FERTILIZATION OF AN OLIGOTROPHIC COASTAL MONTANE LAKE USING HIGH N:P RATIO FERTILIZERS: EFFECTS ON PHYTOPLANKTON AND ZOOPLANKTON COMMUNITY STRUCTURE

by

JOHN WERRING

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Department of Zoology

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date April 29, 1986
ABSTRACT

Comparisons of the response of phytoplankton communities to different methods of nutrient addition used in past whole-lake fertilization studies, suggested that it might be possible to generate predictable changes in the phytoplankton and zooplankton communities of lakes by controlling the frequency, magnitude and N:P ratio of the autochthonous nutrient load. Results obtained by several workers in separate, but related, laboratory and small scale enclosure experiments supported this belief. The evidence strongly suggested that N:P ratios are important in determining the outcome of competitive interactions between algal taxa, with green algae outcompeting blue-green algae at high N:P ratios, while the frequency of nutrient supply is important in determining the size structure of an algal community. There is also evidence that suggests that competitive relationships between zooplankton species are sensitive to changes in the species and size composition of the phytoplankton community. Large cladocerans perform poorly when large algae are present in abundance.

This thesis examines the effects of small, frequent doses of high N:P ratio fertilizers on the littoral and limnetic phytoplankton and zooplankton communities in a small oligotrophic coastal montane lake in the Coastal Range Mountains of British Columbia. The experiments were carried out in-situ in eight large polyethylene enclosures, each measuring 150 m² in area. The enclosures were fertilized three times each week from June to October, 1982 with small doses of NH₄NO₃ and
(NH₄)₂HPO₄ at an N:P atomic ratio of 40:1. Phosphorous was thought to be the nutrient limiting phytoplankton growth in this lake but the results suggest that nitrogen may be more important in this regard. The role of Sphagnum mats surrounding the lake in the control of nitrogen supply to the lake is discussed.

In general, effects of fertilization were more pronounced in the limnetic than the littoral zone. Phytoplankton standing crop increased 4-fold and 7-fold in littoral and limnetic fertilized enclosures, respectively, over controls. Cyanophyceae and Chrysophyceae, which dominated the algal biomass in the lake and controls were almost completely eliminated from all fertilized enclosures by mid-summer and replaced by Chlorophyceae. More than 80% of the algal biomass in fertilized enclosures consisted of algae less than 20 um in size, whereas less than 20% of the biomass in controls and the lake fell into this size range.

Changes in the algal community led to significant changes in the species composition, structure and biomass of the zooplankton community. With the exceptions of Daphnia rosea and Holopedium gibberum all herbivorous zooplankton in all enclosures followed the pattern of species succession that occurred in the lake but at higher densities. Fecundity and body size of all herbivorous zooplankton increased following fertilization, but Daphnia rosea capitalized on the enhanced algal biomass and became the community dominant over the whole summer in fertilized enclosures while in controls and the lake, it ceased to be dominant by late July. Holopedium disappeared
from all enclosures by the end of July. Fish predation and competitive interactions with \textit{Daphnia} probably led to their decline.

Fish predation was generally selective for \textit{Holopedium} and \textit{D. rosea} in control and fertilized enclosures and its role in the disappearance of \textit{Holopedium} and in structuring the zooplankton community in both, is discussed. Adult cutthroat trout (\textit{Salmo clarki clarki}) in fertilized enclosures altered their diet in favour of \textit{Daphnia}. Fish in control enclosures and the lake fed almost exclusively on terrestrial insects. Planted juvenile (fry) cutthroat trout did not survive in any of the enclosures. Avian predation appeared to be responsible for their disappearance suggesting that predation is more important than food to the survival of juvenile fish in lakes.

My results suggest that the phytoplankton and zooplankton communities in freshwaters can be manipulated in a predictable manner based on a control of the pattern of nutrient supply. This knowledge can be of great benefit to the management of lakes for both fish production and ameliorating the effects of eutrophication.
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1.0 INTRODUCTION

1.1 Historical and Theoretical Background

The practice of fertilizing natural lakes in North America developed in response to reports of remarkable increases in fish production following the addition of inorganic fertilizers to fish culture ponds in the southern United States (Swingle, 1947). It was felt that this technology might also be used to increase fish production in natural lakes, however, little was known about the role that nutrients played in the structure and functioning of aquatic ecosystems. Therefore, investigations were launched in an attempt to elucidate the effects of nutrient additions on whole-lake ecosystems.

The first attempt to approach lake fertilization on a scientific basis in North America was made by Juday and Schloemer (1938). This work was later followed by the works of Ball (1948), Smith (1945, 1948, 1955), Langford (1948), Nelson and Edmondson (1955), Baxter (1959), Rabe and Dyer (1964), Donaldson et al. (1971), Parsons et al. (1972), Schindler et al. (1971, 1973), Stockner et al. (1980) and Stockner (1981). As well, lake fertilization studies were being carried out in Scotland (Gross et al., 1944; Holden, 1954; Munro, 1961), Australia (Weatherly and Nicholls, 1955), Poland (Marcjak, 1975; Weglenska et al., 1975; Zdanowski et al., 1975) and Sweden (Jansson, 1978; Lundgrun, 1978; Solander, 1978; Persson, 1978). However, prior to the studies by Schindler et al. (1971, 1973) and Parsons et al. (1972), very little consideration had been
given to studying the effects of nutrient enrichment on the physical, chemical or biological dynamics, or their interactions, in the receiving waters. Nor was any heed given to the methods of fertilizer application (i.e. rate of addition, amount of nutrient added, nutrient ratios) and their potential for inducing either favourable or deleterious responses in the targeted trophic relationships in the recipient lakes. The main objective was usually to determine whether there was an increase in fish production following fertilization. Very few of the publications provide good qualitative or quantitative data dealing with aspects of the lake ecosystem other than fish, such as phytoplankton or zooplankton dynamics. Some reports deal with this superficially (Donaldson et al., 1971; Stockner et al., 1971) while others emphasize changes in the phytoplankton while ignoring corresponding changes in the zooplankton (Schindler et al., 1971, 1973). Thus, while there has been a considerable amount of work done on lake enrichment, our knowledge of its effectiveness as a lake management tool is still very limited.

My research concerns the effects of the addition of inorganic nitrogen and phosphorous, in frequent, small doses and at high N:P ratios, on the water chemistry, phytoplankton composition and zooplankton community structure in a small oligotrophic lake. It also addresses the effects of changes in zooplankton community structure on the survival of planted juvenile cutthroat trout (\textit{Salmo clarki clarki}) and on the diet of adult trout of this species indigenous to the lake. It is my
intention to show that the frequency, magnitude and N:P ratio of nutrient supply to freshwaters can produce predictable changes in the phytoplankton communities of lakes and that these changes can be used to achieve various management goals like increasing fish production or ameliorating the water quality of culturally eutrophied lakes. In order to set the stage for the direction I have taken in this research, I will review lake fertilization as it has been practiced to date.

Lake fertilization, with the objective of increasing the production of fish, usually involves the addition of a combination of nitrogen and phosphorous inorganic fertilizers, although, in some cases, organic fertilizers have also been used (see Maciolek, 1954, and Mortimer, 1954, for a review; Juday and Schloemer, 1938). Early attempts at lake fertilization (prior to 1960) employed large doses of low N:P ratio fertilizers which were added to the recipient lake very infrequently. Nutrient additions often raised in-situ inorganic phosphate levels to as high as 100 ug/liter (Smith, 1948; Holden, 1954; Baxter, 1959), 300 ug/liter (Ball, 1948), or even in excess of 500 ug/liter (Langford, 1948). The ratio of nitrogen to phosphorous of the added fertilizers ranged between 0 and 5:1. Nutrients were usually applied in one yearly dose (Smith, 1945, 1948; Holden, 1954; Weatherley and Nicholls, 1955; Baxter, 1959) or in monthly intervals (Ball, 1948, Morgan, 1961). Most of the publications arising from these early studies document at least some temporal changes in the chemistry and biology of the fertilized lakes (Langford, 1948; Holden, 1954; Nelson and Edmondson, 1955;
Smith, 1969). These data show that, relative to per-enrichment oligotrophic conditions, fertilized waters consistently exhibited the following characteristics:

1) Striking increases in phytoplankton abundance, but almost total dominance by filamentous and toxic forms of blue-green algae (Ball, 1948; Rabe and Gauphin, 1964; Rabe and Dyer, 1964; Smith, 1969).

2) Increased zooplankton abundances but fewer species and different community dominants, especially with disappearances of large filter-feeding cladocerans, like Daphnia (Ball, 1948; Donaldson et al., 1971; Smith, 1969) and replacement by small, raptorial feeders, such as rotifers and copepods (Langford, 1948; Weatherley and Nicholls, 1955; Nelson and Edmondson, 1955; Rabe and Dyer, 1964; Smith, 1969).

3) Short-term increases in the abundances of both phytoplankton and zooplankton (2 weeks - 1 month) (Langford, 1948; Weatherley and Nicholls, 1955; Smith, 1969).

4) Increased fish kills caused by reduced levels of dissolved oxygen following fertilization (Ball, 1948; Tanner, 1960) or toxins produced by blue-green algae (reviewed by Gorham, 1962).
Following the studies of Vollenweider (1968) which clearly illustrated that the degree of eutrophication in freshwaters was a function of the annual rate of nutrient input and of lake morphometry, lake managers modified their fertilization programs in an effort to reduce the level of eutrophication that was associated with earlier fertilization schemes. The amount of inorganic phosphorus per addition was greatly reduced to reflect Vollenweider's (1976) acceptable loading rates for mesotrophic lakes (ca. 3-8 gP/m²/year, see Stockner et al., 1980). Additions were made much more frequently (weekly) to prevent algae from depleting nutrients too rapidly between loading events. Also, N:P ratios were increased to around 10-15:1 to better reflect the average ratio of these nutrients in healthy phytoplankton populations (Redfield, 1958). As a result of these changes, the following patterns of change in the biota of recipient lakes, relative to earlier methods of enrichment, were noted:

1) an increase in overall lake primary production without causing a condition of eutrophication (Parsons et al., 1972; Stockner et al., 1980);

2) enhancement of a much broader range of phytoplankton species, although, this may be more a reflection of more refined sampling and identification techniques rather than a change in the pattern of fertilization;
3) no visible blooms of blue-green algae;

4) a predominance of small phytoplankton species relative to those in the unfertilized lake environment (Schindler, 1971, 1973; Lundgrun, 1978);

5) prolonged increases (3 to 7 months) in algal biomass (Parsons et al. 1972; Schindler et al., 1973; Lundgrun, 1978; Stockner et al., 1980).

