
Nutrients X Fish	0.137	1	0.137	9.434	0.037
Subj w/groups	0.058	4	0.015		
Within Subjects					
Trials	0.951	4	0.238	13.200	0.000
Nutrients X Trials	1.216	4	0.304	16.889	0.000
Fish X Trials	1.388	4	0.347	19.272	0.000
Nutrient X Fish X Trial	1.022	4	0.255	14.191	0.000
Trial X Subj w/groups	0.288	16	0.018		

Multivariate Results:

Source	Multiv. F	df	P
Trials	10.708	4,1	0.225
Nutrients X Trials	20.410	4,1	0.164
Fish X Trials	25.670	4,1	0.147
Nutrient X Fish X Trials	14.649	4,1	0.193

Table 4. Nutrient and fish effects on the proportion of 10-20 µm algal cells in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.561	1	0.561	17.839	0.013
Fish	0.701	1	0.701	22.309	0.009
Nutrients X Fish	0.477	1	0.477	15.159	0.018
Subj w/groups	0.126	4	0.031		
Within Subjects					
Trials	1.247	4	0.312	6.483	0.003
Nutrients X Trials	0.517	4	0.129	2.687	0.069
Fish X Trials	0.873	4	0.218	4.543	0.012
Nutrient X Fish X Trial	0.978	4	0.245	5.089	0.008
Trial X Subj w/groups	0.769	16	0.048		

Multivariate Results:

Source	Multiv. F	df	P
Trials	18.195	4,1	0.174
Nutrients X Trials	02.602	4,1	0.431
Fish X Trials	127.912	4,1	0.066
Nutrient X Fish X Trials	27.137	4,1	0.143

Table 5. Nutrient and fish effects on the proportion of large algal cells (>20 μm) in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.141	1	0.141	7.505	0.052
Fish	0.006	1	0.006	0.330	0.596
Nutrients X Fish	0.069	1	0.069	3.665	0.128
Subj w/groups	0.075	4	0.019		
Within Subjects					
Trials	0.046	4	0.011	0.345	0.844
Nutrients X Trials	0.165	4	0.041	1.250	0.330
Fish X Trials	0.109	4	0.027	0.829	0.526
Nutrient X Fish X Trial	0.057	4	0.014	0.429	0.786
Trial X Subj w/groups	0.528	16	0.033		

Multivariate Results:

Source	Multiv. F	df	P
Trials	9.088	4,1	0.243
Nutrients X Trials	4.772	4,1	0.329
Fish X Trials	28.151	4,1	0.140
Nutrient X Fish X Trials	15.192	4,1	0.190

3.22 Size Distribution of Biomass in the Shallow Enclosures.

As in the deep enclosures, the phytoplankton size distribution was affected by the addition of nutrients and the presence of fish (Fig. 5). In the fertilized enclosures, the relative proportion of small cells (2-10 µm) increased to over 90 percent of total algal biomass with the presence of fish (NF treatment). In contrast, in the fertilized treatments free of fish (N treatments), the 2-10 µm cells never attained more than 50-60 percent of total biomass. The lack of similarity between the N replicates can probably be related to an experimental source of error related to enclosure number 1 (the left panel of the N section of Figure 5) Further discussion on this source of error and its implications can be found in section 4.1). In the non-fertilized treatments, the proportion of cells larger than 20 µm was higher in the control treatments than in the fish treatments.

Statistically, the between-subject ANOVAR analysis showed that the relative contribution of the 2-10 µm cells to the total algal biomass was affected by the presence of fish (p=0.016) but not by fertilization (p=0.303, Table 6). The proportion of 10-20 µm cells was affected by the presence of fish (p=0.002), but not by fertilization (p=0.268). The mean percentage of cells greater than 20 µm was not significantly different with the presence of fish (p=0.647) or with fertilization (p=0.931).

The ANOVAR within-subject found no significant differences in the time trend patterns for either of the three phytoplankton size classes (Table 6, 7, 8). The sole exception was a significant effect of time between the high and low nutrient enclosures (N & C treatments) for the 2-10 µm cells ($p=0.049$, Table 6).

Figure 5. Size distribution of the shallow enclosures during the summer. Replicate enclosures for each treatment are shown side by side.

C= Control or no treatment enclosures, F= enclosures with Fish,

N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

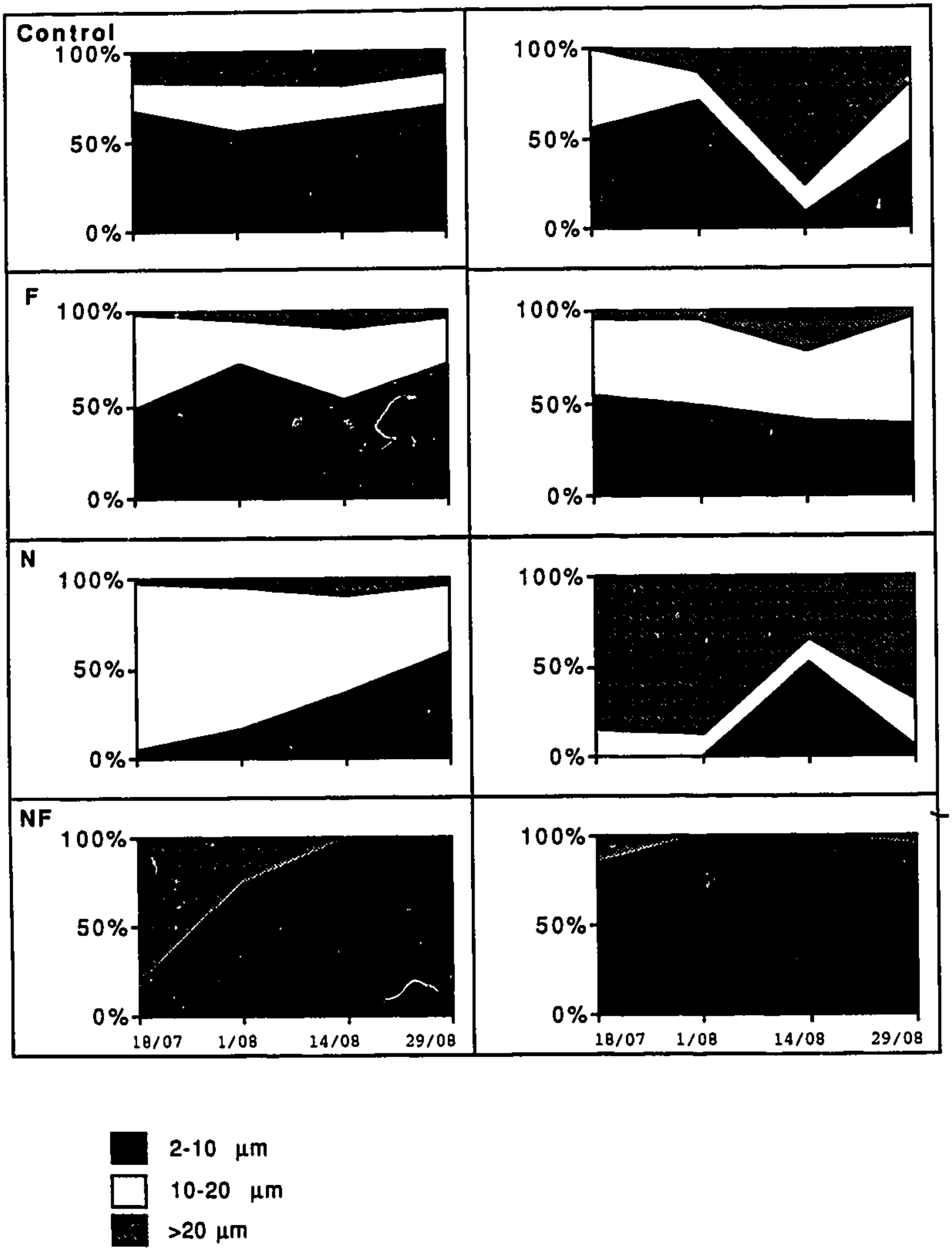

Control
F
N
NF
100%
50%
0%
18/07
1/08
14/08
29/08
2-10 µm
10-20 µm
>20 µm

Table 6. Nutrient and fish effects on the proportion of 2-10 μm algal cells in the shallow enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.141	1	0.141	1.397	0.303
Fish	1.620	1	1.620	16.066	0.016
Nutrients X Fish	1.798	1	1.798	17.823	0.013
Subj w/groups	0.403	4	0.101		
Within Subjects					
Trials	0.368	3	0.123	1.959	0.174
Nutrients X Trials	0.662	3	0.221	3.522	0.049
Fish X Trials	0.223	3	0.074	1.188	0.356
Nutrient X Fish X Trial	0.077	3	0.026	0.408	0.750
Trial X Subj w/groups	0.751	12	0.063		

Multivariate Results:

Source	Multiv. F	df	P
Trials	6.608	3,2	0.134
Nutrients X Trials	25.355	3,2	0.038
Fish X Trials	25.423	3,2	0.038
Nutrient X Fish X Trials	8.007	3,2	0.113

Table 7. Nutrient and fish effects on the proportion of 10-20 µm algal cells in the shallow enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.019	1	0.019	1.654	0.268
Fish	0.674	1	0.674	59.585	0.002
Nutrients X Fish	1.706	1	1.706	150.848	0.000
Subj w/groups	0.045	4	0.011		
Within Subjects					
Trials	0.142	3	0.047	1.555	0.251
Nutrients X Trials	0.041	3	0.014	0.446	0.725
Fish X Trials	0.081	3	0.027	0.888	0.475
Nutrient X Fish X Trial	0.076	3	0.025	0.830	0.503
Trial X Subj w/groups	0.366	12	0.031		

Multivariate Results:

Source	Multiv. F	df	P
Trials	1.539	3,2	0.417
Nutrients X Trials	0.277	3,2	0.841
Fish X Trials	0.738	3,2	0.619
Nutrient X Fish X Trials	0.618	3,2	0.666

Table 8. Nutrient and fish effects on the proportion of large algal cells (>20 µm) in the shallow enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.000	1	0.000	0.009	0.931
Fish	0.012	1	0.012	0.244	0.647
Nutrients X Fish	0.116	1	0.116	2.417	1.195
Subj w/groups	0.192	4	0.048		
Within Subjects					
Trials	0.077	3	0.026	0.538	0.665
Nutrients X Trials	0.342	3	0.114	2.395	0.119
Fish X Trials	0.231	3	0.077	1.621	0.236
Nutrient X Fish X Trial	0.120	3	0.040	0.840	0.498
Trial X Subj w/groups	0.571	12	0.048		

Multivariate Results:

Source	Multiv. F	df	P
Trials	0.872	3,2	0.573
Nutrients X Trials	0.637	3,2	0.659
Fish X Trials	0.797	3,2	0.598
Nutrient X Fish X Trials	0.553	3,2	0.695

3.3 Taxonomic Composition

3.31 General Species Composition

The taxonomic composition differed among each of the 4 treatments. The photographs in figures 6 and 7 represent the same amount of material at the same magnification. The general species composition of these samples are given in Appendix I for the deep treatments and in Appendix X for the shallow treatments. Appendices II to IX are the detailed phytoplankton enumeration data corresponding to the duplicate N, NF, C and F deep enclosures in late summer. Appendices XI, to XVIII are the detailed enumeration data for the shallow late summer N, NF, C and F treatments.

In the deep, fertilized, fishless enclosures (N treatment) the cryptophyte, *Rhodomonas minuta* Skuja dominated the phytoplankton assemblage at the beginning of the summer. By mid summer, and for the rest of the stratified period, both replicates of the treatment were basically a monoculture of the green alga *Schroederia judayi* G. M. Smith (Fig. 6 section N).

Early in the summer, *Cryptomonas* spp. contributed substantially to total algal biomass of the fertilized fish enclosures (NF treatments). Later in summer, two species of the genus *Scenedesmus*, *S. quadricauda* (Turp.) de Brébisson and *S. circumfusus*

Hortob. became predominant. By the end of August, *S. circumfusus* comprised for over 90% of algal biomass (Fig. 6 section NF).

S. circumfusus is not reported in the algal species list of the province of Québec (Poulin et al. submitted). Its identification is based on cell size range, and on the presence of small (1 to 2 µm) erect ornamental spines which deflect away from the cell apex. The species was first described from fish ponds (Komarek & Fott 1983). This first official mention of the species for the province of Québec could be due to either, previous assignation with closely related *Scenedesmus brasiliense*, or to the fact that the species was not previously encountered. A first mention is possible since *S. circumfusus* was specific to the enclosures which had been fertilized and had planktivorous fish.

In the non-fertilized enclosures, no one species was dominant in terms of biomass (Fig. 6, section C & F)(Appendix 1). With the presence of fish (F treatment), armored dinoflagellates (e.g., *Peridinium* spp.) became prevalent, but were not dominant (Fig. 6 section F). They accounted for 10 to 20 percent of total biomass. The control enclosures also developed a diverse algal assemblage with no single dominant taxon (Fig. 6 section C). *Merismopedia tenuissima* Lemmermann *Katablepharis ovalis* Skuja and *Rhodomonas minuta* Skuja were among the frequently encountered taxa.

The taxonomic composition of the planktonic community was more variable in the shallow enclosures. The shallow enclosures did not develop monocultures to the same extent as the deep enclosures (Fig. 7). In addition, the phytoplankton composition of the shallow enclosures varied more through time. In the fertilized fishless enclosures (N treatment), the cyanobacterium *Microcystis aeruginosa* Kütz. dominated the algal assemblage at the beginning of the summer. Later in the season, *Microcystis* was partially replaced by *Schroederia judayi* G. M. Smith. *S. judayi* composed 15-35 % of the total biomass by the end of the summer (Fig. 7 section N).

The algal assemblage of the shallow, fertilized, fish enclosures, (NF treatment), was characterized by two major taxa. *Scenedesmus* cf. *circumfusus* which tended to be larger than in the deep enclosures and *Pseudanabaena* sp, sensu Anagnostidis & Komarek (1988). Typical late summer algal assemblage in the fertilized fish enclosures is represented in figure 7d, section NF.

The shallow non-fertilized enclosures (C and F treatment) had diverse phytoplankton assemblages. No one taxonomic entity dominated the algal assemblage in these enclosures (Fig. 7 section C & F).

Figure 6. Typical late summer algal assemblages in the deep enclosures. Each panel represents a separate treatment. The same amount of material settled (50 ml) and the same magnification (800X) were utilized for each panel.