These changes in the overall pattern of response of phytoplankton in freshwater lakes to two different methods of fertilizer application suggested the possibility of regulating species compositions of phytoplankton and ultimately zooplankton by controlling the rate of addition and N:P ratio of the nutrient load to a water body.

The mechanistic relationships between nutrients, phytoplankton and zooplankton in aquatic ecosystems have all too often been viewed in a relatively simplistic way, i.e. increased nutrient loading on a water body usually increases its capacity to support greater production and maintain larger standing crops of phytoplankton and zooplankton. In reality, the interrelationships are extremely complex. That variations in the chemical composition of natural waters may be important in regulating the abundance, composition and the geographic and periodic distribution of phytoplankton has been recognized since the studies of Pearsall (1930, 1932). Since then, a great deal of research on the link between phytoplankton and water
chemistry has been conducted (for reviews see Lund, 1965; Healey, 1973; Fogg, 1975; Morris, 1980). There have also been extensive investigations concerning the effects of changes in phytoplankton species composition on the population dynamics of individual zooplankton species (e.g. Arnold, 1971; Porter, 1977; Porter and Orcutt, 1980) and on changes in zooplankton community structure (e.g. Gliwicz, 1980; Kerfoot and DeMott, 1980; Richardson and Dodson, 1983).

From the extensive literature detailing relationships between nutrients, phytoplankton and zooplankton, I isolated three properties of freshwater aquatic ecosystems which are relevant to this study.

1) **N:P resource ratios and phytoplankton species composition.**

Schindler (1977) suggested that N:P ratios on the order of 15:1 of nutrients added to natural lakes should not favour the development of "water bloom" blue green algae. The rationale for this suggestion followed experiments (Schindler, 1977) which showed that nutrients added at low N:P ratios (5:1) during whole-lake fertilization experiments, promoted blooms of nitrogen-fixing blue-green algal forms while higher N:P ratios (15:1) did not. However, the addition of nutrients at the higher N:P ratios still resulted in an occasional dominance of the algal community by non-nitrogen fixing, filamentous blue-green algal forms such as *Oscillatoria* (Schindler et al., 1971, 1973). While these blue-green algae did not form visible floating surface scums, their dominance of the algal biomass
could pose a considerable threat to the growth and survival of large cladoceran zooplankton (Arnold, 1971; Porter and Orcutt, 1980; Infante and Litt, 1985) and ultimately change the structure of the zooplankton community (Richman and Dodson, 1983) in a way that might compromise growth and survival in fish. Similar dominances of blue-green algae have been reported in other studies where nutrients were added to lakes in N:P ratios ranging from 10 (Parsons et al., 1972) to 15 (Stockner et al., 1980). In the latter study, floating mats of Anabaena occurred in one of 17 fertilized lakes (Clayoquot Arm, Kennedy Lake), most of the other lakes developed were dominated by the blue-green Merismopedia.

In this regard, Rhee (1978) suggested that differing optimum N:P ratios for growth in green algae and blue-green algae might influence their mutual competition along differing N:P gradients. Later work (Rhee and Gotham, 1980) showed that the specific optimal ratios of cell N and P quotas during normal growth, differed for eight species of algae, ranging from lows of 7 for the diatom Melosira binderana and 9 for the blue-green Microcystis, to as high as 20-30 for three species of chlorococccoid algae. These data suggest, although not conclusively, that green algae might be able to outcompete blue-green algae in a medium which contains much higher N:P ratios than 15:1, as suggested by Schindler (1977).

There is evidence to support this argument. Edmondson (1972) gives data which clearly show that the proportion of blue-green algae in the phytoplankton of Lake Washington
decreased significantly following diversion of sewage inputs to the lake and a subsequent increase in in-situ N:P ratios to as high as 50:1. Barica et al. (1980) found that cyanophytes which normally dominated the phytoplankton in prairie pothole lakes could be completely eliminated by elevating in-situ N:P ratios from 5:1 (the natural lake levels) to more than 50:1 by adding inorganic nitrogen. The resulting algal assemblage consisted predominantly of small chlorophytes and cryptomonads. More recently, Smith (1983) found that blue-green algae (both nitrogen-fixers and non-nitrogen-fixers) formed the dominant component of the algal assemblages for most of the year in hundreds of north temperate lakes whose average summer epilimnetic N:P ratios fell below 29:1.

Hence, it appears that blue-green can still predominate in lake systems where in-situ N:P ratios are greater than those previously suggested (15:1), while less objectionable forms (from a lake manager's standpoint) dominate at much higher N:P ratios. However, data to support this conclusion are few.

2) Small algae grow faster than large algae when environmental conditions for growth are identical (Banse, 1976; Turpin and Harrison, 1980).

The seasonal pattern of algal succession in temperate freshwaters suggests that the frequency of nutrient supply to lakes may be important determining the size structure of algal communities. In temperate freshwaters, small algae tend to dominate the phytoplankton during late spring-early summer.
This is the time when nutrients are available in sufficient concentrations to support rapid growth of small algal forms to the extent that they can outpace losses due to grazing and sinking (Wetzel, 1975; Porter, 1977). Also, because the water column is turning over and snow melt and seasonal rainfall result in higher discharges into lakes, nutrients are replenished frequently. As summer progresses, the autochthonous nutrient supply becomes patchy as rainfall events occur less often. Epilimnetic nutrient concentrations become depleted as stratification sets in and are often too low to allow small algae to maintain the growth rates needed to outpace predation (Porter, 1977). Thus they are replaced by the larger ungrazed algal forms which no longer have to compete with them for nutrients.

If it is true that small algal forms grow faster than larger algae under identical conditions, as suggested by Banse (1976), then it is reasonable to assume that providing a continuous supply of the right combination of nutrients over the summer should favour the growth of small algal forms over larger algae. This has been shown for marine waters. Turpin and Harrison (1980) found that the mean cell diameter of natural phytoplankton communities was related to the time between limiting nutrient additions. Mean cell diameter decreased as frequency of nutrient additions increased. In recent lake fertilization exercises, nutrients were being added to lakes on a weekly basis. This rate of addition does appear to stimulate the growth of small algal forms in some cases (Schindler et al.,
1971, 1973; Lundgrun, 1978), however, Schindler et al. (1971, 1973) and Parsons et al. (1972) both report seasonal dominances by large algae, such as Staurastrum, Dinobryon, Oscillatoria and various euglenoids, following weekly additions.

Given that small algae (2-50 um in size) are preferentially grazed by zooplankton over larger algal forms (Burns, 1968a; Gliwicz and Hillbricht-Ilkowska, 1972; Gliwicz, 1980), one objective of lake managers wishing to increase fish production should be to convert added nutrients into those algal particles on which zooplankton feed. Increasing large net plankton abundances would only serve to inhibit the production of large cladocerans (Burns, 1968b; Porter and Orcutt, 1980) upon which the fish will selectively feed (Zaret, 1980).

3) The role of phytoplankton composition in determining zooplankton community structure. (Gliwicz, 1980; Richman and Dodson, 1983)

Grazer zooplankton species change as the species composition of phytoplankton changes. In temperate lakes, net phytoplankton tend toward predominance during the mid-summer months (Hutchinson, 1967; Porter, 1977). The general pattern of change in the zooplankton is that large cladocerans such as Daphnia and Holopedium, which dominate the zooplankton during early summer, disappear or become less abundant, and are replaced as community dominants by smaller cladocerans and/or copepods. It is believed that smaller cladocerans are more efficient filter-feeders in media containing large amounts of
net phytoplankton, so they outcompete the larger zooplankters for the available grazable phytoplankton (Gliwicz, 1980). Large cladocerans become abundant again in the fall, or when nutrient inputs promote blooms of the rapidly growing small algal species (Porter, 1977; Gliwicz, 1980; Richman and Dodson, 1983). Several laboratory studies have shown that colonial and filamentous algae clog the filtering apparatus of large cladocerans like *Daphnia* (Burns, 1968b; Porter, 1975; Webster and Peters, 1978; Gliwicz and Seidlar, 1980). Cladoceran populations have been known to decline or disappear completely when filamentous algal forms predominate (Burns, 1968b).

Losses of large zooplankters would mean less food for fish in lakes and production could be compromised if the fish do not turn to another food resource. Consequently, from a fisheries standpoint, it would be desirable to maintain the existence of large cladocerans for periods longer than normal patterns of zooplankton succession might dictate. This could be made possible by reducing or eliminating the net phytoplankton in the system and enhancing the small, rapidly growing algae on which the large cladocerans feed.

The extent to which the research discussed above can be applied to whole lake ecosystems has yet to be fully resolved, since the many of these studies have been performed in culture flasks in the laboratory or in small scale enclosure experiments. However, this research does pose some interesting questions of ecological importance.
1) Does the addition of combined nitrogen and phosphorous inorganic fertilizers at high N:P ratios to a water body result in a reduction in or an elimination of the blue-green algae in a system where they form a significant proportion of the algal biomass, such as in culturally eutrophic lakes? To my knowledge, this has not been tested experimentally, however, Barica et al. (1981) did attempt to alter N:P ratios by adding only nitrogen.

2) Can the frequency of nutrient addition to freshwaters be manipulated to produce phytoplankton communities dominated by small algal cells, thereby increasing the efficiency of food chain energy transfer? This has not been shown for freshwater algal communities.

3) If (1) and (2) occur, can these changes affect the outcome of competition between herbivorous zooplankton and thus alter the zooplankton community structure?

4) Can the addition of nutrient to lakes be manipulated to produce zooplankton communities which are dominated over the entire summer by large cladocerans, thereby enhancing the food for fish?

I chose to address these questions by experimentally fertilizing large enclosures in a small, oligotrophic coastal montane lake. The lake exhibited a typical north temperate seasonal pattern of algal succession. In early spring the
dominant algal species were small greens. Blue green algae were rare. The summer and autumn associations were dominated by large ungrazable chrysophytes and colonial blue-green algae, respectively. Zooplankton dominants during the early summer consisted of large cladocerans, giving way to small cladocerans and copepods as summer progressed. Since N:P ratios in the lake at spring overturn, when small green algae were community dominants, were high (40:1), this was the ratio of nutrients I chose to use.

1.2 Research Objectives

My goals in this research focussed on testing theoretical predictions pertaining to the response of aquatic plankton systems in an oligotrophic montane lake to frequent (thrice weekly), small (3.3 ug/liter P) doses of high N:P ratio (40:1) inorganic fertilizers, and on applying the results of these predictions to 1) lake fertilization and the management of trout production in lakes and 2) the control of "water blooms" in lakes subject to cultural eutrophication.