C= Control or no treatment enclosures, F= enclosures with Fish,
N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

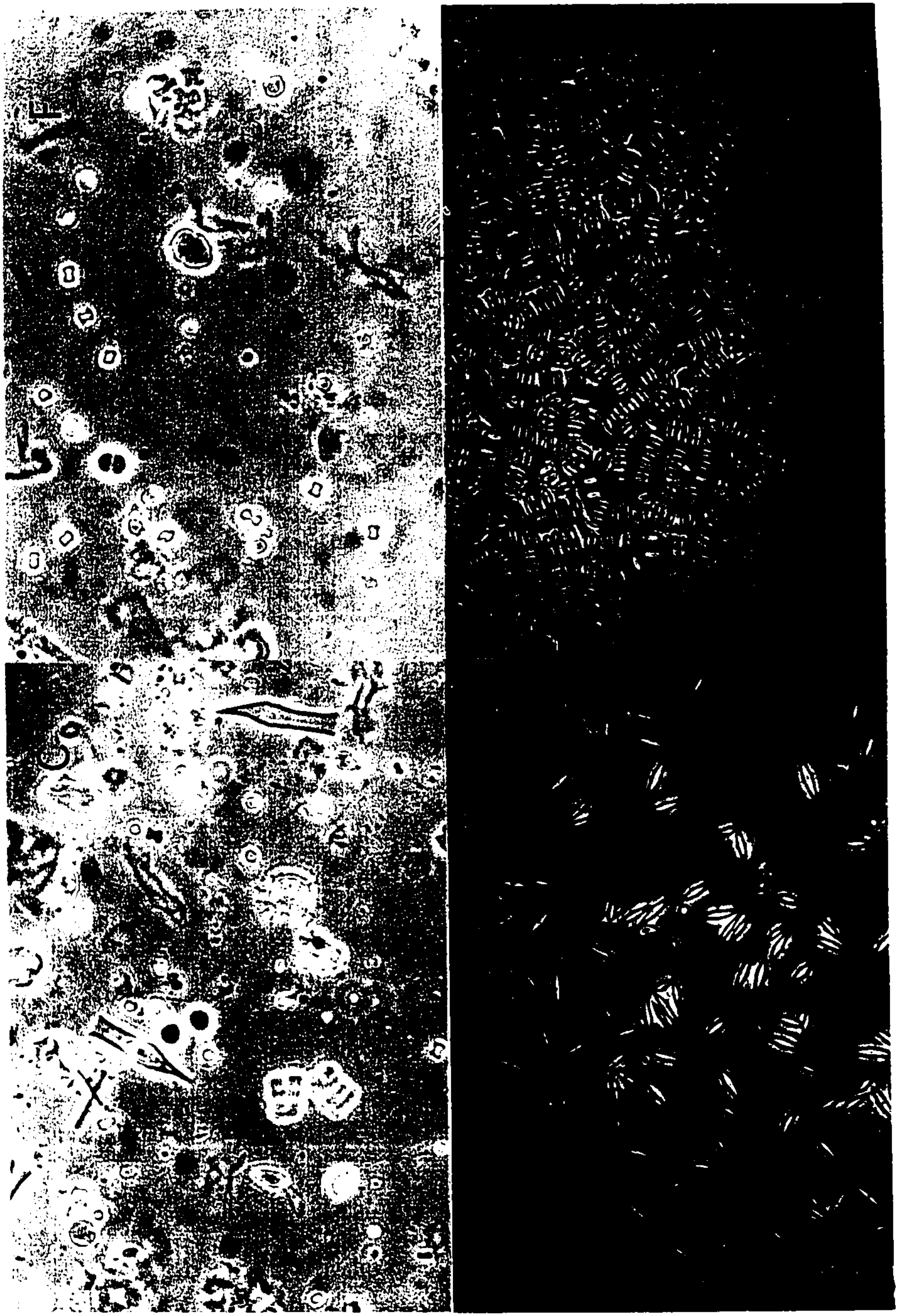
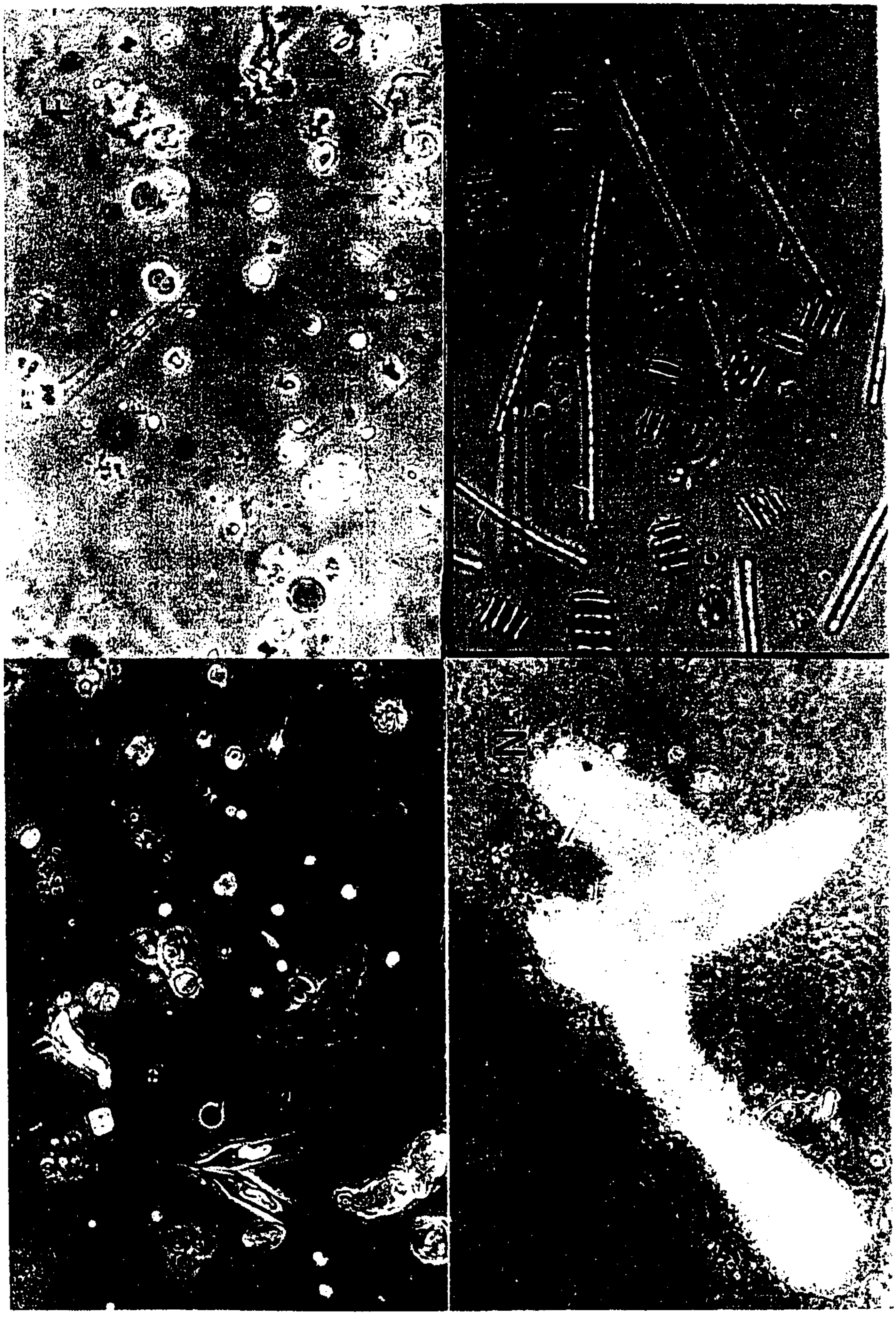


Figure 7. Typical late summer algal assemblages in the shallow enclosures. Each panel represents a separate treatment. The same amount of material settled (50 ml) was utilized for each panel. The same magnification (800X) was utilized for the C, F and NF treatments. The N treatment was photographed at (400X).

C= Control or no treatment enclosures, F= enclosures with Fish,
N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.



3.32 Algal Composition at the Division Level in the Deep Enclosures

The algal biomass of the control enclosures was primarily composed of a variety of Chromophyta (mainly Chrysophyta and Cryptophyta) (Fig. 8). In these enclosures, the relative proportion of Chlorophyta (the green algae) was low, about 1 to 10 percent of total biomass. Addition of fish (F treatment) favored an increase in the proportion of Chlorophyta to 30-40 % of total biomass. Pyrrhophyta gradually replaced the chromophytes.

In the N and in the NF enclosures, the addition of nutrients, and the addition of nutrients and fish increased the proportion of Chlorophyta at the expense of the Chromophyta. For example, at the beginning of the summer, the N enclosures were dominated by a Cryptophyta, the alga *Rhodomonas minuta* By mid summer chlorophytes, mainly *Schroederia*, replaced the Cryptophyta. In the fertilized and fish enclosures (NF treatment), Cryptophyta cells (mainly *Cryptomonas* spp.) were also gradually replaced by Chlorophyta cells (mainly *Scenedesmus* spp.).

The ANOVAR between-subject analysis showed that fertilization ($p<0.001$) and the presence of fish ($p=0.003$) increased the relative proportion of Chlorophyta (Fig. 8, Table 9). Dinoflagellates decreased with nutrients ($p=0.002$) and increased with the presence of fish ($p=0.014$) (Table 10). Cyanobacteria and

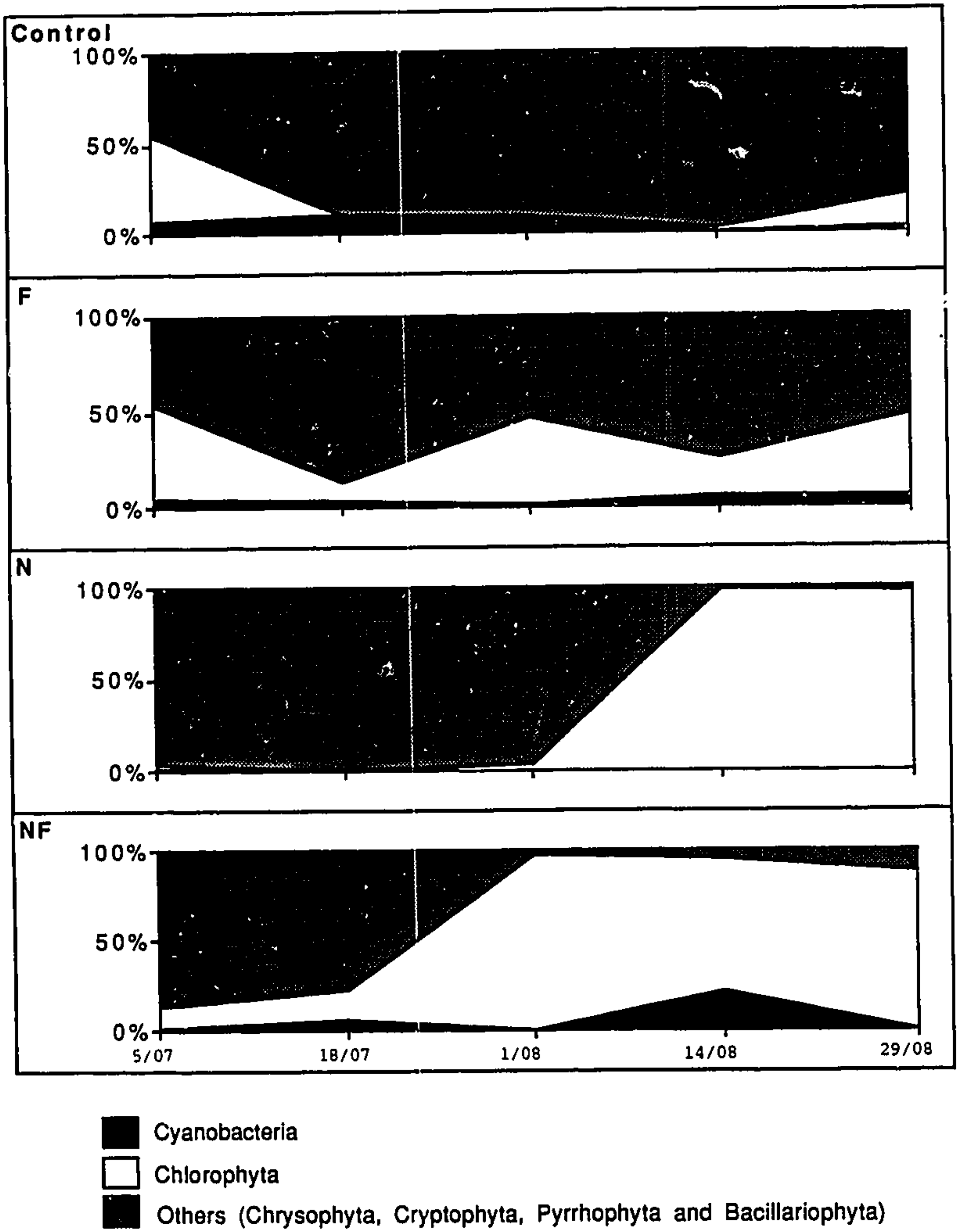
Bacillariophyta (diatoms) were not affected by either fish or nutrients. The Chromophyta were affected by both factors. Table 14 summarizes the between-subject effects for all the algal divisions.

The ANOVAR within-subject analyses for temporal comparisons showed that the trend for the proportion of Chlorophyta biomass differed between the fish and fishless enclosures ($p=0.001$) and between the fertilized and non fertilized enclosures ($p<0.001$). Contrast analysis revealed that the difference in the former case was due to the N and NF linear comparison ($p=0.034$), and in the latter case, to the C and N linear comparison ($p<0.001$).

Figure 8. Distribution of major algal divisions in the deep enclosures during the summer. Each panel represents the mean for each treatment.

C= Control or no treatment enclosures, F= enclosures with Fish,

N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.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5/07
18/07
1/08
14/08
29/08
Cyanobacteria
Chlorophyta
Others (Chrysophyta, Cryptophyta, Pyrrhophyta and Bacillariophyta)

Table 9. Nutrient and fish effects on the relative proportion of Chlorophyta biomass in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	1.878	1	1.878	198.09	0.000
Fish	0.382	1	0.382	40.337	0.003
Nutrients X Fish	0.004	1	0.004	0.376	0.573
Subj w/groups	0.038	4	0.009		
Within Subjects					
Trials	2.452	4	0.613	12.748	0.000
Nutrients X Trials	3.166	4	0.792	16.460	0.000
Fish X Trials	1.559	4	0.390	8.103	0.001
Nutrient X Fish X Trial	0.959	4	0.240	4.986	0.008
Trial X Subj w/groups	0.769	16	0.048		

Multivariate Results:

Source	Multiv. F	df	P
Trials	112.412	4,1	0.071
Nutrients X Trials	42.629	4,1	0.114
Fish X Trials	44.177	4,1	0.112
Nutrient X Fish X Trials	15.328	4,1	0.189

Table 10. Nutrient and fish effects on the proportion of Dinoflagellates in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	0.114	1	0.114	58.711	0.002
Fish	0.033	1	0.033	17.204	0.014
Nutrients X Fish	0.030	1	0.030	15.238	0.017
Subj w/groups	0.008	4	0.002		
Within Subjects					
Trials	0.021	4	0.005	1.434	0.268
Nutrients X Trials	0.017	4	0.004	1.143	0.372
Fish X Trials	0.007	4	0.002	0.486	0.746
Nutrient X Fish X Trial	0.007	4	0.002	0.454	0.768
Trial X Subj w/groups	0.058	16	0.004		

Multivariate Results:

Source	Multiv. F	df	P
Trials	22556.0	4,1	0.005
Nutrients X Trials	15928.9	4,1	0.006
Fish X Trials	9661.7	4,1	0.008
Nutrient X Fish X Trials	6364.8	4,1	0.009

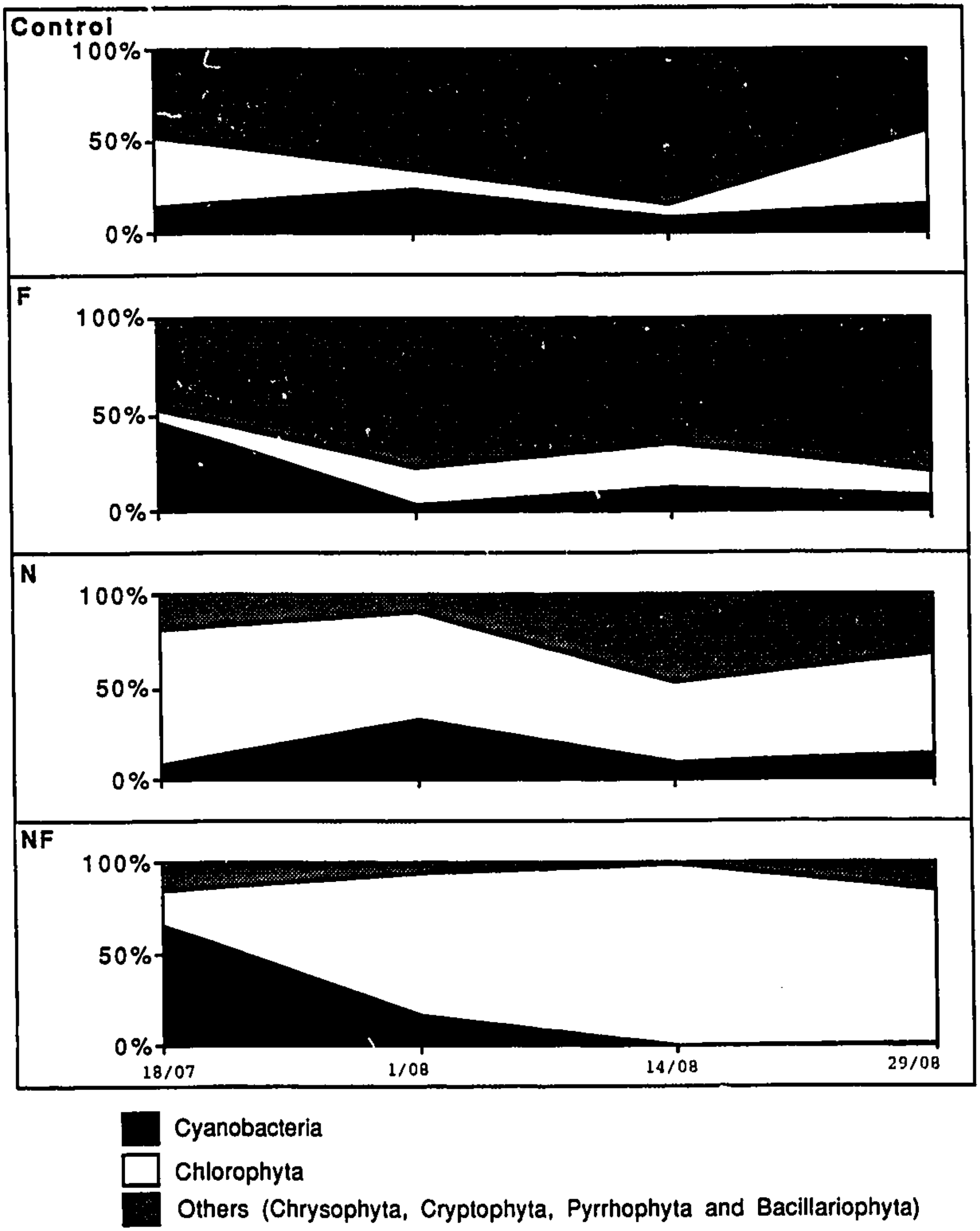
3.33 Algal Composition at the Division Level in the Shallow Enclosures

In the shallow enclosures nutrient loading affected the algal composition at the division level to a higher extent than did the presence of fish (Fig. 9). In the control enclosures, the Chrysophyta was the most important algal division. The contribution of the pyrrhophytes and the diatoms was negligible. With the addition of fish (F treatment), the relative proportion of pyrrhophytes increased up to 10 % of total biomass at the expense of the Chrysophyta. With fertilization, the relative contribution of the Chlorophyta increased from 10-20 % in the control enclosures to 50-80 %.in the N enclosures. The relative proportion of Chlorophyta increased a further 5 to 15 % with the addition of fish in the fertilized enclosures. The relative contribution of Pyrrhophyta to total biomass was negligible in the fertilized enclosures.

Statistically, the ANOVAR between-subject analysis for the shallow enclosures, revealed that fertilization significantly affected the relative proportion of chlorophytes (p=0.009). The presence of fish did not affect the contribution of chlorophytes to total algal biomass (p=0.264). As summarized in Table 14, the presence of fish did not affect the contribution to total biomass of any of the algal divisions.

Figure 9. Distribution of major algal divisions in the shallow enclosures during the summer. Each panel represents the mean for each treatment.

C= Control or no treatment enclosures, F= enclosures with Fish, N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.


Control
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NF
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50%
0%
18/07
1/08
14/08
29/08
Cyanobacteria
Chlorophyta
Others (Chrysophyta, Cryptophyta, Pyrrhophyta and Bacillariophyta)

Table 11. Nutrient and fish effects on the proportion of Chlorophyta biomass in the shallow enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	2.146	1	2.146	22.828	0.009
Fish	0.158	1	0.158	1.682	0.264
Nutrients X Fish	0.349	1	0.349	3.717	0.126
Subj w/groups	0.376	4	0.094		
Within Subjects					
Trials	0.065	3	0.022	1.589	0.244
Nutrients X Trials	0.101	3	0.034	2.447	0.114
Fish X Trials	1.389	3	0.463	33.749	0.000
Nutrient X Fish X Trial	0.488	3	0.163	11.861	0.001
Trial X Subj w/groups	0.165	12	0.014		

Multivariate Results:

Source	Multiv. F	df	P
Trials	1.303	3,2	0.462
Nutrients X Trials	1.139	3,2	0.499
Fish X Trials	26.724	3,2	0.036
Nutrient X Fish X Trials	9.778	3,2	0.094

3.4 Species Diversity

3.41 Species Diversity in the Deep Enclosures

Using Margalef's index as a measure of diversity, the between-subject ANOVAR analysis showed that fertilization ($p<0.001$) and the presence of fish ($p<0.001$) affected algal diversity (Table 12). By mid summer, algal diversity tended to be higher in the non-fertilized treatments (Fig. 10). Diversity increased with the presence of fish in the non-fertilized treatments and decreased with fish in the fertilized treatments.

Figure 10. Algal diversity in the deep enclosures during the summer. Diversity was evaluated with Margalef's index of diversity: d_S = (s-1)/log N where s is the number of species and N is the number of individuals. Errors bar represent the standard deviation of the mean. If error bar is not apparent, standard deviation is smaller than symbol.

C= Control or no treatment enclosures, F= enclosures with Fish,

N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

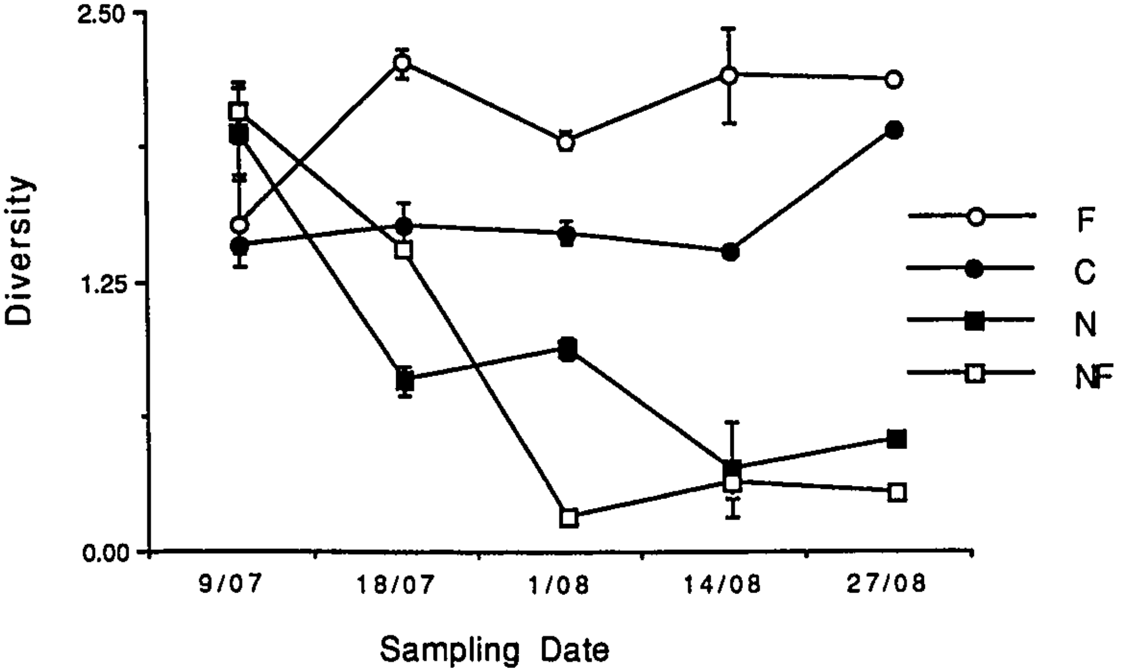

2.50
1.25
0.00
Diversity
9/07
18/07
1/08
14/08
27/08
Sampling Date
F
C
N
NF

Table 12. Nutrient and fish effects on the algal diversity in the deep enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	10.966	1	10.966	3824.06	0.000
Fish	0.313	1	0.313	109.298	0.000
Nutrients X Fish	1.990	1	1.990	694.069	0.000
Subj w/groups	0.011	4	0.003		
Within Subjects					
Trials	4.158	4	1.040	26.787	0.000
Nutrients X Trials	6.285	4	1.571	40.489	0.000
Fish X Trials	2.198	4	0.549	14.157	0.000
Nutrient X Fish X Trial	2.195	4	0.549	14.142	0.000
Trial X Subj w/groups	0.621	16	0.039		

Multivariate Results:

Source	Multiv. F	df	P
Trials	110.573	4,1	0.071
Nutrients X Trials	274.151	4,1	0.045
Fish X Trials	30.394	4,1	0.135
Nutrient X Fish X Trials	48.104	4,1	0.108

3.42 Species Diversity in the Shallow Enclosures

Similar to the deep enclosures, algal diversity in the shallow enclosures was affected by fertilization (p=0.002)(Table 13). However, fish stocking did not influence species diversity (p=0.141). Furthermore, no time interaction was detected (Table 13). In the fertilized treatments, algal diversity generally decreased. The influence of fish, although not statistically significant, was dependent on the nutrient loading (Fig. 11). In the non-fertilized treatments diversity increased in the presence of fish. In the fertilized treatments, fish decreased algal diversity.

Figure 11. Algal diversity in the shallow enclosures during the summer. Diversity was evaluated with Margalef's index of diversity: d_S = (s-1)/log N where s is the number of species and N is the number of individuals. Errors bar represent the standard deviation of the mean. If error bar is not apparent, standard deviation is smaller than symbol.

C= Control or no treatment enclosures, F= enclosures with Fish,

N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

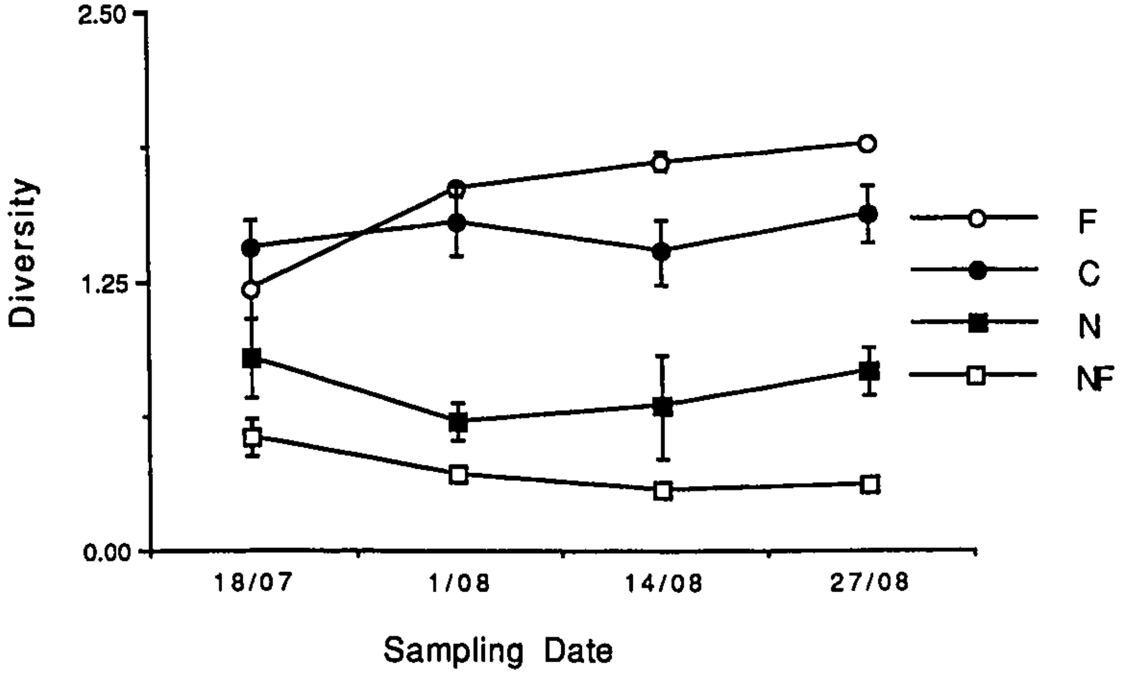

2.50
1.25
0.00
Diversity
18/07
1/08
14/08
27/08
Sampling Date
F
C
N
NF

Table 13. Nutrient and fish effects on the algal diversity in the shallow enclosures during the summer. The effects were evaluated by repeated measures analysis of variance. The main or global effects are reported in the Between-Subject section whereas the temporal effects are reported in the Within-Subject section. The error terms for the multivariate tests are matrices, not individual values.

Univariate Results:

Source	SS	df	MS	F	p
Between Subjects					
Nutrients	10.079	1	10.079	47.204	0.002
Fish	0.718	1	0.718	3.364	0.141
Nutrients X Fish	1.206	1	1.206	5.647	0.076
Subj w/groups	0.854	4	0.214		
Within Subjects					
Trials	0.127	3	0.042	0.811	0.512
Nutrients X Trials	0.640	3	0.213	4.077	0.033
Fish X Trials	0.056	3	0.019	0.355	0.787
Nutrient X Fish X Trial	0.244	3	0.081	1.553	0.252
Trial X Subj w/groups	0.628	12	0.052		

Multivariate Results:

Source	Multiv. F	df	P
Trials	0.389	3,2	0.777
Nutrients X Trials	1.240	3,2	0.476
Fish X Trials	0.363	3,2	0.790
Nutrient X Fish X Trials	1.170	3,2	0.491

3.5 Comparison of the Nutrient and Fish Effects in the Deep and in the Shallow Enclosures

The main effects of nutrients and of fish on the parameters describing phytoplankton community structure are summarized in Table 14. The reported p values are derived from the univariate between-subject effects and represent the level of influence of nutrient loading and of fish stocking. In Table 14, the Chromophytes are comprised here of the Chrysophyta, the Cryptophyta and the Bacillariophyta.

The relative impacts of fish on phytoplankton are more numerous in the deep enclosures than in the shallow enclosures. In many cases, the presence of fish influenced phytoplankton community in the deep, but not in the shallow treatments. As an example, significant influence of fish on total biomass and taxonomic distribution at the division level was detected in the deep, but not in the shallow enclosures.

Table 14. Summary of the effects of fish, nutrients and their interaction on phytoplankton community parameters in both the deep and the shallow enclosures. The reported p values correspond to the univariate between-subject effect.