A secondary goal was to improve upon existing technology for doing in-situ enclosure experiments so as to produce results that are more representative of the research lake as a whole. This was done through the use of limnocorrrals which were large enough to simulate the lake environment, with some of the corrals enclosing parts of the littoral zone and others enclosing parts of the limnetic zone of the lake. To achieve these goals, I formulated the following research objectives.
1) To evaluate the use of large limnocorrals (150 m²), containing several hundred thousand liters of lake water, in simulating the physical, chemical and biological dynamics of the parent lake environment.

2) To determine the effects of fertilization on the physical, chemical and biological dynamics of the lake waters by comparing the changes in these parameters in the littoral and the limnetic fertilized enclosures with their respective untreated controls.

3) To determine whether fertilization at high N:P atomic ratios (> 15:1) will result in a significant reduction in, or a complete elimination of, the blue-green algae that form one of the major algal dominants in this lake's phytoplankton assemblage over the entire summer.

4) To determine whether fertilization using small, frequent doses of nitrogen and phosphorous fertilizers can promote a shift in a phytoplankton assemblage that is dominated throughout the summer by large ungrazed chrysophytes and blue-greens towards one that favours dominance by smaller algal forms that zooplankton can assimilate much easier.

5) If (4) occurs, to determine if, and the extent to which, fertilization with high N:P ratios would lead to an
increase in the standing stock of available edible phytoplankton and to compare these changes in the littoral vs the limnetic zones of the lake.

6) To assess the effects of changes at the primary trophic level on zooplankton biomass and community structure.

7) To assess the effects of any changes in the zooplankton standing stock or community structure arising from experimental nutrient addition on the feeding patterns of cutthroat trout indigenous to the lake.
2.0 MATERIALS AND METHODS

2.1 Study Site

Placid Lake is a small (1.87 ha.), shallow (zmax = 6.5 m), dimictic, coastal montane bog lake situated on the southern slopes of the Coast Mountain range in southwestern British Columbia (Figure 1, Table 1). This lake proved to be a suitable study site because of its shallow depth and accessibility. Its shallow depth helped to keep the cost of materials and the logistics of limnocorral construction within reason, and its accessibility minimized the logistics of limnocorral installation. It is also physically, chemically and biologically similar to hundreds of other coastal mountain lakes in the region. It is located within the bounds of the University of British Columbia Research Forest were lakes are used for research purposes only. The lake has a single indigenous, fish species, cutthroat trout (Salmo clarki clarki).

2.1.1 Climate

The climate for the region is described as marine warm temperate rainy (mesothermal) with no distinct dry season (Feller, 1975). The driest months are July and August which received a mean rainfall of 57 and 70 mm respectively for the years 1977 to 1982 (Krause, 1984). The average monthly precipitation was 194 mm for the same six year period. The year long monthly average for precipitation in 1982, a particularly
Figure 1. Location of study site. From Neill (1978).
Table 1. Morphometric parameters of Placid Lake.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drainage area (ha)</td>
<td>173.70</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>510</td>
</tr>
<tr>
<td>Shoreline (m)</td>
<td>936</td>
</tr>
<tr>
<td>Surface area (ha)</td>
<td>1.87</td>
</tr>
<tr>
<td>Maximum length (m)</td>
<td>195</td>
</tr>
<tr>
<td>Maximum width (m)</td>
<td>195</td>
</tr>
<tr>
<td>Volume (cubic meters)</td>
<td>63,501</td>
</tr>
<tr>
<td>Volume development</td>
<td>1.55</td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td>6.50</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>3.40</td>
</tr>
<tr>
<td>Relative depth (%)</td>
<td>4</td>
</tr>
<tr>
<td>Shoreline development</td>
<td>2.13</td>
</tr>
</tbody>
</table>

* Data from Shepherd (1973)

Area and Volume by Depth Strata

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0-1</th>
<th>1-2</th>
<th>2-3</th>
<th>3-4</th>
<th>4-5</th>
<th>5-6</th>
<th>6+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (m²)</td>
<td>15360</td>
<td>12843</td>
<td>11150</td>
<td>7989</td>
<td>5469</td>
<td>2545</td>
<td>101</td>
</tr>
<tr>
<td>Volume (m³)</td>
<td>16874</td>
<td>13983</td>
<td>11985</td>
<td>9525</td>
<td>6689</td>
<td>3915</td>
<td>529</td>
</tr>
<tr>
<td>% Total Volume</td>
<td>27</td>
<td>22</td>
<td>19</td>
<td>15</td>
<td>10</td>
<td>6</td>
<td>1</td>
</tr>
</tbody>
</table>
wet year, was 235 mm which fell mainly as rain in October through to April. (Snow occasionally accumulates to depths of 30 cm in this region but it rarely remains for more than a few weeks). Placid Lake is normally covered with an intermittent, thin layer of ice, sometimes overlain with snow, from about mid-December until April.

Summers are cool and winters are mild with an average daily mean temperature for the warmest month of about 17 °C. The average daily mean temperature for the coldest month is close to 1 °C (Feller, 1977). These temperatures were recorded at a weather station at an elevation approximately 500 m lower than Placid Lake and therefore may not accurately represent the conditions the lake's elevation. Total daily rainfall (mm) and mean daily temperatures for June - October, 1982 are shown in Figure 2.

2.1.2 Lake Basin Morphology and Morphometry

The geology and soils of the region are described in detail in Efford (1967) and Feller (1975,1977). The most common rock type in the area is quartz diorite displayed in large, smooth superficially weathered surfaces relatively free of open joints suggesting that the bedrock is impermeable and not easily eroded. Soils in the area are predominantly humo-ferric podzols with textures predominantly sandy loam and loamy sand, with soils adjacent to streams and in some valleys being described as deep (> 1 m) and slightly moist. Soils elsewhere are shallow and dry to slightly moist.
Figure 2. Rainfall and temperature data for 1982
Figure 2. Rainfall and Temperature Data for the University Research Forest for June - October, 1982
Placid Lake's watershed is bounded on the southeast, east and northeast sides by steep, tree-covered mountains rising to over 1000 m elevation. To the north and northwest is a gently rising tree-covered valley which eventually drops very slightly to two other lake basins, Eunice Lake to the north-northeast and Gwendoline Lake to the northwest. The west to southwest is bounded by a long ridge at about 700 m elevation which is not actually part of the drainage basin but acts as a barrier to wind flow. To the south is a fairly steep, heavily tree-covered valley slope which descends immediately southwards and eventually opens onto a gently rolling glacial outwash plain.

Prevailing winds in the region are predominantly from the south to north west. The lake is protected on the south by dense forest and on the west and northwest sides by steep slopes. Hence, it can be sharply stratified during the summer. During periods of heavy summer rainfall, lake waters can rise as much as 1.5 m in less than 24 hours. This sometimes results in disruption of stratification. It can, at times, break down completely allowing complete mixing of epilimnetic and hypolimnetic waters for a brief period. If mixing occurs, stratification is usually quickly restored if the heavy rainfall does not continue.

Since the lake basin is situated on basal glacial till in a valley scoured by Pleistocene glacier movement (Feller 1975,1977) and since the basin is shallow and irregular in shape (Figure 3), it is probably a kettle lake as defined by Wetzel (1975). The lake itself is developing into a quaking bog lake
Figure 3. Bathymetric map of Placid Lake showing locations of the enclosures and the vegetation. From Shepherd (1973).
with thick mats of *Sphagnum* sp. around two-thirds of the shoreline and extending as much as 5 m out into the open water (Figure 3). Lagg zones (Wetzel 1975) exist around the periphery of the lake. The lake has what appears to be a false bottom, a loosely aggregated, flocculent sediment several meters thick (> 1 m, W.E. Neill, personal communication). This is probably a result of the presence of the *Sphagnum* mat and its ongoing release of much particulate organic matter into the open water. In several places around the lake, logs imbedded in the *Sphagnum* mat protrude out into the open water and/or down into the sediments. There is one distinct inlet stream on the north side of the lake. A minor runoff channel to the west carries water into the lake only during periods of high rainfall. The inlet stream's flow is probably less than 900 cubic cm/sec during summer dry spells (personal observation). The outlet stream is to the south.

2.1.3 Chemical Features

Most montane coastal lake waters of British Columbia are characterized by a low dissolved solids content averaging of 46 ppm (Northcote and Larkin, 1956). Many are as low as 25 ppm (Northcote and Larkin, 1963). They are mostly small, comparatively deep, mildly acidic and unproductive (Neill, 1981).

The chemical composition of Placid Lake water (Table 2) reflects the nature of the hard, erosion resistant bedrock, the high annual rainfall of the west coast climatic region and the
Table 2. Mean summer water chemistry values for Placid Lake (July-August, 1982). All values in ug/liter unless otherwise stated.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>* Total dissolved solids (ppm)</td>
<td>24.4</td>
</tr>
<tr>
<td>pH</td>
<td>6.25</td>
</tr>
<tr>
<td>Total phosphorous</td>
<td>6.20</td>
</tr>
<tr>
<td>Total dissolved phosphorous</td>
<td>5.0</td>
</tr>
<tr>
<td>Soluble reactive P (ortho-P)</td>
<td>&lt;3.0</td>
</tr>
<tr>
<td></td>
<td>(range 1-15)</td>
</tr>
<tr>
<td>Total Kjeldahl nitrogen</td>
<td>220</td>
</tr>
<tr>
<td>Nitrate nitrogen</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>(range &lt;20-140)</td>
</tr>
<tr>
<td>Nitrite nitrogen</td>
<td>&lt;5.0</td>
</tr>
<tr>
<td>Ammonia nitrogen</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>(range 6-130)</td>
</tr>
<tr>
<td>Organic nitrogen</td>
<td>164</td>
</tr>
<tr>
<td>Specific conductivity (umhos/cm @ 25 C)</td>
<td>16.2</td>
</tr>
<tr>
<td>Color (Pt units)</td>
<td>25</td>
</tr>
<tr>
<td>Secchi disc depth (m)</td>
<td>6.0</td>
</tr>
<tr>
<td>* Total alkalinity (ppm CaCO3)</td>
<td>6.3</td>
</tr>
<tr>
<td>* Free CO2 (ppm CaCO3)</td>
<td>24.5</td>
</tr>
<tr>
<td>Hypolimnetic O2 (mg/liter @ 5m)</td>
<td>5.1</td>
</tr>
</tbody>
</table>

* Data from Shepherd (1973) for August 3 1972
shallow soils of the area. The total dissolved solid content of the mid-summer epilimnion (upper 4 m) averages 24 ppm. Nutrient concentrations are particularly low, especially soluble reactive phosphorous (PO$_4^-$-P). Only on one occasion was PO$_4^-$-P measurable in large quantities in the waters of the lake (15 ug/liter) and that was in the upper 2 m during a heavy rainfall. Feller (1977) gives measurements of PO$_4^-$-P in precipitation (as rain) as high as 40 ug/liter and ortho-P values much higher in surface runoff in unlogged watersheds. I suspect that much of this nutrient in the rain is a result of prevailing winds picking up dry, nutrient rich dust and fertilizer residues from the farmland of the Fraser River valley to the south. Since precise information about the size of tributary watersheds, stream discharge, surface runoff and groundwater supply was not available, I did not attempt to calculate a nutrient budget for the lake. However, considering Feller's data, it is likely that infrequent high nutrient input events might occur during periods of rainfall in the dryer months of the year. Krause (1984) gives a very rough estimate of nutrient input to the lake, and her data suggest that nutrient supply to the lake is generally very low (eg., a mean of 0.47 ug/liter of phosphorous for the month of August in 1982).