	Deep enclosures			Shallow enclosures		
	Fish	Nutrients	FXN	Fish	Nutrients	FXN
Total biomass	* *	* * *	ns	ns	* *	ns
Division distribution						
Chlorophyta	* *	* * *	ns	ns	* *	ns
Cyanobacteria	ns	ns	ns	ns	ns	ns
Pyrrhophyta	*	* *	*	ns	*	ns
chromophytes	* *	* *	ns	ns	*	ns
Bacillariophyta	ns	ns	ns	ns	ns	ns
Size distribution						
2-10 µm	* *	ns	*	*	ns	*
10-20 µm	* *	*	*	* *	ns	* * *
>20 µm	ns	ns	ns	ns	ns	ns
Algal diversity	* * *	* * *	* * *	ns	* *	ns

*   p≤ .05
* *   p≤ .01
* * * p≤ .001
ns non-significant

Chapter Four

Discussion

4.1 Effects of Planktivorous Fish on Algal Biomass

In lakes, it has been shown that algal biomass increases with nutrient loading (e.g., Nicholls & Dillon 1978). The significant enhancement in phytoplankton biomass observed in both the deep and the shallow enclosures with nutrients was therefore expected.

The influence of fish on algal biomass is, in contrast, a controversial topic (e.g., DeMelo et al. 1992; Carpenter & Kitchell 1992). Planktivory has been reported to have both a significant (Lazzaro et al. 1992) as well as an insignificant (McQueen et al. 1990) influence on algal biomass.

In this study, algal biomass increased with the presence of fish in the deep enclosures. One explanation may be that the presence of planktivorous fish indirectly influences algal biomass by modifying zooplankton community structure (Carpenter et al. 1985). Changes in the zooplankton community structure can result in a modification of the amount of algae suppressed by zooplankton grazing (Mazumder et al. 1990). The presence of large mesozooplankton (e.g., cladocerans like *Daphnia*) with high grazing rates have been hypothesized to reduce algal biomass regardless of lake trophic status (McQueen et al. 1986).

The zooplankton community of the deep fishless enclosures were dominated by the large cladocera *Daphnia middendorffiana* (A.

Mazumder, unpublished data). By actively removing *Daphnia* from the water column, planktivorous fish are hypothesized to indirectly favor an increase in algal biomass because algae are relieved from *Daphnia* grazing. In this study, the zooplankton community of the deep enclosures with fish, were dominated by rotifers (small microzooplankton of 41-200 µm). Cladocerans were absent from the fish treatments. Increased microzooplankton biomass in the presence of planktivorous fish is consistent with others experimental results (e.g., Lazzaro et al. 1992). Microzooplankton (dominant in the fish enclosures) have lower grazing rates than the mesozooplankton (dominant in the fishless enclosures)(Mazumder et al. 1990). Fish may thus favor an increase in total algal biomass by removing the algal cells from mesozooplankton grazing pressure. Increased phytoplankton densities (increased number of cells) in the fish enclosures reflects the changes in grazing pressure (Fig. 12 & 13). Similar increases in phytoplankton densities have been reported with the presence of fish by Northcote et al. (1990).

Furthermore, the high algal biomass in the deep enclosures with fish (Fig. 2) may be the result of the interaction between thermal structure, algal growth and loss rates. In contrast to the shallow enclosures, the deep enclosures were thermally stratified. Stratification theoretically leads to a higher proportion of small cells because large cells are lost via sedimentation and not recirculated within the epilimnion (Cushing 1989). Since small cells have faster growth rates (e.g., Reynolds 1984) and lower loss rates, small cells would tend to accumulate in the epilimnion.

The absence of a fish effect in the deep enclosures during mixing in October supports the view that thermal stratification plays a key role. This observation combined with the absence of a fish effect in the non-stratified shallow enclosures suggests that during mixing, physical factors may override food web effects.

Additional factors could account for the absence of a fish effect in the shallow enclosures. There was a greater variation in algal biomass within shallow replicates. Among the sources of variability, two were inherent to the shallow fertilized enclosures (N and NF treatments). The N treatments developed blooms of the cyanobacterium *Microcystis aeruginosa. Microcystis* forms patchy macroscopic colonies which tend to float at the surface of the water column. Due to this patchiness, sampling of *Microcystis* and thus, estimation of algal biomass was difficult. An experimental source of variation was that one of the fertilized enclosures (enclosure number 1) appeared to be leaky and exchanged water with the lake. This leakage was determined by measurements of Na levels since addition of $NaNO_3$ leads to predictable accumulations of Na over the season. Na is essentially a conservative ion, stays in solution and does not affect phytoplankton growth. Lower levels of Na in one of the fertilized shallow enclosures (N treatment) indicated exchange of enclosure water with surrounding lake water (Lean & Mazumder pers. comm.). Furthermore, the non-significant effect of fish on phytoplankton biomass in the shallow enclosures can be related to the absence of, large *Daphnia* populations in the shallow fish enclosures.

In addition, a fish kill occurred at the beginning of August in one of the shallow enriched enclosures with fish (NF treatment). The cause of the fish kill was difficult to determine. Some strains of *Microcystis* are toxic to vertebrates (Prescott 1973) and this could be responsible for the fish kill. Concomitantly, pH levels increased to approximately 9 wich may have contributed to mortalities. In this poorly buffered system, with nutrient enrichment, the high rates of photosynthetic uptake of CO_2 leads to increases in pH. For experimental purposes, each individual dead fish (≈100% of stocked population) was immediately replaced with another one of similar length and weight.

In the deep enclosures, the impact of planktivory was most pronounced in the fertilized enclosures (Fig. 2). In the nutrient enriched conditions, phytoplankton biomass increased 2 to 5 times with the presence of fish. It increased only 2 times in the non-fertilized enclosures. Chlorophyll-*a* values followed the same general pattern as total biomass (Lean & Mazumder In press). It is hypothesized that the high increase in algal biomass in the fertilized fish enclosures is related to the high efficiency and rapid growth of small cells. Particulate organic carbon was also significantly higher in the enclosures with fish, particularly under the fertilized conditions (Lean & Mazumder In press). The increase of organic material in the fish enclosures is not accounted for by differences in total phosphorus levels since epilimnetic total phosphorus levels were not consistently higher in the presence of fish (Lean & Mazumder In press).

There is controversy over the mechanism by which the presence of planktivorous fish can affect algal biomass and the overall phytoplankton community structure. Several studies suggest that the removal of macrozooplankton results in the increase in small rotifer densities which, subsequently, leads to an increase in phytoplankton productivity and biomass due to the lower grazing rate of rotifers (Lazzaro et al. 1992; Carpenter et al. 1985). Other studies suggest that the predatory influences of fish on phytoplankton community structure via changes in zooplankton community and overall grazing can be confounded by the influence of the addition of nutrients by fish (McQueen et al. 1992) and zooplankton. Per unit of biomass, small zooplankton are reported to have a greater nutrient regeneration capacity than bigger zooplankton (Vanni 1987). Increases in algal biomass could thus be due to fish and zooplankton excretion.

The present study was designed to test whether or not fish alter phytoplankton community structure and under what physical and chemical conditions the alteration occurs. The actual mechanism underlying the results, whether phytoplankton community is modulated by zooplankton or fish excretions rather than grazing pressure cannot be ascertained.

Figure 12. Total number of algal cell X 10 ^{6} in the deep enclosures during the summer. Error bars represent the standard deviation of the mean of the replicate enclosures.
C= Control or no treatment enclosures, F= enclosures with Fish,
N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.

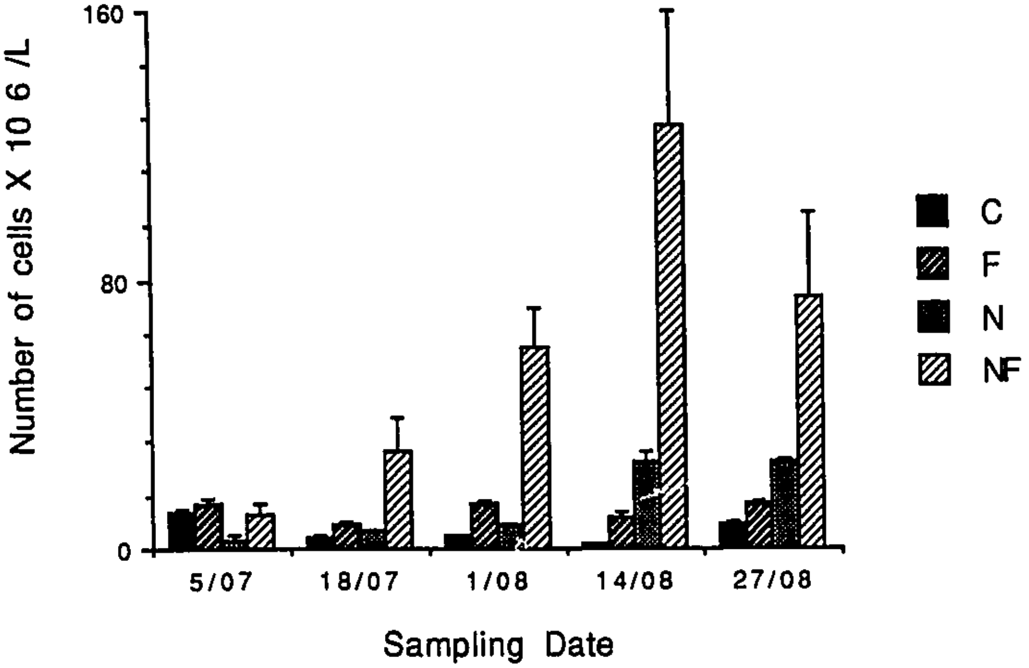
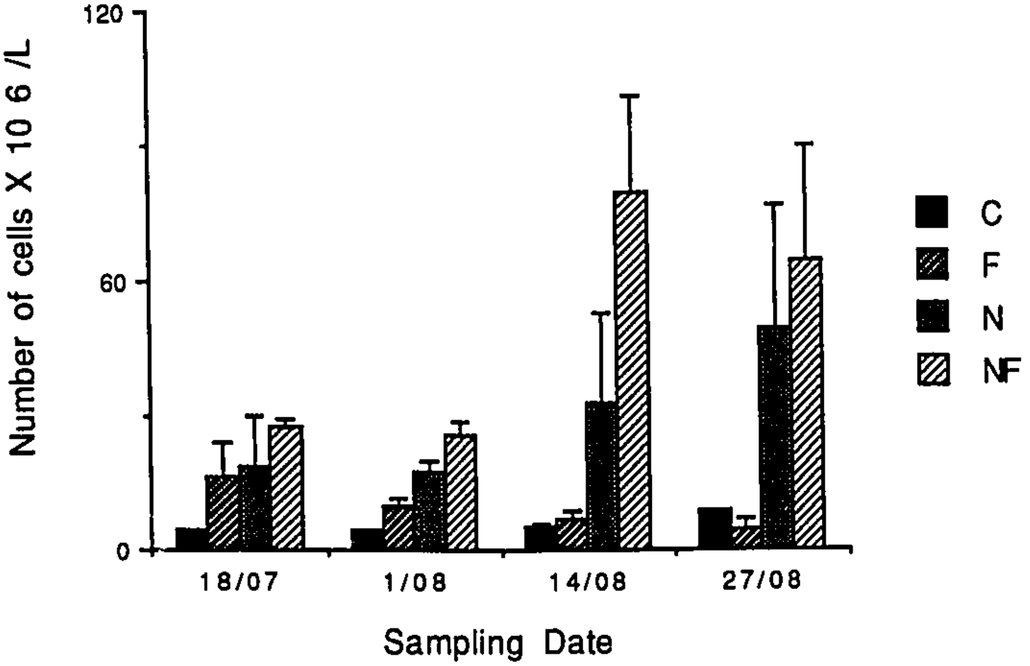

160
80
0
Number of cells X 10 6 /L
5/07
18/07
1/08
14/08
27/08
Sampling Date
C
F
N
NF

Figure 13. Total number of algal cell X 10 ^{6} in the shallow enclosures during the summer. Error bars represent the standard deviation of the mean of the replicate enclosures.

C= Control or no treatment enclosures, F= enclosures with Fish,

N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.


120
60
0
Number of cells X 10 6 /L
18/07
1/08
14/08
27/08
Sampling Date
C
F
N
NF

4.2 The Effects of Planktivorous Fish on Phytoplankton Size Distribution

The analysis of size spectra of aquatic communities is a practical way to partition total biomass while avoiding taxonomic problems (Sprules et al. 1983). Size spectra have been related to community processes such as growth rates (e.g., Sheldon et al. 1977) and loss rates (Smayda 1970). In aquatic systems, mean algal cell size generally increases with nutrient loading (e.g., Watson & Kalff 1981) although picoplanktonic cyanobacteria (0.2-2.0 µm) have been reported to contribute significantly to total phytoplankton biomass in some hypereutrophic systems (Voros et al. 1991).

For the same amount of algal biomass, Secchi depth (a measure of water clarity) will be higher if the biomass is mainly due to big cells rather than small cells. In a review of long term data from 15 lakes, McQueen et al. (1990) reported a significant negative relation between Secchi depth and planktivore biomass. McQueen also reported a non-significant relationship between the deviations of the phosphorus - chlorophyll model and planktivorous fish biomass. These results imply that a change in the size distribution of algal biomass can occur even though total algal biomass may not be affected by planktivorous fish. Shifts in algal size distribution may, perhaps, be the main factor underlying the significant negative relationship between planktivorous fish and Secchi depth.

In both the shallow and the deep enclosures, the presence of fish significantly increased the relative proportion of 2-10 µm cells (see tables 6 to 11). Analogous reductions in the size distribution of particulate phosphorus in the presence of fish were obtained in similar enclosure experiments conducted under mesotrophic conditions (Mazumder et al. 1988). Shorter PO_4^{3-} turnover time reflected the increase in the proportion of small cells in the fish enclosures (Mazumder et al. 1988). Planktivory can thus modify nutrient cycling by modifying the structure of the food web components. Various processes are hypothesized to account for the increase in the proportion of small cells in the fish enclosures. High nutrient regeneration by abundant microzooplankton and feeding selectivity of the microzooplankton on the nanoplankton size-group are some of the hypothesized mechanisms (Mazumder et al. 1990).

4.3 Effects of Planktivorous Fish on Algal Taxonomic Composition

Many environmental factors influence the composition of algal assemblages at the broad level of division. The succession from Chrysophyta and Cryptophyta to Chlorophyta and finally to Cyanobacteria along a gradient of fertilization is a well-described phenomenon for temperate dimictic lakes (Reynolds 1984). It is hypothesized that the contrasting composition of algal assemblages originates from varying physical conditions, grazing pressure and nutrient availability (Sommer et al. 1986).

In the enclosures, both nutrient loading and the presence of fish influenced the distribution of algal biomass among the divisions. In the beginning of the summer, flagellated cryptophytes (*Cryptomonas*, *Rhodomonas*) dominated the fertilized deep enclosures. By mid summer, both fertilized treatments (N and NF) were basically Chlorophyta monocultures (over 80 % of total biomass was composed of chlorophytes). High dominance of Chlorophyta in fertilized enclosures has been reported in other enclosures studies (e.g., Vanni 1987; Lazzaro et al. 1992).

In the deep enclosures, neither the diatoms nor the Cyanobacteria were affected by fertilization. However, in contrast, in the shallow enclosures the relative proportion of cyanobacteria increased. Cyanobacteria are reported to significantly increase their contribution to total algal biomass when total algal biomass reaches 3 to 5 $g \cdot m^3$ (Pick & Lean 1987). Since fertilization rates were the same for both deep and shallow treatments, Cyanobacteria growth in the shallow enclosures can be attributed to either increased nutrient availability in the shallow enclosures or to unfavorable growth conditions in the deep enclosures. Even if nutrient requirements are met, unfavorable physical conditions (e.g., water column stability) may restrict cyanobacterial growth (Paerl 1988). Presence of fish also influenced the non-dominant divisions, for example, fish favored an increase in the relative contribution of pyrrhophytes.

Due to the high taxon pool in aquatic systems, the species composition of algal communities is not easily predicted by taking into account the lake's physical, chemical and biological status. With the exception of a few models for specific algal divisions (e.g., Harris 1986) the current state of our theories does not permit precise prediction of the species composition of phytoplankton assemblages.

4.4 Effects of Planktivorous Fish on Algal Taxonomic Richness

On a local scale, relationships between the number of different living organisms and various environmental gradients have led to several hypotheses (e.g., individualistic continuum, Gauch & Whittaker (1972); resource-partitioning (niche), Pianka (1981); stress-tolerance, Grime (1979); resource ratio, Tilman (1982). However, none of these hypotheses have been able to adequately explain and predict variations in the number of species as a function of a single or several independent variables.

Various methods have been elaborated in order to evaluate the number of species present in a given habitat. Species richness, a simple count of the number of species is one of the most simple and intuitive ways to evaluate the number of species. However, evaluating species richness presents problems in many systems. For example, to adequately enumerate the number of plankton species is a laborious task. Difficulties in taxonomic classification, the high number of organisms and the morphological variability of these organisms all contribute to the difficulty of adequately evaluating plankton richness.

Typically, biological communities are composed of a few common species and of several scarce ones (Stiling 1992). Therefore, evaluating richness with respect to the number of organisms counted, is a simple way of taking into account some of the inherent difficulties of enumeration. Several diversity indices have been developed in order to take into account one aspect or another of the distribution of organisms in communities. Of the myriad of indices that have been elaborated none has gained wide acceptance and each index has its limits ànd its drawbacks (Wolda 1981). Even though there are many problems with the interpretation of diversity indices, an index of diversity was employed here because it is a practical way to standardize, and thus compare the number of species present in each treatment.

Margalef's (1958) index of diversity was selected for various reasons. Margalef's index stems from cybernetics or information theory (Margalef 1958) which, when transposed to ecosystems, assumes the existence of an interaction network between all the environmental components. Margalef's index of diversity was also favored over other indices because of its simplicity and its broad use in limnological studies (e.g., Reynolds 1984). Using Margalef's index of diversity, ds, Reynolds (1984) showed seasonal variations (ds increases as water column becomes stratified) and trophic variations (ds is lower in eutrophic and higher in oligotrophic lakes) of phytoplankton diversity.

With a few exceptions (Northcote et al. 1990), the influence of fish on algal diversity remains largely uninvestigated. In this experiment, diversity, estimated with Margalef's index, decreased with the presence of fish in the fertilized conditions. Diversity increased with presence of fish in the non-fertilized treatments. The same pattern in algal diversity was repeated in both the deep and the shallow enclosures (Fig. 10 & 11). Field manipulations of herbivorous zooplankton have provided evidence for an effect of zooplankton grazing on algal diversity (e.g., McCauley & Briand 1979). The relative impacts of grazing on diversity are, however, difficult to evaluate since in most studies algal biomass was categorized into edible and the inedible functional groups. Diversity per se was not reported.

Fertility or resource richness of the environment is one of the best qualitative local scale predictors of species richness. A reduction in richness with increasing fertility and standing stock has been reported in various habitats (e.g., Agusti et al. 1991; Abramsky & Rosenzweig 1984; Al-Mufti et al. 1977). Typically, species richness rapidly increases with fertilization in areas of low nutrient availability. Richness reaches a plateau at a certain fertility level, after which it declines at a relatively constant proportion with increased fertility.

Enclosure data on species richness follows the general fertility (biomass) versus diversity curve described by Tilman (Fig. 14). The same type of general relationship between total algal biomass and algal richness has been reported by Nicholls et al. (1992) in Ontario lakes and by Agusti et al. (1991) for Florida lakes.

The biomanipulation hypothesis states that planktivory modulates algal biomass. Therefore, one would expect each treatment to follow sequentially on the biomass axis of the biomass-species richness plot. Figure 15 shows the distribution of the average species richness with respect to each of the four treatments. As predicted, the non-fertilized enclosures are grouped at the beginning of the curve. Since planktivory leads to an increase in algal biomass in the non-fertilized enclosures, the fish enclosure data are to the right of the control enclosure data along the fertility-biomass gradient. Since planktivory also indirectly enhances biomass in the fertilized treatments, the fertilized fish treatments are grouped further to the right on the fertility-biomass axis.

Changes in algal diversity can thus be hypothetically related to the changes in total biomass which can be modulated by planktivory. In the non-fertilized enclosures the presence of fish, or absence of large zooplankton, does not limit the growth of edible (e.g., McCauley & Briand 1979) algae. Scarcity of nutrients can prevent the dominance of specific algae (e.g., Harris 1986). Consequently, overall diversity increases because no one specific taxon is able to dominate the algal assemblage and out compete the others taxa. In the fertilized environment large cells can take advantage of available nutrients (Lean & White 1983). Consequently, the best nutrient storing taxa (usually large cells) should dominate the community and overall diversity should decrease. Diversity is further decreased in the presence of fish because algal biomass and the relative number of cells increased. Planktivory can thus be hypothesized as a deterministic vector of phytoplankton richness.

Figure 14. Species richness and total algal biomass relationship during the summer. Each datum point is the mean for the two replicate enclosure at one given time during summer. Taxa contributing less than one percent to total algal biomass were not taken into account in species richness evaluation. Shallow and deep treatments are tabulated.

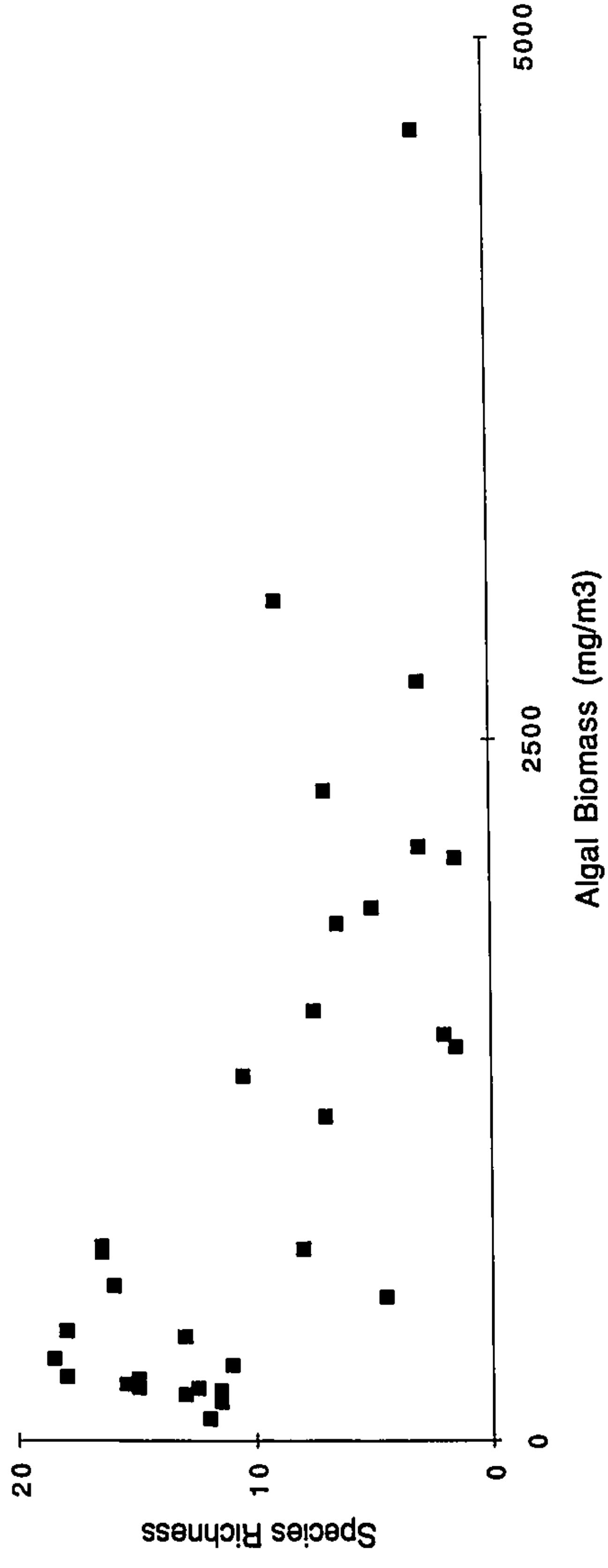
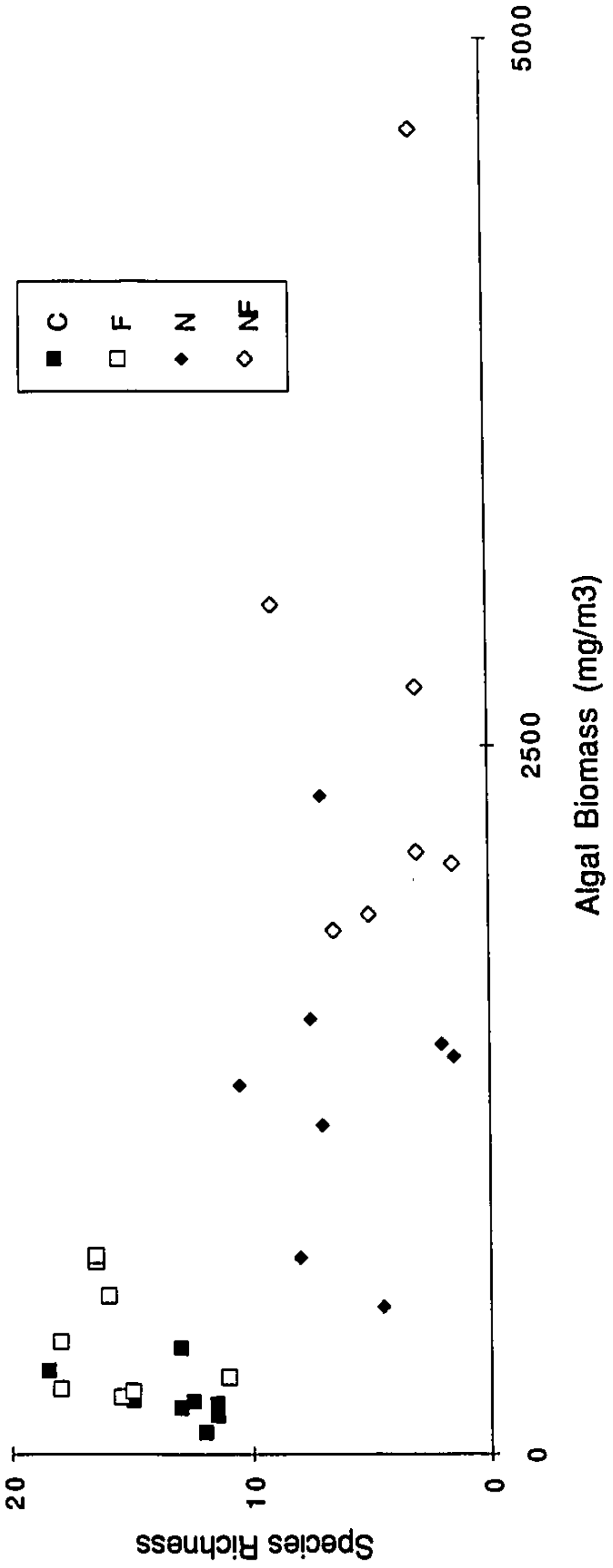

Species Richness
20
10
0
0
2500
5000
Algal Biomass (mg/m3)

Figure 15. Species richness and total algal biomass relationship with respect to fertilization and the presence of planktivorous fish during the summer. Each point is the mean for the two replicate enclosure at one given time during summer. Taxa contributing less than one percent to total algal biomass were not taking into account in species richness evaluation. Shallow and deep treatments are tabulated.

C= Control or no treatment enclosures, F= enclosures with Fish,
N= enclosures with Nutrient additions, NF= enclosures with Nutrient additions and Fish.


Species Richness
0
10
20
Algal Biomass (mg/m3)
0
2500
5000
C
F
N
NF

Chapter Five

General Conclusions

In this experiment, the presence of planktivorous fish influenced overall phytoplankton community structure. Fish altered total biomass, size and taxonomic distribution, as well as diversity. Algal biomass increased with the presence of fish in the deep enclosures, but not in the shallow ones. The relative proportion of small cells increased with fish and the composition of algal assemblages at both the species level and the broad division level were modified with the presence of fish. Fish also influenced algal diversity. Diversity increased with presence of fish in the non-fertilized treatments and decreased with fish in the fertilized treatments. These modifications of phytoplankton community structure triggered by the presence of planktivorous fish imply that biological factors can modify the structure of aquatic ecosystems. The biotic as well as the abiotic components of the environment can thus shape food web structure.

The results of this study support the hypothesis that both food web structure and abiotic factors affect phytoplankton community (Carpenter et al. 1987). The biomanipulation hypothesis (Shapiro et al. 1975) suggests that the presence of planktivorous fish triggers a shift in the structure of the food web which affects lower trophic levels. The changes in the trophic structure can in turn affect the physical characteristics of lakes (Shapiro & Wright 1984). Planktivore biomass has been negatively correlated with water clarity for North American stratified lakes (McQueen et al. 1990). Regardless of the mechanism by which fish may influence the food web, the present study concludes that presence of planktivorous fish can have a significant influence on phytoplankton community structure.

Based on the enclosures experiment, this study also suggests that the relative impact of planktivory on phytoplankton community structure may be modulated by thermal stratification and nutrient loading. The specific influence of planktivorous fish on phytoplankton community structure may therefore be best determined by taking into account lake trophic status and thermal stratification.

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Appendix

Appendix I. List of taxonomic abbreviations

ah spp	*Aphanocapsa* species
an cic	*Anabaena circinalis* Rabenh.
ar inc	*Arthrodesmus incus* (Bréb.) Hass. *ex* Ralfs
at nid	*Aphanothece nidulans* P.Richter
ca sp1	*Chlamydomonas* species no. 1
ca sp2	*Chlamydomonas* species no. 2
cc dis	*Chroococcus dispersus* (Keissler) Lemm.
cc dvm	*Chroococcus dispersus* var. *minor* G. M. Sm.
cf lon	*Chrysosphaerella longispina* Lauterb.
ch spp	*Chromulina* species
ch sp2	*Chromulina* species no. 2
ch sp4	*Chromulina* species no. 4
cp spp	*Chrysophyte* species
cr ero	*Cryptomonas erosa* Ehrenb.
cr erv	*Cryptomonas erosa* var. *reflexa* Marsson
cr spp	*Cryptomonas* species
cs par	*Chrysochromulina parva* Lackey
cu rec	*Crucigenia rectangularis* (Näg.) Gay
cu tet	*Crucigenia tretrapedia* (Kirchn.) W. & G. S. West
cy sp1	*Cyclotella* species no. 1
cy sp2	*Cyclotella* species no. 2
di bav	*Dinobryon bavaricum* Imhof
di cre	*Dinobryon crenulatum* W. & G. S. West
do spp	*Diatoma* spp.
ds pul	*Dictyosphaerium pulchellum* Wood
el gel	*Elakatothrix gelatinosa* Wille
gy spp	*Gymnodinium* species
ka ova	*Katablepharis ovalis* Skuja
ke s10	*Kephyrion* species
me ten	*Merismopedia tenuissima* Lemm.
mi aer	*Microcystis aeruginosa* Kütz.
oc sp1	*Ochromonas* species no. 1
oc sp2	*Ochromonas* species no. 2
os xxx	*Pseudanabaena* species
pe tet	*Pediastrum tetras* (Ehrenb.) Ralfs
pr inc	*Peridinium inconspicuum* Lemm.
qa lac	*Quadrigula lacustris* (Chodat) G. M. Sm.
ra lin	*Rhabdoderma lineare* Schmidle & Lauterb.
rh min	*Rhodomonas minuta* Skuja

rz eri	*Rhizosolena eriensis* H. L. Sm.
sa min	*Salpingoeca species*
sc wis	*Scenedesmus quadricauda* (Turp.) de Brébisson
sc wos	*Scenedesmus circumfusus* Hortob
se min	*Selenastrum minutum* (Näg.) Collins
so pla	*Spondylosium planum* (Wolle) W. & G. S. West
sp cor	*Spiniferomonas cornutus*
sr jud	*Schroederia judayi* G. M. Smith
su uvl	*Synura uvella* Ehrenb.
sy spp	*Synura* species
ta fen	*Tabellaria* cf.*fenestrata* (Lyngb.) Kütz
te min	*Tetraëdron minimum* (A. Braun) Hansg.