Nitrogen appears to be in good supply relative to phosphorous, with the nitrogen species most utilized by phytoplankton (NH$_4^+$ and NO$_3^-$) occurring at a ratio of about 40:1 nitrogen to phosphorous (as PO$_4^-$-P) at spring overturn. However, very shortly after spring overturn (within 1-2 weeks), inorganic
nitrogen concentrations are sharply reduced.

The water is only lightly colored and very slightly acidic. The mean pH in 1982 (6.25) was somewhat higher than that quoted by Shepherd (1973) for August 1973, (5.75), but is in line with other lakes in the area (Efford, 1963, Marmorek, 1983). It is possible that Shepherd's pH values were taken near the edge of the Sphagnum mats where pH around the plants may be as low as 4.5 (Clymo, 1966). Secchi disc depth is always at or near the maximum depth of the lake. Free CO$_2$ is the dominant form of available inorganic carbon. Alkalinity is low (0.13 meq/liter).

2.1.4 Flora

The watershed lies within the dry subzone of the Coastal Western Hemlock biogeoclimatic zone of British Columbia (Efford, 1967). The area was logged in the 1950's and is now covered mostly by second growth Western Hemlock, Douglas-fir, red alder and some white birch. Feller (1977) gives a description of common understory species in these forests.

The dominant vegetation around and in the lake are species typically associated with Sphagnum mats. Bog cranberry (Vaccinium oxycoccus) and Labrador tea (Ledum groenlandicum) were the most common plant found growing on the Sphagnum. In the lake, submersed macrophytes include Potamogeton natans, Scirpus subterminalis, and Depanocladus exannulatus (Shepherd, 1973, Figure 3). Water lilies, Nuphar polysepalum, can be found in small stands all around the shoreline.

The phytoplankton species number in the hundreds but only
those that were encountered in water column samples were recorded (Appendix 1). Appendix 1 may not be a complete account of the limnetic plankton species but the major genera are represented. The phytoplankton assemblage is characteristic of oligotrophic lakes (Hutchinson, 1967; Wetzel, 1975) and includes such indicator organisms as the chrysophyceans (Dinobryon sp., Mallomonas, Synura sp., Oochromonas sp.), chlorophyceans (Botryococcus, Sphaerocystis and Gloeocystis). Numerically, the dominant phytoplankters are small green flagellates of the genus Chlamydomonas and small chlorococcoids.

Mid-summer dominants which make up more than 30% of the phytoplankton biomass, include several species of chrysophytes and cyanophytes. Seasonally, the numerically abundant chrysophytes include Dinobryon (spring, summer and fall), Synura (late summer), Chrysophaella longispina (mid summer) and Oochromonas (all summer). Cyanophytes become more dominant late in summer and early fall when lake N:P ratios drop considerably (< 15:1, N:P). They are always moderately abundant throughout the summer.

2.1.5 Fauna

Only fauna directly linked to this study are mentioned below: avian predators on fish, the fish, other aquatic vertebrates and zooplankton. Benthic fauna were not studied. Although nymphs and larval stages of several major groups of aquatic insects occur in the lake, they were rarely encountered in samples taken from the water column, so they too are not
considered.

Avian predators on the fish consisted of two species, the Belted Kingfisher (*Megaceryle alcyon*) and the Great Blue Heron (*Adrea herodias*). A single pair of kingfishers appeared to be residents at the lake, and appeared to regularly patrol its surface several times each day. Occasionally, a heron would appear on the lake during the early mornings and in the late afternoons. Both species were observed capturing adult and juvenile fish from the littoral zone of the lake. No piscivorous mammals were observed in the watershed, but evidence of long abandoned "otter slides" suggests they were once present.

The aquatic fauna are listed in Table 3. The sole fish species is cutthroat trout (*Salmo clarki clarki*). Shepherd (1973) made Schnabel estimates by trap netting and diving and estimated the population at around 300, consisting mostly of 2 and 3 year old individuals. The fish are small (3+ fish attain a mean fork length of 23 cm), and slender (mean body depth at front of dorsal fin, 4.2 cm.) suggesting that growth is food limited.

Salamanders of the species *Taricha granulosa* are common in the lake. Salamanders do not normally persist in water bodies containing fish (Zaret, 1980), though Sprules (1974) found *Ambystoma* and fish in several British Columbia lakes and ponds. Neish (1970) found both *Ambystoma gracile* and *Taricha granulosa* in Marion Lake, which also contains fish. These salamanders are nocturnal feeders, a strategy probably developed to avoid fish
Table 3. Faunal characteristics of Placid Lake. Crustacean zooplankton densities are mean densities for June to October 1982 for the entire water column.

<table>
<thead>
<tr>
<th>Fish</th>
<th>Population size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salmo clarki clarki</td>
<td>300 (Shepherd, 1973)</td>
</tr>
<tr>
<td>Others</td>
<td></td>
</tr>
<tr>
<td>Salamander Taricha granulosa</td>
<td>350 (approximately)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Crustacean zooplankton</th>
<th>Density No./liter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia rosea</td>
<td>2.5</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>2.3</td>
</tr>
<tr>
<td>Diaphanosoma brachyurum</td>
<td>2.4</td>
</tr>
<tr>
<td>Polyphemus pediculus</td>
<td>0.08</td>
</tr>
<tr>
<td>Ceriodaphnia quadrangula</td>
<td>0.16</td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td>0.50</td>
</tr>
<tr>
<td>Scaphaloberis kingii</td>
<td>rare</td>
</tr>
<tr>
<td>Chydorus spp.</td>
<td>0.01</td>
</tr>
<tr>
<td>Diaptomus kenai</td>
<td>0.01</td>
</tr>
<tr>
<td>Diacyclops thomasi</td>
<td>3.9</td>
</tr>
<tr>
<td>Tropocyclops prasinus</td>
<td>rare</td>
</tr>
</tbody>
</table>
predation. *Taricha granulosa* has a skin toxin which may make protect it from predation by the cutthroat trout in Placid Lake.

The zooplankton in Placid Lake (Table 3) are the same assemblage that occurs throughout the region (Northcote and Clarotto, 1975) independent of fish composition or fish abundance (Neill, 1981). This assemblage differs from lake to lake only in the co-existing copepod species. The zooplankton biomass is generally dominated by the filter-feeding cladocerans *Holopedium gibberum* and *Daphnia rosea*.

2.2 Experimental Methods

2.2.1 Limnocorral Design and Installation

Eight large limnocorrals were installed in Placid Lake in early May, 1982. The purpose of these enclosures was to isolate sections of the nearshore (from here on referred to as "littoral") and offshore (from here on referred to as "limnetic") zones of the lake from the main body of the lake. It was hoped that the same physical, chemical and biological processes occurring in the lake would manifest themselves within the enclosed areas.

The enclosures were constructed of translucent, 10 mil polyethylene sheeting suspended from tubular floats made from p.v.c. plastic irrigation pipes, 3m long and 15 cm in diameter placed end on end (Figure 4a). The pipes were "sealed" by gluing 15 cm diameter p.v.c. plastic discs over the open ends making them watertight and buoyant. The lengths of pipe were
Figure 4. Limnocorral design
Figure 4. Design of the enclosure frames and method of attaching one enclosure to the other.

(a) Enclosure Frame

Wooden Braces
2m X 0.05m X 0.10m

p.v.c. plastic pipes
3m X 0.15m

6 mm Nylon Lashing
Double Wrap Around
2 per side

(b) Attaching one enclosure to the other.

Enclosure 1 lain flat

Enclosure 2

0.5 m overlay

10 m
15 m
then enclosed in a prefabricated "collar" constructed by folding over the top 1m of plastic sheeting and sealing it to the main enclosure body with a hot pressing iron. The pipes were lashed together using 180 cm wooden two by fours to lend an element of rigidity to the structure. Elbow joints made of 15 cm dia p.v.c. plastic were used at corner joints.

The enclosures measured 10 m wide by 15 m long by 9 m deep (3 m deeper than the lake) and were sealed into the lake sediments so as to leave the area (m$^2$) of exposed sediments equal to the surface area of the enclosures. The bottoms of the enclosure walls were sealed into the sediments and anchored by placing granite boulders (weighing 10 - 15 kg each) every 0.5 m along the bottom of the enclosure sides. Since the bottom sediments were a flocculent gytta, the weight of the boulders caused the plastic to sink about 0.5 m into the mud, effecting a complete seal. Roughly 2m of excess sheeting was left as slack in the sides to allow the enclosures to rise and fall with fluctuating lake levels (recall that the lake level could rise as much as 1.5 m in less than 24 hours during a heavy rain).

The enclosures were positioned in the lake so as to make them as morphometrically as similar as possible (see Figure 3) given the problems of logs protruding out into the water column. The littoral enclosures were also placed in areas where the Sphagnum mat around the lake was not undercut. The littoral enclosures were sealed to the face of the Sphagnum mat by driving large wooden tent stakes through the plastic and into the mat. The "limnetic" enclosures were heat sealed, on land,
to the outer margins of the "littoral" enclosures (Figure 4b).

The enclosures were assembled at a wooden dock at the east end of the lake. Upon installation, the sides of the enclosures were lashed to the flotation frame and small rocks were tied to that part of the plastic sheet that was to be the bottom of the walls. The enclosures were then towed into place by boat and secured to shore. The "skirt" weights were then freed so that they would sink to the bottom, thus enclosing the existing water column. Divers then sealed the bottom edges into the sediments. Subsequent sampling for phytoplankton and zooplankton showed that all species existing in the open lake water were proportionally and numerically represented in all of the enclosures.

2.2.2 Experimental Treatments

The eight enclosures were arranged into two location blocks (littoral vs limnetic, 4 each), and two of the enclosures within each block were treated with fertilizer. The other four enclosures served as controls (Table 4, Figure 3). Hatchery reared cutthroat trout fry were added to all eight enclosures in order to provide a standardized set of fish for growth and survival estimations; however those fish quickly disappeared from all of the enclosures.