Appendix II. Details of the species composition of the deep treatments in late summer. Each listed taxa contributes to more than one percent of total biomass.

Control enclosures (Fig. 6 section C)	Fish enclosures (Fig. 6 section F)	Nutrient fertilized enclosures (Fig. 6 section N)	Nutrient fertilized enclosures with Fish (Fig. 6 section NF)
Chlorophyte sp.	*Chromulina spp.* *	*Cryptomonas spp.*	*Cryptomonas spp.*
Chromulina spp. *	*Ankistrodesmus sp.*	*Schroederia judayi* *	*Scenedesmus cirumfusus* *
Cryptomonas erosa	*Cosmarium sp.*		*Scenedesmus quadricauda*
Cryptomonas ovata	*Chroococcus spp.*		*Gymnodinium sp.* *
Gymnodinium spp.	*Cryptomonas erosa*		
Mallomonas cf. *caudata*	*Cryptomonas ovata*		
Mallomonas spp.	*Cyclotella spp.*		
Merismopedia tenuissima *	*Elakatothrix gelatinosa*		
Ochromonas spp. *	*Gymnodinium spp.*		
Pediastrum tetras	*Katablepharis ovata*		
Rhodomonas minuta	*Ochromonas spp.* *		
Synura uvella	*Oocystis spp.* *		
Tabellaria cf. *fenestrata*	*Peridinium inconspicuum* *		
Tetraëdron minimum *	*Quadrigula lacustris*		
	Scenedesmus circumfusus		
	Selenastrum minutum		
	Tetraëdron minimum *		
Taxa represented in the figure, but not contributing to more than 1% of total biomass	Taxa represented in the figure, but not contributing to more than 1% of total biomass	Taxa represented in the figure, but not contributing to more than 1% of total biomass	Taxa represented in the figure, but not contributing to more than 1% of total biomass
Peridinium (empty cell) *	*Chroococcus sp.* *	cf. *Chromulina spp.* *	*Cryptomonas sp.* *
Katablepharis ovata *	cf. *Chlamydomonas* *	*Rhodomonas minuta* *	
Dinobryon divergens *			
Salpingoeca sp. *			
Oocystis sp. *			

* taxon appears on figure 6

Appendix III. Phytoplankton enumeration data for enclosure number 9.
(deep enclosure with nutrient additions).

```
 09a 29aout          1
DATE ANALYSED...02-08-1992
SUBSAMPLE VOLUME (ml) ..       10.00
TRANSECT WIDTH (Um)..            226
COUNTING AREA...               ROUND
CHAMBER LENGTH (mm)               26
COUNT OBJECTIVES             10x, 20x, 40x
-----------------------------------------------------------------------------
 TAXON          CELLS       BIOMASS   COL CELLS COL    LEN    WID   D  # TRANS MAG
                (L-1)     (mg.m-3)             LENGTH   Um     Um   Um
---------------------------------------------------------------------------
ah spp 1s        18071       0.009    0     1    0.0    1.0    0.0  0  1  2  40.0
sr jud 2e     26528390    1519.244    0  2202    0.0   17.5    2.5  0  1  3  40.0
sc wis 2e        36142       4.769    2     8   35.0    7.0    3.0  0  1  2  40.0
oo sp2 2e        18071       0.681    1     1   15.0    8.0    3.0  0  1  2  40.0
te min 2t        18071       0.000    0     1    0.0    6.0    6.0  0  1  2  40.0
sc wos 2e       108427       7.448    6    24   25.0    6.2    2.3  0  1  2  40.0
cp s32 4e       162640       1.526    0     9    0.0    7.0    1.6  0  1  2  40.0
cv spp 5e        18071       0.664    0     1    0.0    7.8    3.0  0  1  2  40.0
cy spl 7s        54213       0.766    0     3    0.0    3.0    0.0  0  1  2  40.0
-----------------------------------------------------------------------------
TOT CNT       26962090    1535.1080      2226
```

Appendix IV. Phytoplankton enumeration data for enclosure number 10. (deep enclosure with nutrient additions).

```
 10a 29aout          1
DATE ANALYSED...02-08-1992
SUBSAMPLE VOLUME (ml) ..      10.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...              ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES            10x, 20x, 40x
-------------------------------------------------------------------------
 TAXON        CELLS      BIOMASS  COL CELLS COL    LEN    WID  D  # TRANS MAG
              (L-1)    (mg.m-3)            LENGTH   Um     Um  Um
-----------------------------------------------------------------------
ah spp 1s      18071      0.009   0    1    0.0    1.0    0.0  0  1  2   40.0
sr jud 2e   23046683   1319.852   0 1913    0.0   17.5    2.5  0 11  3   40.0
sc wos 2e      18071      1.241   1    4   25.0    6.2    2.3  0  1  2   40.0
cp s32 4e     126498      1.187   0    7    0.0    7.0    1.6  0  1  2   40.0
cp s33 4s      36142      2.365   0    2    0.0    5.0    0.0  0  1  2   40.0
ch spp 4s     126498      0.271   0    7    0.0    1.6    0.0  0  1  2   40.0
cv spp 5e     542133     19.927   0   30    0.0    7.8    3.0  0  1  2   40.0
cr ero 5e      18071     17.734   0    1    0.0   17.0   10.5  0  1  2   40.0
cy spl 7s      54213      0.766   0    3    0.0    3.0    0.0  0  1  2   40.0
-------------------------------------------------------------------------
TOT CNT     23986383  1363.3540      1965
```

Appendix V. Phytoplankton enumeration data for enclosure number 11.
(deep enclosure with nutrient additions and fish).

```
 11 a  29 aout          sample 1
DATE ANALYSED...11-06-1991
SUBSAMPLE VOLUME (ml) ..       1.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...              ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES            10x, 20x, 40x
-----------------------------------------------------------------------------
 TAXON       CELLS       BIOMASS   COL CELLS COL    LEN    WID  D  # TRANS MAG
              (L-1)      (mg.m-3)            LENGTH  Um     Um  Um
-----------------------------------------------------------------------------
an cic 1r     120474       0.048   1     8    4.0    0.4    0.4  0  1  3  40.0
sc wis 2e    3493748     316.346  29   118   12.4    6.8    2.5  0  3  3  40.0
sc wos 2e   36503640    1530.196 303   933    8.7    6.5    2.0  0  3  3  40.0
rh min 5c     481896      44.882   0     4    0.0   12.2    5.4  0  1  3  40.0
-----------------------------------------------------------------------------
TOT CNT     40599752   1891.4730       337
```

Appendix VI. Phytoplankton enumeration data for enclosure number 12.
(deep enclosure with nutrient additions and fish).

```
 12 a 29 aout         1
DATE ANALYSED...02-03-1992
SUBSAMPLE VOLUME (ml) ..       1.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...              ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES            10x, 20x, 40x
--------------------------------------------------------------------------------
 TAXON       CELLS       BIOMASS  COL CELLS COL    LEN    WID  D  # TRANS MAG
             (L-1)      (mg.m-3)            LENGTH  Um     Um  Um
------------------------------------------------------------------------------
pi spp 1s      240948     10.645   1    25  34.0    1.5    0.0  0  1  3  40.0
sc wos 2e   104451000   2932.769 289   668   8.2    5.9    2.0  0  8  2  40.0
ch spp 1s     1927585     27.251   0     8   0.0    3.0    0.0  0  2  3  40.0
cs par 4e     1445688     18.421   0     6   0.0    3.6    2.6  0  2  3  40.0
rh min 5c     1445688     55.352   0     6   0.0    8.7    4.1  0  3  3  40.0
cr ero 5e      481896    479.719   0     2   0.0   16.3   10.8  0  1  3  40.0
--------------------------------------------------------------------------------
TOT CNT    109992800   3524.1562       312
```

Appendix VII. Phytoplankton enumeration data for enclosure number 13. (control or no treatment deep enclosure).

13 a 29 aout 1
DATE ANALYSED...02-08-1992
SUBSAMPLE VOLUME (ml) .. 10.00
TRANSECT WIDTH (Um).. 226
COUNTING AREA... ROUND
CHAMBER LENGTH (mm) 26
COUNT OBJECTIVES 10x, 20x, 40x

TAXON	CELLS (L-1)	BIOMASS (mg.m-3)	COL	CELLS	COL LENGTH	LEN Um	WID Um	D Um	#	TRANS	MAG
ah spp 1s	722844	0.654	0	20	0.0	1.2	0.0	0	1	1	40.0
cc dvm 1s	72284	2.170	2	28	89.9	1.6	0.0	0	1	1	40.0
sr jud 1e	36142	0.833	0	1	0.0	11.0	2.0	0	1	1	40.0
at nid 1r	36142	2.725	1	75	60.0	2.0	0.8	0	1	1	40.0
me ten 1s	108427	2.299	3	36	30.0	1.5	0.0	0	1	1	40.0
at spp 1e	36142	0.852	1	15	65.0	3.0	1.0	0	1	1	40.0
pi spp 1s	36142	0.194	1	20	45.0	0.8	0.0	0	1	1	40.0
el gel 2d	18071	0.207	4	6	40.0	9.0	1.8	0	1	4	20.0
gr sp1 2s	36142	82.792	1	35	64.0	5.0	0.0	0	1	1	40.0
se min 2e	36142	0.828	0	1	0.0	7.0	2.5	0	1	1	40.0
sc wos 2e	72284	1.514	2	4	20.0	5.0	2.0	0	1	1	40.0
su uvl 4e	18071	11.000	4	31	69.0	6.0	5.0	0	1	4	20.0
oc sp3 4s	36142	4.088	0	1	0.0	6.0	0.0	0	1	1	40.0
di sva 4e	72284	3.488	0	2	0.0	9.0	3.2	0	1	1	40.0
ma cau 4e	36142	55.967	0	1	0.0	17.5	13.0	0	1	1	40.0
cp s22 4e	180711	4.546	0	5	0.0	5.0	3.1	0	1	1	40.0
oc sp1 4s	542133	31.393	0	15	0.0	4.8	0.0	0	2	1	40.0
ch spp 4s	1662542	6.964	0	46	0.0	2.0	0.0	0	1	1	40.0
ch spp 4e	433707	0.500	0	12	0.0	2.2	1.0	0	1	1	40.0
cs par 4e	72284	0.606	0	2	0.0	4.0	2.0	0	3	1	40.0
sa spp 4e	72284	1.703	0	2	0.0	5.0	3.0	0	1	1	40.0
ma sp3 4e	72284	9.462	0	2	0.0	10.0	5.0	0	1	1	40.0
oc sp4 4e	72284	13.625	0	2	0.0	10.0	6.0	0	1	1	40.0

```
cp sp4 4e      72284     13.625   0    2    0.0   10.0    6.0  0  1  1  40.0
cr ero 5e      31624     24.813   0    7    0.0   18.5    9.0  0  2  4  20.0
cr ova 5e      13553     15.328   0    3    0.0   15.0   12.0  0  1  4  20.0
cr pus 5e      49696     16.490   0   11    0.0   15.0    6.5  0  1  4  20.0
ka ova 5e      36142      1.022   0    1    0.0    6.0    3.0  0  1  1  40.0
rh min 5c     505991      7.451   0   14    0.0    9.0    2.5  0  1  1  40.0
gy spp 6e       4518      5.109   0    1    0.0   15.0   12.0  0  1  4  20.0
ta fen 7k      34335      3.399  19   57  180.0   66.0    1.0  1  1  5  10.0
do spp 7r      36142      5.813   0    1    0.0   12.8    4.0  0  1  1  40.0
--------------------------------------------------------------------------------
TOT CNT     5265920    331.4594        190
```

Appendix VIII. Phytoplankton enumeration data for enclosure number 14. (control or no treatment deep enclosure).

```
 14 a 30 aout        1
DATE ANALYSED...01-31-1992
SUBSAMPLE VOLUME (ml) ..       10.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...               ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES             10x, 20x, 40x
-----------------------------------------------------------------------------
 TAXON        CELLS       BIOMASS  COL CELLS COL    LEN    WID  D  # TRANS MAG
              (L-1)      (mg.m-3)            LENGTH  Um     Um  Um
----------------------------------------------------------------------------
an spp 1r        3614      0.766   1    6   65.0    5.0    3.0  0  1  5  20.0
ah spp 1s     1843253      1.285   0  102    0.0    1.1    0.0  0  1  2  40.0
me ten 1s      524062      3.066  29  324   52.0    1.0    0.0  0  1  2  40.0
cc dvm 1s      162640      0.766   9   81   12.0    1.0    0.0  0  1  2  40.0
at spp 1e       72284      1.135   4   60   74.0    2.0    1.0  0  1  2  40.0
mi aer 1s       18071      0.757   1   80   98.0    1.0    0.0  0  1  2  40.0
gr spl 2s       18071      2.810   1   11    0.0    3.0    0.0  0  1  2  40.0
te min 2t       54213      1.822   0    3    0.0    4.2    4.0  2  1  2  40.0
pe tet 2t       18071      3.903   1    3   55.0    6.0    6.0  2  1  2  40.0
oo spp 2e      180711      5.365  10    9   15.0    7.0    3.0  0  1  2  40.0
el gel 2d      162640      0.830   9   12   29.0    6.5    1.5  0  1  2  40.0
ak fal 2d      108427      0.581   0    6    0.0    8.0    1.6  0  1  2  40.0
se min 2r      198782     12.630   0   11    0.0    7.9    3.2  0  1  2  40.0
mo spp 4e        7228      0.999   0    4    0.0   66.0    2.0  0  1  5  10.0
sa spp 4e       72284      0.114   0    4    0.0    3.0    1.0  0  1  2  40.0
sy uvl 4e      126498      1.314   0    7    0.0    4.5    2.1  0  1  2  40.0
di sp4 4e      108427      3.066   0    6    0.0    6.0    3.0  0  2  2  40.0
de sp5 4e       18071      0.852   0    1    0.0   10.0    3.0  0  1  2  40.0
ch spp 4s     2349244      9.840   0  130    0.0    2.0    0.0  0  1  2  40.0
ch spp 4e      144569      0.275   0    8    0.0    3.0    1.1  0  1  2  40.0
cs par 4e      505991      4.239   0   28    0.0    4.0    2.0  0  1  2  40.0
oc spl 4s      813200     47.089   0   45    0.0    4.8    0.0  0  1  2  40.0
cr ero 5e       54213     43.686   0   15    0.0   19.0    9.0  0  1  5  20.0
```

```
cr mar 5e      39756     20.650   0   11    0.0  15.5   8.0  0  2  5  20.0
cr ova 5e       7228      8.175   0    2    0.0  15.0  12.0  0  1  5  20.0
cr erv 5e      46985     47.253   0   13    0.0  20.0   9.8  0  2  5  20.0
rh min 5c     415635      8.104   0   23    0.0   9.5   2.8  0  2  2  40.0
ka ova 5e      18071      2.725   0    1    0.0   8.0   6.0  0  1  2  40.0
gy spp 6s      18071      6.898   0    1    0.0   9.0   0.0  0  2  2  40.0
ta fen 7k      32528      3.816  18   64  150.0  66.0   1.0  1  1  5  10.0
sy spp 7r      39756      0.749   0   11    0.0   6.0   2.0  0  1  5  20.0
cy spp 7s     126498     14.306   0    7    0.0   6.0   0.0  0  2  2  40.0
rz eri 7r     216853      3.709   0   12    0.0   2.0   3.3  0  1  2  40.0
------------------------------------------------------------------------------
TOT CNT      8525948   263.5767       534
```

Appendix IX. Phytoplankton enumeration data for enclosure number 15.
(deep enclosure with fish).