The fertilizers used were commercial grade soluble diammonium hydrogen phosphate, \((\text{NH}_4)_2\text{HPO}_4\), and reagent grade soluble ammonium nitrate, \(\text{NH}_4\text{NO}_3\). All fertilized enclosures received weekly doses of 10 ug/liter of P and 400 ug/liter N
(Table 4). The fertilizers were dissolved in lake water and applied evenly over the surface area of the enclosures using a pressurized garden insecticide dispenser.

Considering the arrangement of the enclosures (each littoral plus limnetic unit divided by a thin plastic sheet), I feared possible contamination of an unfertilized enclosure should it be in juxtaposition with a fertilized enclosure. Hence, I sacrificed this element of randomization in assigning treatments to enclosures. Also, because one set of four enclosures was on the south side of the lake and the other set was on the northwest side (Figure 3), I felt that each location should have its own series of treatments and controls should this factor prove to be a significant source of variation in subsequent statistical analyses.

The fish added to each enclosure were progeny of adult trout captured from the lake by trap net in October of 1981. The young were reared at the Abbotsford Trout Hatchery (British Columbia Fish and Wildlife Branch) near Abbotsford, B.C. Based on an estimated fecundity of 120 eggs per female, 30 female and 10 male fish were taken as brood stock. I intended to stock each enclosure with 250 juvenile trout and have 1500+ fish for emergency purposes. Of the 30 females taken in late October 1981, 12 fish had already spawned, 5 fish were nearing spawning condition and the rest showed no evidence of being ready to spawn until the following January. Due to adult mortalities, discordant times of spawning, and juvenile mortalities, I finally had 427 cutthroat trout fry, half of which had been
Table 4. Experimental treatments.

<table>
<thead>
<tr>
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<td>58</td>
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<td></td>
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<td>8</td>
<td>698</td>
<td>5.0</td>
<td>&quot;</td>
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</table>

a) determined by transect depth sounding and calculation.

b) amount of nutrient added weekly from June 1 to September 30 1982. Total weekly additions were divided into three and added to enclosures on Monday Wednesday and Friday.

c) released into enclosures on June 14, 1982.
spawned in November 1981 and raised at cold temperatures (ca. 4 °C) to slow down growth, and half of which had been spawned in February 1982 and raised at high temperature (ca. 25 °C) so they could achieve sizes similar to their earlier spawned brethren.

2.2.3 Sampling Methods

Zooplankton, phytoplankton, plant pigment and water chemistry samples were all drawn from the enclosures by means of a 10 m long, 2.5 cm diameter clear plastic hose connected to a battery operated bilge pump that delivered 25 liters per minute. Zooplankton, phytoplankton and plant pigment samples were taken weekly. Water chemistry measurements were taken every two weeks. All samples were taken on a Tuesday between 11 a.m. and 2 p.m. Fifty liter (2 minute) samples were taken in a depth stratified regimen by pumping from the top, middle and bottom (respectively) of each of the following depth strata: 0-2, 2-4 and 4-6 m. In the case of an enclosure being only 5 m deep, a one minute sample was taken from the 4-5 m depth. The hose and bilge pump method of sampling has been shown to have excellent replicability and small sampling bias with respect to the zooplankton in the research forest lakes (Peacock, 1981; Neill, 1981; Marmorek, 1983).
Each fifty liter sample of water was pumped through a 90 um nytex mesh net fitted with a cod-end. Samples were preserved in a sucrose-formaldehyde mixture (Haney and Hall, 1975) and enumerated by species, size, sex, reproductive condition and number of eggs per female. Body size was estimated for the first twenty specimens of each species counted. Cladocerans were measured from the anterior tip of the carapace (excluding helmets or protuberances) to the most distal part of the carapace (excluding tail spines). Copepods were measured from the anterior tip of the cephalothorax to the most distal part of the urosome (excluding caudal rami). Samples with high zooplankton densities were subsampled using the splitting device described in Northcote and Clarotto (1975). Successive subsamples were counted until at least 200 individuals of each species were recorded. All samples were counted at 25X magnification with a Wild M5, binocular dissecting scope using a 10X ocular fitted with a micrometer.

Zooplankton biomass was estimated from the counts and measurements using a length-weight regression formula developed in our lab by D. Robinson and C.J Walters (unpublished). Normal probability plots and the g-statistics of these data indicated rejection of the hypothesis that these data came from a population whose members follow a normal distribution, therefore, to meet the assumptions of analysis of variance, the estimates were subjected to a log-transformation to correct for non-normality. The data were then analyzed using three-way
(time x treatment x location), two-way (time x treatment) and one-way (time) analyses of variance.

The overall mean lengths for each of the zooplankton categories **Daphnia rosea** (adults, juveniles and females with eggs), **Diaphanosoma brachyurum** (combined adults and juveniles) and **Diaptomus oregonensis** (adults, females and juveniles) were computed and the untransformed data subjected to a two factor (littoral-limnetic or fertilized-unfertilized) Kruskall-Wallis non-parametric one way analysis of variance.

The overall mean brood sizes of **D. rosea**, **D. brachyurum**, **H. gibberum**, **C. quadrangula**, **B. longirostris**, **Diaptomus oregonensis**, and **Diacyclops thomasi** were computed and the untransformed data subjected to the same test.

(2) Phytoplankton

Phytoplankton samples were taken from each of the three depth strata mentioned above. Water from each stratum was pumped through a 90 um nytext net (to remove large zooplankters and debris) into a 10 liter plastic bucket and swirled to ensure adequate mixing. A 100 ml glass jar was inverted into the bucket and a sample drawn and preserved in Lugol's solution. In the lab, a 60 ml subsample was left to stand in a 100 ml graduated cylinder to allow settling of the plankton for 36 hours, after which the top 40 ml was siphoned away. The remaining 20 ml were transferred to a 25 ml cylindrical, plexiglass counting chamber (5cm high, 2.5 cm dia., with a slide cover slip for the bottom), allowed to stand for a further 36
hours and subsequently counted using a Wild Model M-40 inverted microscope at 400X. The scope was equipped with a 10X ocular unit with a 100 μm² grid in the eyepiece.

Cells were enumerated and identified to genus and, where possible, to species. Edmondson (1956), Prescott (1962) and Stein (1975) were used for taxonomic identification. Up to twenty cells of each type were measured for maximum length and maximum width. Forty grids (each 100 μm²) were counted for each sample. Krause (1984) undertook intensive replicate counting using this method to determine the minimum number of fields and cells needed for quantitative accuracy. She found that 20 to 40 fields were required to achieve a ±5% accuracy (with 95% confidence) depending on cell size dimensions, with the larger cells requiring more fields. Krause set a standard of 30 fields. I have chosen 40 fields. If a species or category numbered 200 cells prior to 40 grids being counted, then further enumeration of that species or category was terminated. Once 40 grids had been counted, the entire chamber was scanned at 200X for rare and/or large forms.

Cell volumes were computed using measured maximum dimensions and the geometric shape (cylinder, sphere, fusiform, etc...) that most resembled each cell shape. Lengths of filaments were taken to the limit of the grid dimensions. Large diatoms were measured in their entirety. Dinobryon colony volumes were computed as the sum of the volumes of individual loricas. Colonies of cells were counted and measured as single cells. Algal cells were also classified according to their
maximum dimension into the following size classes: <2, 2-6, 6-10, 10-14, 14-20, 20-30, 30-40, 40-80, >80 um.

Total algal volumes were converted to biomass assuming all cells had a specific gravity of 1.0. Algal biomass estimates were log-transformed to correct for non-normality and subjected to two-way (time x location) and one-way (time) analyses of variance.

(3) Plant Pigments

Replicated (x2) 250 ml subsamples were taken from each pumped water sample, and filtered in the field using a small hand pump, 4.25 Whatman GF/C glass fiber filters and MgCO$_3$. The filters were folded, stored in the dark and frozen within 2 hours. The filters were later ground in 90 % acetone with the aid of a teflon Ter Meulin tissue grinder and left to sit refrigerated in the dark for 20-25 hours. Pigments were then measured flourometrically using a Turner Model 111 Flourometer. The flourometer was standardized with acetone extracts of commercially grown spinach leaves in which plant pigments had been determined spectrophotometrically. The results are expressed as total pigment, chlorophyll a and phaeophytin. All plant pigment data were transformed (1/square root) to correct for non-normality and subjected to three-way and two-way analyses of variance.
(4) Water Chemistry

For water chemistry, a 1 liter water sample was taken in a sterilized, opaque plastic bottle from each depth stratum. The samples were placed on ice in a 50 liter plastic garbage pail lined with black plastic and taken directly to the British Columbia Ministry of the Environment's environmental laboratory at B.C. Research on the University of B.C.'s campus. There, the samples were subjected to chemical analyses within 24 hours.

True color (Pt units), specific conductance (umhos/cm) and pH were all measured according to *Standard Methods* (1971). Total phosphorous and total dissolved phosphorous and orthophosphate were determined using the automated colorimetric: ascorbic acid reduction method according to *Standard Methods* with some modification (Brynjolfson, 1973). Total Kjeldahl nitrogen was quantified by the Nesslerization method. Determination of ammonia nitrogen was by the method of the automated Berthelot reaction (Technicon Instruments Corporation, Industrial Method No. 154-71W). Nitrate nitrogen plus nitrite nitrogen quantification involved the cadmium reduction method plus diazotization whereas singular Nitrite nitrogen was detailed by diazotization alone. Nitrate nitrogen was isolated by calculation ($\text{mg/l N}(\text{NO}_3) = \text{mg/l N}(\text{NO}_2+\text{NO}_3) - \text{mg/l N}(\text{NO}_2)$).

Temperature (°C) and oxygen (mg/l) were obtained weekly using a Yellow Springs Instruments Model 56 Oxygen-Temperature-Salinity meter. The oxygen probe was air calibrated and corrected for elevation. Data were taken starting at the surface and working down at successive 0.5 m intervals.
3.0 RESULTS

3.1 Physical Parameters

3.1.1 Temperature

Summer temperature profiles for Placid Lake in 1982 demonstrate a weak, unstable pattern of stratification (Figure 5). Warming of surface waters began in early June resulting in the onset of stratification. A weak thermocline was established at about 3.5 m by mid-June. A two week period (June 30 - July 15) of cool, clear weather resulted in cooling of the epilimnetic waters from 20 °C to 16 °C eliminating stratification. The period following was characterized by alternating phases of (1) calm conditions, during which microstratification developed within superficial layers, and (2) more disturbed phases, when the epilimnion became more homogeneously mixed. Around August 3-5 a heavy rain caused the newly stratified layer to destabilize, allowing whole or partial mixing of the lake water while reducing epilimnetic temperatures once again. Towards late August, microstratification was again established at about 2m. Then another period of cool weather and heavy rain (September 8-12) resulted in decreased epilimnetic temperatures which persisted until a definite autumnal circulation occurred in late September. There appeared to be a stable water mass at about 4m which would probably represent the upper limits of the metalimnion in a deeper lake, so for lack of a better distinction, waters above 4 m were
Figure 5. Placid Lake water temperatures (degrees Celsius) for summer 1982
designated the epilimnion and waters below 4m, the hypolimnion. This seasonal temperature pattern was identical for all enclosed waters, thus only one temperature profile is presented.

3.1.2 Dissolved Oxygen

Seasonal dissolved oxygen (DO) profiles were similar in all control enclosures and the lake (Figure 6). The waters were well oxygenated at all depths throughout the season except during late September at 6m (just above the mud-water interface) in the lake and in control enclosure 2, when a short period of near anoxia occurred (0.6 mg/liter, 0.6% saturation). The DO concentration throughout the summer in the control enclosures and the lake ranged from 8-12 mg/liter (55-100 % saturation) to a depth of 3 m, to 2-4 mg/liter (20-40 % saturation) below 4 m.

The DO profiles for the fertilized enclosures (Figure 6) differed from the control enclosures in two ways. First, dissolved oxygen concentrations in the upper four meters were considerably higher than in controls. Second, all fertilized enclosures exhibited near anoxia within 0.5 m of the bottom in late September. The littoral fertilized enclosures differed little from the controls with respect to epilimnetic DO concentrations. Enclosure 3 exhibited an extended epilimnetic maximum of 11 mg/liter (120 % saturation) through late July and all of August. Enclosure 7 approximated the control series. The limnetic fertilized enclosures had significantly higher epilimnetic DO concentrations than controls (mean 12 mg/liter, 125 % saturation) with values reaching as high as 14 mg/liter.
Figure 6. Depth-time isopleths of dissolved oxygen. Values are mg/liter.
Dissolved Oxygen µg/L

Enclosure 1
(littoral control)

Enclosure 3
(littoral fertilized)

Enclosure 2
(limnetic control)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 7
(littoral fertilized)

Enclosure 6
(limnetic control)

Enclosure 8
(limnetic fertilized)
Distinct DO maxima were present in enclosures 3 and 8 at about 3-4 m in late August.

3.1.3 Transparency

Control enclosures and the lake did not differ markedly in their transparency. The Secchi disc was usually visible on the bottom of the lake but disc visibility was slightly reduced in the lake and limnetic control enclosure 2 in early August (Figure 7). Secchi disc visibility in the fertilized enclosures changed dramatically compared to controls following fertilization. Secchi disc depths began to decrease in August, reaching 3.0 m in the littoral fertilized enclosures and 1.5-2.0 m in the limnetic fertilized enclosures.

3.1.4 Summary of Physical Results

In summary, there were no major differences in temperature, dissolved oxygen and Secchi disc visibility profiles between the control enclosures and the lake. Note too, that these parameter profiles were similar for both littoral and limnetic control enclosures. The similarities in temperature and DO suggest that wind mediated mixing and diffusion that occurred in the lake also occurred in the enclosures. Super-saturated oxygen concentrations were recorded in the epilimnia of the fertilized enclosures. Also, hypolimnetic oxygen depletion extended further into the water column in the fertilized enclosures than in controls. Secchi disc visibility began to change as a result
Figure 7. Secchi disc depths
Secchi depth (m)

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
of the fertilization in mid-August. Changes in disc visibility were more pronounced in the limnetic than in the littoral fertilized enclosures.

3.2 Chemical Parameters

3.2.1 Conditions in Lake Waters

Concentrations of dissolved inorganic and dissolved and particulate organic nutrients in Placid Lake were low in 1982, in the range for ultra-oligotrophic lakes proposed by Vollenweider (1968).

Soluble reactive phosphorous (SRP) was undetectable (<3 ug/liter) in the water column on almost all occasions (Figure 8). Low level orthophosphate analysis performed on June 22 samples revealed that, on that date, <3 ug/liter was in fact <1 ug/liter. Measurable quantities of SRP were detected only in the early part of the summer, and in the epilimnion during two separate storm events in August and September. (The inability to detect this nutrient made it difficult to evaluate vertical and chronological changes in concentration over the summer, however, when the nutrient did occur in detectable quantities, its concentration was uniform over all depths. The observation that concentrations of the inorganic and organic fractions of other, detectable, nutrients did not change with depth suggests that uniformity over depth also occurred for SRP over the entire season.)

Total dissolved phosphorous (TDP) (Figure 9) and
Figure 8. Depth-time isopleths of ortho-phosphate. Values are ug/liter.
Ortho-phosphate ug/L

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
particulate phosphorous (PP) (Figure 10) concentrations in the lake ranged from 3-8 and 1-5 ug/liter, respectively. Highest concentrations of these nutrients occurred in the epilimnion during rain events. Values of PP were also high in the hypolimnion, which may be indicative either of seston sedimentation or of deep-water phytoplankton production.

Nitrate nitrogen (NO$_3$-N) (Figure 11) was undetectable (<20 ug/liter) on almost all occasions. Nitrite nitrogen (NO$_2$-N) never exceeded 5 ug/liter, the analytical limit of detection. Seasonally, ammonia (NH$_3$-N) concentrations (Figure 12) ranged from 5-20 ug/liter. Concentrations of NH$_3$-N were lower in late summer than in early summer, probably as a result of depletion by mid to late summer blooms of algae. There was also evidence of hypolimnetic accumulation of NH$_3$-N during a short period of low oxygen concentrations near the bottom in the latter part of summer. Total nitrogen (TKN) (Figure 13) and total organic nitrogen (TON) (Figure 14) concentrations were always < 200 ug/liter. The highest concentrations of TON (average 190 ug/liter) occurred in the hypolimnion from August to September.

The pH of the water column (Figure 15) was circumneutral (6.0 - 7.0) and was nearly constant over all depths and over time. It increased slightly during mid-summer as compared to early summer.
Figure 9. Depth-time isopleths of total dissolved phosphorous. Values are ug/liter.
Total Dissolved P (ug/L)

Enclosure 1 (littoral control)

Enclosure 2 (limnetic control)

Enclosure 3 (littoral fertilized)

Enclosure 4 (limnetic fertilized)

Enclosure 5 (littoral control)

Enclosure 6 (limnetic control)

Enclosure 7 (littoral fertilized)

Enclosure 8 (limnetic fertilized)
Figure 10. Depth-time isopleths of particulate phosphorous. Values are ug/liter.
Particulate P ug/L

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
Figure 11. Depth-time isopleths of nitrate nitrogen. Values are ug/liter.
Nitrate Nitrogen ug/L

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
Figure 12. Depth-time isopleths of ammonia nitrogen. Values are ug/liter.
Ammonia Nitrogen ug/L
Figure 13. Depth-time isopleths of total Kjeldahl nitrogen. Values are ug/liter.
Total Kjeldahl Nitrogen ug/L
Figure 14. Depth-time isopleths of organic nitrogen. Values are ug/liter.
Organic Nitrogen ug/L

Enclosure 1
(littoral control)

Enclosure 3
(littoral fertilized)

Enclosure 2
(limnetic control)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 7
(littoral fertilized)

Enclosure 6
(limnetic control)

Enclosure 8
(limnetic fertilized)
Figure 15. Depth-time isopleths of pH. Note the change in scale of the Y-axis on the plots for the limnetic fertilized enclosures.
Hydrogen ion Concentration

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
3.2.2 Effects of Enclosure

There were no detectable changes in any of the chemical characteristics of the lake water as a result of enclosure and isolation from the main lake. Chemical profiles for all nutrients and pH in the unfertilized control enclosures mirrored those presented for the lake over the entire season (Figures 8 - 15).

3.2.3 Effects of Fertilization

(1) Phosphorus

Addition of approximately 10 ug PO$_4$-P/liter (of epilimnion water) per week, divided into three equal doses, resulted in detectable levels of SRP in all of the fertilized enclosures (Figure 8). Early summer epilimnetic SRP concentrations were strikingly close to the amounts I was adding on a weekly basis (10 ug/liter). In July, micro-stratification of the epilimnion resulted in a sharp density gradient at about 2 m (Figure 5). This may explain why the in situ concentrations of SRP in the 0-2 m range doubled to 20 ug/liter in the limnetic fertilized enclosures (Figure 8). This increase suggests that the added phosphate was not immediately incorporated into the seston. Concentrations of SRP became undetectable in the fertilized enclosures from mid-August to the end of the season even though fertilizer was still being added at the same rate and concentrations as before.
The two littoral fertilized enclosures exhibited little variation in TDP or SRP content with depth (Figure 8 and 9). Early summer TDP (8-10 ug/liter) values, however, were higher than in controls in proportion to increases in levels of detectable SRP. Late summer TDP and SRP concentrations were lower (5-8 ug/liter and <3 ug/liter, respectively) and similar to those found in the controls and lake for the same period.

The seasonal profiles of TDP and SRP concentrations in the two limnetic fertilized enclosures were identical to those in the littoral enclosures. However, early summer TDP (20-30 ug/liter) concentrations were 7.5 times control values but decreased (8-9 ug/liter) to only double lake values in late summer. Early summer SRP values (20 ug/liter) decreased from over 20 times control values to equal late summer control values (<3 ug/liter).

Particulate phosphorous fractions (Figure 10) increased in all fertilized enclosures during late summer. These increases were paralleled by the disappearances of available P (SRP, TDP). The average increase in PP of the littoral fertilized enclosures was up to 3 times (6-9 ug/liter) higher than in the two littoral controls. Increases in the PP concentrations in the two limnetic fertilized enclosures were up to 10 times (25-30 ug/liter) higher than in the two limnetic controls.
(2) Nitrogen

Total nitrogen (TKN) concentrations in all of the fertilized enclosures were higher than in the controls over the entire season (Figure 14). Maximum epilimnetic concentrations of TKN occurred in the latter part of the summer. Concentrations in the littoral fertilized enclosures reached 300 ug/liter, almost double control values. Epilimnetic values in the limnetic fertilized enclosures reached 600 - 650 ug/liter, four times higher than control values and twice as high as in the littoral fertilized enclosures. These late summer increases in TKN were chiefly due to large increases in the organic fractions of nitrogen, and were coincident with increased phytoplankton production. The uniformity of nutrient concentrations with depth in early August confirms my earlier suggestion that almost complete mixing of the water column can occur in this lake during summer storm events.