15a 30aout 1
DATE ANALYSED...02-01-1992
SUBSAMPLE VOLUME (ml) .. 10.00
TRANSECT WIDTH (Um).. 226
COUNTING AREA... ROUND
CHAMBER LENGTH (mm) 26
COUNT OBJECTIVES 10x, 20x, 40x

TAXON	CELLS (L-1)	BIOMASS (mg.m-3)	COL	CELLS	COL LENGTH	LEN Um	WID Um	D Um	#	TRANS	MAG
ra lin 1r	433707	3.066	0	12	0.0	4.0	1.5	0	1	1	40.0
ah spp 1s	36142	0.530	1	28	75.0	1.0	0.0	0	1	1	40.0
at cla 1r	108427	2.895	3	51	88.0	2.0	1.0	0	1	1	40.0
ah spp 1s	1409546	2.491	0	39	0.0	1.5	0.0	0	3	1	40.0
me ten 1s	108427	1.142	3	22	35.0	1.4	0.0	0	1	1	40.0
cc dvm 1s	252996	0.284	7	15	40.0	1.0	0.0	0	1	1	40.0
mi aer 1s	144569	2.365	4	125	150.0	1.0	0.0	0	1	1	40.0
co spp 2e	36142	43.601	0	1	0.0	16.0	12.0	0	1	1	40.0
te min 2t	1843253	117.968	0	102	0.0	8.0	8.0	1	1	2	40.0
se min 2r	325280	25.292	0	9	0.0	11.0	3.0	0	1	1	40.0
qa lac 2r	144569	24.525	4	12	33.0	18.0	2.0	0	1	1	40.0
el gel 2d	180711	2.271	5	6	33.0	10.0	2.0	0	1	1	40.0
oo sp2 2e	216853	11.127	6	6	18.0	8.0	3.5	0	2	1	40.0
sc wos 2e	361422	12.545	10	31	8.8	6.6	1.8	0	2	1	40.0
cu tet 2t	10843	2.776	3	12	23.0	8.0	8.0	1	1	5	20.0
ke s12 4e	108427	0.908	0	3	0.0	4.0	2.0	0	1	1	40.0
ke s10 4e	36142	0.145	0	1	0.0	3.0	1.6	0	2	1	40.0
oc sp3 4s	72284	8.175	0	2	0.0	6.0	0.0	0	1	1	40.0
ch spp 4e	361422	0.681	0	10	0.0	2.5	1.2	0	2	1	40.0
oc sp1 4s	650560	31.040	0	18	0.0	4.5	0.0	0	2	1	40.0
cs par 4e	433707	2.575	0	12	0.0	3.5	1.8	0	2	1	40.0
sa spp 4e	144569	0.151	0	4	0.0	2.0	1.0	0	1	1	40.0
cp s19 4e	180711	2.912	0	5	0.0	9.5	1.8	0	2	1	40.0

```
di bav 4e      36142      0.038   0    1   0.0    2.0    1.0  0  1  1  40.0
ch min 4s    2674524     34.154   0   74   0.0    2.9    0.0  0  5  1  40.0
cp sp1 4s     180711     20.438   0    5   0.0    6.0    0.0  0  3  1  40.0
cp sp7 4s      72284     10.394   0    2   0.0    6.5    0.0  0  2  1  40.0
ma cau 4e      18071      2.271   0    5   0.0   15.0    4.0  0  1  5  20.0
cp s11 4e      10843      1.635   0    3   0.0    8.0    6.0  0  1  5  20.0
ma sp6 4e      10843      1.362   0    3   0.0   15.0    4.0  0  1  5  20.0
ka ova 5e     252996      5.770   0    7   0.0    4.0    3.3  0  1  1  40.0
cr ero 5e      43371     38.627   0   12   0.0   21.0    9.0  0  1  5  20.0
cr ova 5e      46985     29.890   0   13   0.0   15.0    9.0  0  1  5  20.0
gy spp 6e     140955    159.415   0   39   0.0   15.0   12.0  0  1  5  20.0
cy sp1 7r     108427     10.645   0    3   0.0    5.0    5.0  0  1  1  40.0
cy sp2 7s      36142     32.701   0    1   0.0   12.0    0.0  0  1  1  40.0
ta fen 7k       1506      0.244   1    3  85.0   18.0    6.0  1  1  6  10.0
-------------------------------------------------------------------------------
TOT CNT     11234501    647.0505        433
```

Appendix X. Phytoplankton enumeration data for enclosure number 16.
(deep enclosure with fish).

16 a 30 aout 1
DATE ANALYSED...02-03-1992
SUBSAMPLE VOLUME (ml) .. 10.00
TRANSECT WIDTH (Um).. 226
COUNTING AREA... ROUND
CHAMBER LENGTH (mm) 26
COUNT OBJECTIVES 10x, 20x, 40x

TAXON	CELLS (L-1)	BIOMASS (mg.m-3)	COL	CELLS	COL LENGTH	LEN Um	WID Um	D Um	#	TRANS	MAG
ah spp 1s	180711	1.360	5	54	100.0	1.1	0.0	0	1	1	40.0
ch spp 1s	4084070	17.107	0	113	0.0	2.0	0.0	0	1	1	40.0
me ten 1s	216853	0.833	6	44	45.0	1.0	0.0	0	1	1	40.0
ch spp 1e	867413	1.363	0	24	0.0	3.0	1.0	0	1	1	40.0
oc spp 1s	325280	36.788	0	9	0.0	6.0	0.0	0	2	1	40.0
mi spp 1s	144569	1.360	4	54	99.0	1.1	0.0	0	1	1	40.0
ah spp 1s	2060106	1.436	0	57	0.0	1.1	0.0	0	1	1	40.0
at spp 1e	108427	1.449	3	23	85.0	1.3	1.6	0	2	1	40.0
cc dvm 1s	108427	0.114	3	6	25.0	1.0	0.0	0	1	1	40.0
co spp 2e	93367	73.330	0	31	0.0	15.0	10.0	0	1	6	20.0
cu tet 2t	10843	1.832	3	12	33.0	6.5	6.5	1	2	5	20.0
ci kut 2s	18071	15.745	5	130	71.0	4.0	0.0	0	1	5	20.0
gr sp5 2s	9036	4.087	2	8	90.0	6.0	0.0	0	1	4	20.0
qa lac 2r	72284	2.725	2	4	33.0	6.0	2.0	0	1	1	40.0
se min 2r	108427	6.898	0	3	0.0	9.0	3.0	0	1	1	40.0
ki lun 2d	252996	0.470	0	7	0.0	4.2	1.3	0	1	1	40.0
te min 2t	1662542	162.929	0	46	0.0	10.0	9.8	1	1	1	40.0
ak fal 2d	108427	9.225	0	3	0.0	13.0	5.0	0	1	1	40.0
sc wos 2e	469849	51.504	13	35	32.0	6.0	3.6	0	1	1	40.0
oo spp 2e	252996	9.061	7	7	19.0	7.6	3.0	0	1	1	40.0
el gel 2d	108427	1.665	3	4	55.0	11.0	2.0	0	1	1	40.0
ma spp 4e	57225	16.180	0	19	0.0	15.0	6.0	0	2	6	20.0
ke sl1 4e	36142	0.303	0	1	0.0	4.0	2.0	0	1	1	40.0

```
di bav 4e     108427     0.170  0   3  0.0   3.0   1.0  0  1  1  40.0
cp spl 4s     325280    36.788  0   9  0.0   6.0   0.0  0  1  1  40.0
cs par 4e    1698684    14.231  0  47  0.0   4.0   2.0  0  1  1  40.0
cp s14 4e     144569     3.406  0   4  0.0   5.0   3.0  0  1  1  40.0
cr ero 5e      81320   100.464  0  27  0.0  19.5  11.0  0  2  6  20.0
cr ova 5e      33130    18.284  0  11  0.0  15.3   8.3  0  3  6  20.0
rh min 5c     397564     6.473  0  11  0.0   9.2   2.6  0  2  1  40.0
ka ova 5e     397564    19.984  0  11  0.0   6.0   4.0  0  1  1  40.0
gy spp 6s      24095     6.459  0   8  0.0   8.0   0.0  0  2  6  20.0
pr inc 6e      93367    66.486  0  31  0.0  13.6  10.0  0  1  6  20.0
cy sp2 7s      36142    13.796  0   1  0.0   9.0   0.0  0  1  1  40.0
cy spl 7s     108427     7.096  0   3  0.0   5.0   0.0  0  1  1  40.0
-------------------------------------------------------------------------
TOT CNT    14805052    711.4006    535
```

Appendix XI. Details of the species composition of the shallow treatments in late summer. Each listed taxa contributes to more than one percent of total biomass.

Control enclosures (Fig. 7, section C)	Fish enclosures (Fig. 7, section F)	Nutrient fertilized enclosures (Fig. 7, section N)	Nutrient fertilized enclosures with Fish (Fig. 7, section NF)
*Chromulina spp.**	*Aphanothece clathrata*	*Chroococcus dispersus*	*Cryptophyte sp.*
Chroococcus limneticus	*Chromulina spp.* *	*Cryptomonas erosa*	*Pseudanabaena sp.* *
Chrysosphaerella longispina *	*Chroococcus dispersus* *	*Microcystis aeruginosa* *	*Scenedesmus cirumfusus* *
Crucigenia tetrapedia	*Chrysosphaerella longispina*	*Sphaerocystis schroeteri*	*Scenedesmus quadricauda*
Cryptomonas spp.	*Cosmarium spp*	*Schroederia judayi*	
Cyclotella spp.	*Cryptomonas spp.*	*Tetraëdron minimum*	
Katablepharis ovalis	*Elakatothrix gelatinosa*		
Ochromonas spp.	*Gloeocystis planctonica*		
Oocystis sp. *	*Gymnodinium spp.*		
Scenedesmus circumfusus	*Katablepharis ovalis*		
Sphaerocystis schroeteri	*Merismopedia tenuissima* *		
Tabellaria cf.*fenestrata*	*Ochromonas spp.* *		
Tetraëdron minimum *	*Pediastrum tetras*		
	Peridinium inconspicuum *		
	Sphaerocystis schroeteri		
	Spineferomonas cornutus		
	Spondylosium planum *		
	Scenedesmus cirumfusus		
	Tetraëdron minimum		

Taxa represented in the figure, but not contributing to more than 1% of total biomass	Taxa represented in the figure, but not contributing to more than 1% of total biomass
Merismopedia tenuissima *	*Fragilaria sp.*
Dinobryon divergens *	*Tetraëdron minimum* *
Crytomonas erosa *	*Dinobryon sociale var. americanum**
Sphaerocystis schroeteri *	
cf. *Cosmarium* *	

* taxon appears on figure 7

Appendix XII. Phytoplankton enumeration data for enclosure number 1. (shallow enclosure with nutrient additions).

```
 01 a 14 aout         1
DATE ANALYSED...11-14-1992
SUBSAMPLE VOLUME (ml) ..      1.00
TRANSECT WIDTH (Um)..          226
COUNTING AREA...             ROUND
CHAMBER LENGTH (mm)             26
COUNT OBJECTIVES          10x, 20x, 40x
------------------------------------------------------------------------------
 TAXON        CELLS       BIOMASS   COL CELLS COL    LEN    WID  D  # TRANS MAG
              (L-1)      (mg.m-3)            LENGTH   Um     Um  Um
----------------------------------------------------------------------------
cc dis 1s      180711       3.101   0    1    0.0    3.2    0.0  0  1  2  40.0
cc dis 1s     1626400      83.714   9   27   12.3    3.2    0.0  0  1  2  40.0
me ten 1s      722844       2.519   4   20    8.0    1.1    0.0  0  1  2  40.0
so pla 2e      301185     193.782   5    8   16.0   12.0    8.0  0  1  6  20.0
ca spl 2s      361422       6.201   0    2    0.0    3.2    0.0  0  1  2  40.0
sc wos 2e      903555      24.884   5   13    8.0    7.0    1.7  0  1  2  40.0
cu tet 2t      361422      13.011   2    8   12.0    3.0    3.0  1  1  2  40.0
qa lac 2r      361422       6.182   2    4   11.0    9.0    1.1  0  1  2  40.0
sh sch 2s     2891377     469.694  16   98   12.0    3.7    0.0  0  1  2  40.0
sr jud 2r     8493421     157.829   0   47    0.0   14.0    1.3  0  1  2  40.0
cu rec 2e      542133       4.542   3   16   10.1    3.0    1.0  0  1  2  40.0
te min 2t    24396000     389.360   0  135    0.0    4.2    3.8  1  1  2  40.0
ds pul 2s     1264978      78.724   7   13   15.0    4.0    0.0  0  2  2  40.0
ch spp 4s    10842663     124.626   0   60    0.0    2.8    0.0  0  1  2  40.0
oc spl 4s     3794932     429.197   0   21    0.0    6.0    0.0  0  2  2  40.0
su uvl 4e     3252799     472.510  18  118   15.0    8.0    2.3  0  1  2  40.0
cp spp 4s      180711       4.415   0    1    0.0    3.6    0.0  0  1  2  40.0
ta fen 7k      271067     100.294   9   37  130.0   60.0    3.0  1  1  6  10.0
sy spp 7r      662607     122.817   0   11    0.0   59.0    2.0  0  1  6  20.0
------------------------------------------------------------------------------
TOT CNT     61411650    2687.4010       358
```

Appendix XIII. Phytoplankton enumeration data for enclosure number 2. (shallow enclosure with nutrient additions).

```
 02 a 14 aout         1
DATE ANALYSED...11-12-1992
SUBSAMPLE VOLUME (ml) ..       1.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...              ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES             10x, 20x, 40x
--------------------------------------------------------------------------------
 TAXON        CELLS       BIOMASS   COL CELLS COL    LEN    WID   D  # TRANS MAG
              (L-1)      (mg.m-3)            LENGTH   Um     Um  Um
--------------------------------------------------------------------------------
mi aer 1s     248478   202.3568   22 8354 100.0    1.6    0.0   0  9  8   10.0
ca sp2 2e     180711     2.9310    0    1   0.0    6.4    2.2   0  1  2   40.0
sr jud 2r     180711     2.2709    0    1   0.0   16.0    1.0   0  1  2   40.0
ch spp 4s    1445689     9.2099    0    8   0.0    2.3    0.0   0  1  2   40.0
cr spp 5e     650560   127.7371    0   18   0.0   15.0    5.0   0  1  5   20.0
rh min 5c     903555    41.3963    0    5   0.0    7.0    5.0   0  1  2   40.0
--------------------------------------------------------------------------------
TOT CNT      3609704    385.9020         55
```