Concentrations of NO$_3$-N in the fertilized enclosures increased dramatically following fertilization (Figure 11). Epilimnetic NO$_3$-N concentrations ranged from 100 - 200 ug/liter and 300 - 500 ug/liter in the littoral fertilized and limnetic fertilized enclosures, respectively. NO$_3$-N accumulated more in the limnetic than in the littoral fertilized enclosures as the season progressed (100 - 500 ug/liter), but rapidly declined to normal lake levels at fall overturn (early October). Since 180 ug/liter of NO$_3$-N were added weekly, only a small percentage remained in solution; however, build up of NO$_3$-N was still progressive over the summer.
The NH₄-N added (as NH₄NO₃ and (NH₄)₂HPO₄) to the fertilized enclosures resulted in higher epilimnetic levels of NH₄-N beginning immediately after initiation of fertilization on June 1st, 1982 (Figure 12). 220 ug/liter of NH₄ were added weekly, so, as was the case for NO₃, only a small percentage remained in solution. Levels of NH₄-N in the littoral and limnetic fertilized enclosures were, respectively, 3-5 and 20-25 times higher than in controls during the early summer. Though there was some accumulation of the nutrient in epilimnetic waters in June and July, the nutrient disappeared rapidly from the system after addition, much more rapidly in the littoral than in the limnetic enclosures.

Seasonal total organic nitrogen (TON) concentrations in the fertilized enclosures differed substantially from control values (Figure 13). The epilimnetic concentrations of TON in late summer reached 200-250 ug/liter in the littoral fertilized enclosures and 400-500 ug/liter in the limnetic fertilized enclosures, 2-2.5 and 4-5 times higher than in their respective controls.

(3) Hydrogen Ion Concentration

Hydrogen ion concentrations (pH) in both the littoral and limnetic fertilized enclosures did not change, compared to controls, following nutrient addition (Figure 15).
3.2.4 Summary of Chemical Results

Enclosure had no detectable effect on the distributions or concentrations of the major nitrogen and phosphorous fractions in the water column. However, chemical changes resulting from nutrient addition were evident in all fertilized enclosures, and were greater in the limnetic than in the littoral enclosures.

Major responses to fertilization occurred in the particulate nitrogen and phosphorous fractions, and in the conspicuous accumulations of ammonium and nitrate nitrogen in the limnetic fertilized enclosures.

Additions of 10 ugP/liter of epilimnion/week, made in 3 equal doses weekly, resulted in detectable levels of SRP in the water column until mid-August when phytoplankton demands apparently exceeded supply. Most of the added phosphate ended up in the particulate fraction, although slight increases occurred in the total dissolved P fraction in the limnetic fertilized enclosures.

Concentrations of added nitrate increased dramatically soon after fertilization, often exceeding 100 and 300 ug/liter in the littoral and limnetic fertilized enclosures, respectively. Concentrations of nitrate remained high until fall overturn in mid-October. Similarly, epilimnetic concentrations of added ammonia increased soon after fertilization, exceeding 50 ug/liter and 200 ug/liter in the littoral and limnetic enclosures. However, concentrations of this nutrient had decreased significantly by the end of August.

Hydrogen ion concentration in the epilimnion did not change
as a result of either enclosure or fertilization.

3.3 PHYTOPLANKTON STANDING CROP, SPECIES AND SIZE COMPOSITION

3.3.1 Standing crop

(1) Effects of Enclosure

Total algal biomass as determined by cell volumes did not exceed 400 ug/liter (Figure 16) and did not differ significantly between lake and the control enclosures (Table 5). Mid-summer maximum chlorophyll a concentrations in both the lake and controls did not exceed 0.6 - 0.8 ug/liter (Figure 17 and Table 6). Concentrations of chlorophyll a increased with increasing depth (Table 6) (significant at p < 0.05). Seasonal mean standing crops at all depths in the controls were not significantly different from those in the lake or between littoral and limnetic controls (Table 7). Seasonal fluctuations in chlorophyll a in each of 3 depth strata in the controls were in phase with those occurring at all depths in the lake (Figures 18 - 20), differing only slightly in the magnitude of change. Mean summer standing crops in 1982 (0.44 ± 0.04 ug/liter and 0.40 ± 0.02 ug/liter for the lake and controls, respectively) were similar to those in 1980 and 1981 in nearby Eunice Lake (0.39 ± 0.05 ug/liter, Marmorek, 1983).

Significant differences in the concentrations of phaeophytin a and total pigment in the 2-4 m stratum were noted in the control vs lake comparison (Table 7). This difference
Figure 16. Algal biomass as determined by cell volume.
Table 5: Results of one way analysis of variance on total biomass of phytoplankton (not excluding detritus) in the 0-2 m depth stratum as determined by cell volumes. Numbers in brackets are probabilities of no significant treatment effect (F_1, i) for lake vs control means, F_1, oo for control vs fertilized means, and F_1, oo. Data for the Littoral fertilized vs Limnetic fertilized comparison were not transformed because the large standard deviation (11478) associated with the mean for the limnetic fertilized enclosure precluded analysis by transformation.

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<th>Limnetic Controls</th>
<th>Littoral Fertilized</th>
<th>Limnetic Fertilized</th>
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<td>891 ± 1.20</td>
<td>705 ± 1.22</td>
<td>1914 ± 1.21</td>
<td>3027 ± 1.36</td>
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<th>Littoral Control vs Littoral Fertilized</th>
<th>Littoral Control vs Limnetic Control</th>
<th>Littoral Control vs Littoral Fertilized</th>
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<td>ns (0.331)</td>
<td>F (0.000)</td>
<td>ns (0.333)</td>
<td>Lim (0.004)</td>
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ns = not significant at \( \alpha = 0.05 \)

F, Litt., Lim, or C = interaction significant at \( \alpha = 0.01 \)
Figure 17. Depth-time isopleths of Chlorophyll a. Values are ug/liter.
Chlorophyll a µg/L

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
Table 6. Mean seasonal concentrations of plant pigments at all depths and in all treatments ± SE (ug/liter).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment arithmetic means ± SE (ug/liter)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Depth (m)</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td></td>
</tr>
<tr>
<td>0-2</td>
<td>0.36 ± 0.032</td>
</tr>
<tr>
<td>2-4</td>
<td>0.40 ± 0.038</td>
</tr>
<tr>
<td>4-6</td>
<td>0.56 ± 0.141</td>
</tr>
<tr>
<td>Phaeophytin a</td>
<td></td>
</tr>
<tr>
<td>0-2</td>
<td>0.49 ± 0.012</td>
</tr>
<tr>
<td>2-4</td>
<td>0.71 ± 0.041</td>
</tr>
<tr>
<td>4-6</td>
<td>1.20 ± 0.169</td>
</tr>
<tr>
<td>Total Pigment</td>
<td></td>
</tr>
<tr>
<td>0-2</td>
<td>0.85 ± 0.032</td>
</tr>
<tr>
<td>2-4</td>
<td>1.10 ± 0.065</td>
</tr>
<tr>
<td>4-6</td>
<td>1.76 ± 0.200</td>
</tr>
<tr>
<td>ALL</td>
<td>1.24 ± 0.106</td>
</tr>
</tbody>
</table>
Table 7. Results of analysis of variance on $1/\sqrt{\text{of treatment means}}$ shown in Table 6. Numbers in brackets are probabilities of no significant treatment effect ($F_{i,j,k}$ for lake vs control grand means, $F_{i,j,k}$ for lake vs control depth means, $F_{i,j,k}$ for control vs fertilized grand means, $F_{i,j,k}$ for control vs fertilized depth means, $F_{i,j,k}$ for all other grand means, and $F_{i,j,k}$ for all other depth comparisons).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment Comparison</th>
<th>Depth (m)</th>
<th>Lake Control vs Control Fertilized</th>
<th>Littoral Control vs Control Fertilized</th>
<th>Littoral Control vs Limnetic Control Fertilized</th>
<th>Limnetic Control vs Limnetic Fertilized</th>
</tr>
</thead>
<tbody>
<tr>
<td>$1/\sqrt{\text{Chl a}}$</td>
<td>0-2</td>
<td>ns (0.350)</td>
<td>F (0.000)</td>
<td>ns (0.640)</td>
<td>Lim (0.002)</td>
<td>F (0.000)</td>
</tr>
<tr>
<td></td>
<td>1/2-4</td>
<td>ns (0.060)</td>
<td>F (0.000)</td>
<td>ns (0.070)</td>
<td>Lim (0.000)</td>
<td>F (0.000)</td>
</tr>
<tr>
<td></td>
<td>4-6</td>
<td>ns (0.860)</td>
<td>F (0.000)</td>
<td>Lim (0.020)</td>
<td>Lim (0.030)</td>
<td>ns (0.310)</td>
</tr>
<tr>
<td></td>
<td>ALL</td>
<td>ns (0.580)</td>
<td>F (0.000)</td>
<td>ns (0.058)</td>
<td>Lim (0.000)</td>
<td>F (0.000)</td>
</tr>
<tr>
<td>$1/\sqrt{\text{Phae a}}$</td>
<td>0-2</td>
<td>ns (0.690)</td>
<td>F (0.000)</td>
<td>Litt (0.005)</td>
<td>Lim (0.000)</td>
<td>F (0.000)</td>
</tr>
<tr>
<td></td>
<td>1/2-4</td>
<td>C (0.006)</td>
<td>F (0.000)</td>
<td>Litt (0.008)</td>
<td>Lim (0.000)</td>
<td>F (0.040)</td>
</tr>
<tr>
<td></td>
<td>4-6</td>
<td>ns (0.570)</td>
<td>F (0.000)</td>
<td>ns (0.660)</td>
<td>Lim (0.000)</td>
<td>ns (0.290)</td>
</tr>
<tr>
<td></td>
<td>ALL</td>
<td>ns (0.400)</td>
<td>F (0.000)</td>
<td>Litt (0.020)</td>
<td>Lim (0.000)</td>
<td>F (0.000)</td>
</tr>
<tr>
<td>$1/\sqrt{\text{Total Pigment}}$</td>
<td>0-2</td>
<td>ns (0.470)</td>
<td>F (0.000)</td>
<td>ns (0.160)</td>
<td>Lim (0.000)</td>
<td>F (0.000)</td>
</tr>
<tr>
<td></td>
<td>1/2-4</td>
<td>C (0.005)</td>
<td>F (0.000)</td>
<td>ns (0.220)</td>
<td>Lim (0.000)</td>
<td>F (0.030)</td>
</tr>
<tr>
<td></td>
<td>4-6</td>
<td>ns (0.600)</td>
<td>F (0.000)</td>
<td>ns (0.790)</td>
<td>Lim (0.001)</td>
<td>ns (0.120)</td>
</tr>
<tr>
<td></td>
<td>ALL</td>
<td>ns (0.380)</td>
<td>F (0.000)</td>
<td>ns (0.330)</td>
<td>Lim (0.000)</td>
<td>F (0.000)</td>
</tr>
</tbody>
</table>

ns = not significant at $\alpha = 0.05$
F, Litt, Lim, or C = interaction significant at $\alpha = 0.01$
Figure 18. Cumulative concentrations of chlorophyll a and phaeophytin a in the 0-2 m depth stratum. Note the change in scale of the Y-axis on the plots for the limnetic fertilized enclosures.
LEGEND

- Chlorophyll a
- Phaeopigments

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
Figure 19. Cumulative concentrations of chlorophyll a and phaeophytin a in the 2-4 m depth stratum. Note the change in scale of the Y-axis on the plots for the limnetic fertilized enclosures.
Figure 20. Cumulative concentrations of chlorophyll a and phaeophytin a in the 4-6 m depth stratum
can be entirely attributed to higher phaeophytin values which appeared at that depth in the controls (Table 6, Figure 19). This may have been caused by seston settling out of the epilimnion and decomposing on the thermal discontinuity barrier at 3.5-4 m.