Appendix XIV. Phytoplankton enumeration data for enclosure number 3. (shallow enclosure with nutrient additions and fish).

```
 03 a 13 aout          1
DATE ANALYSED...05-07-1992
SUBSAMPLE VOLUME (ml) ..        1.00
TRANSECT WIDTH (Um)..            226
COUNTING AREA...               ROUND
CHAMBER LENGTH (mm)               26
COUNT OBJECTIVES             10x, 20x, 40x
---------------------------------------------------------------------------
 TAXON         CELLS       BIOMASS   COL CELLS COL    LEN    WID   D  # TRANS MAG
               (L-1)      (mg.m-3)            LENGTH   Um     Um  Um
---------------------------------------------------------------------------
os xxx 1r      361422      15.356    2    23   25.0    2.4    1.4  0  3  2  40.0
sc wos 2e    77705760    2001.283  430  1020    8.0    6.4    1.8  0  3  2  40.0
sc wis 2e     7409154     933.333   41   137    9.0    8.0    3.0  0  1  2  40.0
ch spp 4s      722844       3.028    0     4    0.0    2.0    0.0  0  1  2  40.0
cp spp 4e    23673152       0.000    0   131   12.0    2.7    0.0  0  1  2  40.0
cy spl 7s      542133      13.244    0     3    0.0    3.6    0.0  0  1  2  40.0
---------------------------------------------------------------------------
TOT CNT   110414500    2966.2430        611
```

Appendix XV. Phytoplankton enumeration data for enclosure number 4. (shallow enclosure with nutrient additions and fish).

```
 04 a 27 aout          1
DATE ANALYSED...05-15-1992
SUBSAMPLE VOLUME (ml) ..        1.00
TRANSECT WIDTH (Um)..            226
COUNTING AREA...               ROUND
CHAMBER LENGTH (mm)               26
COUNT OBJECTIVES             10x, 20x, 40x
-----------------------------------------------------------------------------
 TAXON        CELLS       BIOMASS  COL CELLS COL    LEN    WID  D  # TRANS MAG
              (L-1)      (mg.m-3)             LENGTH  Um     Um  Um
---------------------------------------------------------------------------
os xxx 1r    1084266       74.315    6  187 235.0    2.8    1.0  0  2  2  40.0
sc wos 2e   93969760     1237.952  520 1043   8.0    6.4    1.4  0  2  2  40.0
cu tet 2t     361422       14.345    2   27  15.0    2.1    1.4  1  1  2  40.0
sc wis 2e    1264978       45.127    7   23  10.0    6.4    1.8  0  1  2  40.0
ch spp 4s    1084266        3.311    0    6   0.0    1.8    0.0  0  2  2  40.0
cp spp 4e    1807111       23.299    0   10   0.0    7.6    1.8  0  1  2  40.0
cy spl 7s    1084266       26.488    0    6   0.0    3.6    0.0  0  4  2  40.0
-----------------------------------------------------------------------------
TOT CNT    100656100    1424.8360        557
```

Appendix XVI. Phytoplankton enumeration data for enclosure number 5. (control or no treatment shallow enclosure).

05 a 15 aout 1
DATE ANALYSED...05-01-1992
SUBSAMPLE VOLUME (ml) .. 10.00
TRANSECT WIDTH (Um).. 226
COUNTING AREA... ROUND
CHAMBER LENGTH (mm) 26
COUNT OBJECTIVES 10x, 20x, 40x

TAXON	CELLS (L-1)	BIOMASS (mg.m-3)	COL	CELLS	COL LENGTH	LEN Um	WID Um	D Um	#	TRANS	MAG
ah spp 1s	240948	0.517	0	20	0.0	1.6	0.0	0	2	3	40.0
cc dis 1s	349375	2.222	29	86	12.0	1.6	0.0	0	2	3	40.0
at nid 1r	12047	0.341	1	12	15.0	3.0	1.0	0	1	3	40.0
mi aer 1s	36142	0.915	3	66	28.0	1.3	0.0	0	1	3	40.0
me ten 1s	469849	3.459	39	412	33.0	1.1	0.0	0	2	3	40.0
pi spp 1s	36142	1.447	3	56	45.0	1.6	0.0	0	1	3	40.0
ra lin 1r	168664	4.918	14	39	16.0	6.8	1.4	0	3	3	40.0
cc dvm 1s	373470	3.274	31	89	15.0	1.8	0.0	0	2	3	40.0
se min 2r	12047	0.256	0	1	0.0	7.5	1.9	0	1	3	40.0
te min 2t	518038	8.687	0	43	0.0	4.3	3.9	1	3	3	40.0
sc wos 2e	60237	0.698	5	9	19.0	4.8	1.6	0	2	3	40.0
sr jud 2r	24095	0.392	0	2	0.0	6.4	1.8	0	1	3	40.0
el gel 2d	120474	1.356	10	16	16.0	10.5	1.6	0	2	3	40.0
di cre 4e	36142	1.400	8	8	18.0	6.4	3.4	0	2	4	20.0
ch spp 4e	156616	0.246	0	13	0.0	3.0	1.0	0	3	3	40.0
oc spl 4s	722844	41.857	0	60	0.0	4.8	0.0	0	3	3	40.0
cs par 4e	108427	0.908	0	9	0.0	4.0	2.0	0	2	3	40.0
sa min 4s	60237	1.731	0	5	0.0	3.8	0.0	0	6	3	40.0
su uvl 4e	36142	13.063	3	14	30.0	8.0	4.3	0	1	3	40.0
ch spp 4s	1710731	7.166	0	142	0.0	2.0	0.0	0	2	3	40.0
cr ero 5e	9036	7.664	0	2	0.0	20.0	9.0	0	1	4	20.0
rh min 5c	60237	1.192	0	5	0.0	8.4	3.0	0	2	3	40.0
ka ova 5e	156616	5.542	0	13	0.0	6.6	3.2	0	2	3	40.0

sy spp 7r	27107	1.405	0	6	0.0	66.0	1.0	0	2	4	20.0
rz eri 7r	180711	3.304	0	15	0.0	4.4	2.3	0	6	3	40.0
cy spl 7s	265043	7.029	0	22	0.0	3.7	0.0	0	3	3	40.0
TOT CNT	5951417	120.9897		504							

Appendix XVII. Phytoplankton enumeration data for enclosure number 6. (control or no treatment shallow enclosure).

```
 06 a 15 aout          1
DATE ANALYSED...05-05-1992
SUBSAMPLE VOLUME (ml) ..      10.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...              ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES            10x, 20x, 40x
-------------------------------------------------------------------------------
 TAXON        CELLS        BIOMASS  COL CELLS COL    LEN   WID  D  # TRANS MAG
              (L-1)      (mg.m-3)             LENGTH  Um    Um  Um
-------------------------------------------------------------------------------
cc dis 1s      60237       1.478    5   22  12.0    2.2   0.0  0  2  3   40.0
ah spp 1s      84332       0.353    0    7   0.0    2.0   0.0  0  2  3   40.0
cc dvm 1s      36142       1.766    3   35  30.0    2.0   0.0  0  1  3   40.0
me ten 1s     252996       1.842   21  169  15.0    1.2   0.0  0  3  3   40.0
os xxx 1s      12047       1.362    1   27   1.0    2.0   0.0  0  1  3   40.0
ra lin 1r     156616       8.954   13   68  25.0    7.1   1.4  0  2  3   40.0
te min 2t     228901       3.369    0   19   0.0    4.6   3.2  1  2  3   40.0
pe tet 2t      24095       1.245    2    8  12.0    3.8   3.4  1  1  3   40.0
so pla 2e      12047      10.900    1    1  15.0   12.0  12.0  0  1  3   40.0
el gel 2d      48190       0.199    4    4  15.0    7.0   1.5  0  1  3   40.0
ch sp2 4s      24095       0.101    0    2   0.0    2.0   0.0  0  1  3   40.0
oc spl 4s     132522       7.674    0   11   0.0    4.8   0.0  0  2  3   40.0
ch spp 4s    2240817       9.386    0  186   0.0    2.0   0.0  0  1  3   40.0
cf lon 4e     939698     176.309   78  130  66.0    8.6   5.0  0  2  3   40.0
ka ova 5e     192758       6.614    0   16   0.0    6.4   3.2  0  2  3   40.0
rh min 5c      48190       0.908    0    4   0.0    8.0   3.0  0  1  3   40.0
cy spl 7s      84332       2.060    0    7   0.0    3.6   0.0  0  2  3   40.0
cy sp2 7s      24095      24.053    0    2   0.0   12.4   0.0  0  1  3   40.0
rz eri 7r      24095       0.057    0    2   0.0    3.0   1.0  0  1  3   40.0
-------------------------------------------------------------------------------
TOT CNT      4626204     258.6312        384
```

Appendix XVIII. Phytoplankton enumeration data for enclosure number 7. (shallow enclosure with fish).

```
 07 a 14 aout         1
DATE ANALYSED...05-04-1992
SUBSAMPLE VOLUME (ml) ..      10.00
TRANSECT WIDTH (Um)..           226
COUNTING AREA...              ROUND
CHAMBER LENGTH (mm)              26
COUNT OBJECTIVES           10x, 20x, 40x
----------------------------------------------------------------------------------
 TAXON         CELLS      BIOMASS  COL CELLS COL    LEN    WID  D  # TRANS MAG
               (L-1)     (mg.m-3)            LENGTH  Um     Um  Um
---------------------------------------------------------------------------------
me ten 1s      72284       1.090   6  100  38.0    1.2    0.0  0  2  3   40.0
pi spp 1s      12047       0.775   1   30  45.0    1.6    0.0  0  1  3   40.0
ah spp 1s     144569       0.131   0   12   0.0    1.2    0.0  0  2  3   40.0
cc dis 1s     120474       1.363  10   27  15.0    2.0    0.0  0  2  3   40.0
cc dvm 1s      96379       3.126   8  121  45.0    1.6    0.0  0  2  3   40.0
te min 2t    1385452      20.394   0  115   0.0    4.6    3.2  1  2  3   40.0
sr jud 2r      12047       0.066   0    1   0.0    7.0    1.0  0  1  3   40.0
sc wos 2e     108427       2.100   9   24  15.0    4.8    1.7  0  2  3   40.0
sc wis 2e      12047       0.219   1    2  15.0    4.8    1.9  0  1  3   40.0
el gel 2d      48190       0.226   4    4  12.0    7.0    1.6  0  1  3   40.0
sp cor 4s      48190       2.790   0    4   0.0    4.8    0.0  0  1  3   40.0
cs par 4e      96379       0.807   0    8   0.0    4.0    2.0  0  2  3   40.0
ch spp 4s    1867348       7.822   0  155   0.0    2.0    0.0  0  2  3   40.0
ch spp 4e      60237       0.095   0    5   0.0    3.0    1.0  0  2  3   40.0
oc sp2 4s      48190       2.790   0    4   0.0    4.8    0.0  0  1  3   40.0
oc spl 4s     445754      25.812   0   37   0.0    4.8    0.0  0  2  3   40.0
sa min 4s      48190       0.827   0    4   0.0    3.2    0.0  0  1  3   40.0
cf lon 4e      48190       4.651   0    4   0.0    8.0    4.8  0  1  3   40.0
cr ero 5e      18071      15.328   0    4   0.0   20.0    9.0  0  1  4   20.0
cr erv 5e       4518       4.023   0    1   0.0   21.0    9.0  0  1  4   20.0
ka ova 5e     168664       4.522   0   14   0.0    5.0    3.2  0  2  3   40.0
rh min 5c      36142       1.050   0    3   0.0    9.6    3.4  0  1  3   40.0
```

```
gy spp 6e      27107    17.031   0    6    0.0  12.0  10.0  0  2  4  20.0
pr inc 6e      13553     6.898   0    3    0.0  12.0   9.0  0  1  4  20.0
ta fen 7k      18071     3.927   8   19  180.0  61.0   3.0  1  2  4  10.0
sy spp 7r      45178     2.129   0   10    0.0  60.0   1.0  0  2  4  20.0
rz eri 7r     108427     0.213   0    9    0.0   2.5   1.0  0  2  3  40.0
cy spl 7s      36142     0.883   0    3    0.0   3.6   0.0  0  1  3  40.0
---------------------------------------------------------------------------
TOT CNT      5150263   131.0873       449
```

Appendix XIX. Phytoplankton enumeration data for enclosure number 8. (shallow enclosure with fish).

08 a 14 aout 1
DATE ANALYSED...05-05-1992
SUBSAMPLE VOLUME (ml) .. 10.00
TRANSECT WIDTH (Um).. 226
COUNTING AREA... ROUND
CHAMBER LENGTH (mm) 26
COUNT OBJECTIVES 10x, 20x, 40x

TAXON	CELLS (L-1)	BIOMASS (mg.m-3)	COL	CELLS	COL LENGTH	LEN Um	WID Um	D Um	#	TRANS	MAG
pi spp 1s	90356	8.099	5	107	55.0	2.0	0.0	0	2	2	40.0
cc dvm 1s	72284	0.621	4	38	17.0	1.2	0.0	0	1	2	40.0
cc dis 1s	198782	6.131	11	24	12.0	3.0	0.0	0	2	2	40.0
me ten 1s	180711	1.033	10	82	25.0	1.1	0.0	0	2	2	40.0
ah spp 1s	126498	0.182	0	7	0.0	1.4	0.0	0	2	2	40.0
an cic 1r	18071	27.088	1	9	18.0	9.6	4.7	0	1	2	40.0
ar inc 2r	13553	26.984	0	3	0.0	15.0	13.0	0	1	6	20.0
cl sp4 2d	36142	0.342	0	2	0.0	10.0	1.9	0	1	2	40.0
te min 2t	2186604	38.222	0	121	0.0	4.6	3.8	1	2	2	40.0
sc wis 2e	18071	0.484	1	2	15.0	6.4	2.0	0	1	2	40.0
el gel 2d	90356	0.728	5	13	15.0	7.0	1.3	0	2	2	40.0
sc wos 2e	162640	3.100	9	20	15.0	6.4	1.6	0	2	2	40.0
pe tet 2t	54213	1.665	3	9	15.0	3.2	3.2	1	1	2	40.0
di bav 4e	22589	0.981	0	5	0.0	6.4	3.6	0	2	6	20.0
ch sp2 4s	36142	0.151	0	2	0.0	2.0	0.0	0	2	2	40.0
ch spp 4e	90356	0.142	0	5	0.0	3.0	1.0	0	2	2	40.0
oc sp1 4s	596346	34.532	0	33	0.0	4.8	0.0	0	2	2	40.0
cs par 4e	578275	4.845	0	32	0.0	4.0	2.0	0	2	2	40.0
sp cor 4s	18071	2.480	0	1	0.0	6.4	0.0	0	1	2	40.0
ke s10 4e	18071	0.620	0	1	0.0	6.4	3.2	0	1	2	40.0
ch spp 4s	3885288	16.275	0	215	0.0	2.0	0.0	0	1	2	40.0
sa min 4s	18071	0.310	0	1	0.0	3.2	0.0	0	1	2	40.0
cr ero 5e	9036	7.664	0	2	0.0	20.0	9.0	0	1	6	20.0

```
ka ova 5e     325280     21.800   0   18    0.0    8.0    4.0  0  2  2  40.0
gy spp 6e      18071     11.354   0    4    0.0   12.0   10.0  0  1  6  20.0
pr inc 6e      27107     13.795   0    6    0.0   12.0    9.0  0  2  6  20.0
ta fen 7k      22589      5.489  10   27  180.0   60.0    3.0  1  2  6  10.0
sy spp 7r      49696      2.342   0   11    0.0   60.0    1.0  0  2  6  20.0
cy spl 7s      72284      1.240   0    4    0.0    3.2    0.0  0  1  2  40.0
rz eri 7r     234924      0.554   0   13    0.0    3.0    1.0  0  2  2  40.0
do spp 7r      36142     38.369   0    2    0.0   33.0    6.4  0  1  2  40.0
--------------------------------------------------------------------------------
TOT CNT      9306618   277.6228        547
```