Concentrations of phaeophytin a were significantly higher overall in the littoral compared to the limnetic control enclosures (Tables 6 and 7). This difference was particularly due to higher mean phaeophytin a concentrations at 0-2 and 2-4 m in the littoral enclosures (Figure 18 and 19). The mean value for these enclosures is forced upward by the slightly higher concentrations of phaeophytin a in littoral enclosure 5 compared to littoral enclosure 1 at both of these depths. These higher concentrations were likely caused by wind generated resuspension of littoral sediments in control enclosure 5. Enclosure 5 had a gently sloping bottom with a near shore depth of only 0.25 m compared to its counterpart, littoral control enclosure 1, which had a 1 m drop to the sediments in the near shore area. Thus, a greater area of littoral sediment in enclosure 5 was exposed to turbulent mixing by wind generated currents, thus resulting in higher concentrations of suspended particulate matter.

The exceptionally high value of phaeophytin a at 4-6 meters on August 17th in enclosure 6 (Figure 20) was a result of contamination of the sample with bottom sediments that were sucked up by the pump.

Variations in the live chlorophyll a as a percentage of the total plant pigment concentration may be an index of viability
for the algal population. Temporal or spatial reductions in the percentage of live chlorophyll can be an indication that a greater proportion of the algal population is dying off at some times or in some places. Temporal fluctuations in the percentage of live chlorophyll a in the controls did not differ from those occurring in the lake (Figure 21). Seasonal means were not significantly different between littoral and limnetic controls or between controls and the lake (Table 8). However, the mean percentage of live chlorophyll a decreased significantly at 4-6 m both in the controls (39.0 ± 1.9% at 0-2 m, 37.0 ± 2.6% at 2-4 m, and 28.0 ± 1.8% at 4-6 m) and in the lake (38.8 % at 0-2 m, 35.0 % at 2-4 m, and 29.5 % at 4-6 m). This pattern suggests that while the biomass of phytoplankton as measured by chlorophyll a was greatest in the hypolimnion (Table 6), a greater percentage of that biomass may have existed as nonfunctional pigment in the form of decomposing detritus. Many of the cells in the hypolimnion may have been dead or dying.

(2) Effects of Fertilization

Phytoplankton standing crops increased several fold after fertilization (Figures 16 and 17). An epilimnetic maximum concentration of 15 ug Chl a/liter was reached in the limnetic fertilized enclosures in late August.

Maximum epilimnetic concentrations of chlorophyll a in the littoral fertilized enclosures averaged only 2.5 ug Chl a/liter with enclosure 3 values almost double those for littoral enclosure 7. However, the total pigment concentrations in both
Figure 21. Proportions of live chlorophyll a in the 0-2, 2-4 and 4-6 meter depth strata
LEGEND

0-2 meters

2-4 meters

4-6 meters

Lake

Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
Table 8. Results of one way analysis of variance on measurements of the seasonal mean proportion of live Chlorophyll a in all of the enclosures and the lake. Numbers in brackets are probabilities of no significant treatment effect ($F_{1,i}$ for lake vs control means, $F_{1,n}$ for control vs fertilized means, and $F_{i,1}$ for all other comparisons.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment arithmetic means ± SE (ug/liter)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lake</td>
</tr>
<tr>
<td>Proportion Live Chlor a</td>
<td>0.349 ± 0.019</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Treatment Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake vs Control</td>
</tr>
<tr>
<td>Littoral Control vs Littoral Fertilized</td>
</tr>
<tr>
<td>Littoral Control vs Limnetic Control</td>
</tr>
<tr>
<td>Control vs Fertilized</td>
</tr>
<tr>
<td>Limnetic Control vs Limnetic Fertilized</td>
</tr>
<tr>
<td>Limnetic Control vs Limnetic Fertilized</td>
</tr>
</tbody>
</table>

| ns (1.000) | ns (.864) | ns (0.220) | ns (1.00) | ns (0.689) | ns (0.475) |

ns = not significant at $\alpha = 0.05$
enclosures at 0-2 m were about the same (Figure 18). The low ratio of chlorophyll a to phaeophytin a in enclosure 7 during the latter part of the summer was due to domination of the algal community at that time by chrysophytes, which have a preponderance of carotenoid pigment (Reynolds, 1984) and contain very little chlorophyll.

Epilimnetic concentrations of chlorophyll a in all of the fertilized enclosures were significantly higher than in controls (Table 6 and 7, Figures 17 and 18-20). Concentrations in the littoral enclosures were not significantly different from littoral controls at 4-6 m, since enclosure 7 had only a modest response to fertilization. Chlorophyll a values in the littoral fertilized enclosures were significantly lower than in the limnetic fertilized enclosures at all depths (Tables 6 and 7). Also, chlorophyll a in the littoral fertilized enclosures did not peak as sharply as in the limnetic fertilized enclosures during late August (Figures 18-20) except at 4-6 m (Figure 20).

Total algal biomass in limnetic fertilized enclosure 8 began to increase exponentially in the 0-2 m stratum, apparently in response to nutrient addition, about 1 week earlier than in all other fertilized enclosures (Figure 16 and 18). The sudden decline in biomass that occurred in early September was paralleled by a dramatic increase in the biomass and abundance of phytoplankton at 2-4 m, (Figure 19) which suggests that the algae settled out of the 0-2 m stratum. An exceptionally high value of 39.4 ug Chl a/liter was recorded at 2-4 m at that time.

Temporal fluctuations in the percentage of live chlorophyll
a in the fertilized enclosures were not significantly different from those occurring in the controls and lake (Figure 21). However, a much higher percentage of live chlorophyll a occurred in littoral fertilized enclosure 3 in late August and limnetic fertilized enclosure 8 for the 3 weeks in August at 2-4 meters when the metalimnetic biomass maxima (mentioned above) occurred.

Seasonal mean percentages of live chlorophyll a in the fertilized enclosures were not significantly different between littoral or limnetic locations, or between the controls and the lake (Table 8). As in the control-lake series, percentages also decreased significantly with depth (42.8 ± 1.6 % at 0-2 m, 31.4 ± 1.7 % at 2-4 m and 28.6 ± 1.3 % at 4-6 m). However, recall that the major portion of the biomass in the fertilized enclosures occurred in the upper 4 m (Table 6) where the percentage of live chlorophyll a was the greatest. This pattern suggests that a greater proportion of the total biomass of the phytoplankton in the fertilized enclosures was living, viable plant material compared with controls and the lake.

3.3.2 Species Composition

(1) In The Lake

The phytoplankton species present in Placid Lake seem typical of those found in bog lakes (Welch, 1952) and of other small coastal lakes in the area. All of the genera and many of the species identified in this study (Appendix 1) have been reported to appear in nearby Marion Lake (Dickman, 1968).
Although most of the following analysis deals primarily with data from the 0-2 m depth stratum, there was no evidence that the species composition changed with depth in this shallow lake.

The number of species of limnetic phytoplankton is small (ca. 120) with few species in each genera. Qualitatively, the Chlorophyceae predominate in the number of species followed by Cyanophyceae, Chrysophyceae and finally Cryptophyceae. Bacillariophyceae play an insignificant role in the composition of summer plankton associations but are probably present in large numbers during the spring bloom.

Most of the taxa in the lake, with the exception of the Cryptophyceae, had seasonal cycles of peak abundance (Figure 22). Small Chlorophyceans, such as *Chlamydomonas* spp., *Oocystis* sp., *Nannochloris*, *Chlorella ellipsoïda* (Gerneck), palmellar stages of *Chlamydomonas*, *Sphaerocystis schroetleri* (Chodat) and *Gloeocystis planktonica* (West) dominated the biomass in June through late July in the lake, but contributed little to the standing stock for the rest of the summer.

Coincident with the collapse of the chlorophytes, came an increase in the chrysophytes. This mid-summer bloom began with the appearance of *Ochromonas* (Wyssoztski), *Synura uvella* (Ehrenberg) and *S. sphagnicola* (Korshnikov) and progressed in time to include *Chrysophaella longispina* (Lauterborn), *Dinobryon sertularia* (Ehrenberg), and *D. sociale* (Ehren.). *Dinobryon* spp. were the only perennial chrysophytes in the lake, occurring at all times in the plankton at moderate densities (10^3 to 10^4 cells/ liter). All of the other species of chrysophytes bloomed
Figure 22. Phyletic composition of algal biomass
and then disappeared.

In late August when nitrogen to phosphorous ratios (total inorganic N : total dissolved P) in the epilimnion decreased significantly (N:P = 6:1) from mid summer values (N:P = 27:1), the algal association became dominated by the colonial cyanophytes Chroococcus limneticus (Lemm.), C. Prescottii (Drouet and Daily) and Merismopedia elegans (A. Braun). Even before this "bloom" (by Placid Lake standards), these species formed a large component of the summer phytoplankton assemblage.

(2) Effects of Enclosure

Seasonal phyletic compositions of the total algal volumes in the control enclosures were essentially the same as in the lake (Figure 22). An exception was that the collapse of the early summer Chlorophycean bloom in enclosure 2 was followed in July with a bloom of the cyanophyte Merismopedia elegans. No chrysophyte bloom developed in this enclosure.

The littoral controls exhibited a dominance of diatoms rather than greens in the June 16th sample. These may have been remnants of a spring bloom of diatoms (for which I have no direct evidence) but were most likely stirred up from littoral sediments by SCUBA divers who, a day before the samples were taken, had been working inside the enclosures inspecting for a proper bottom seal between the littoral and limnetic enclosures.
(3) Effects of Fertilization

Seasonal changes in the phyletic composition of the algal biomass in the two littoral fertilized enclosures were basically similar to those in the controls and the lake (Figure 22) except for four major differences.

1) The mid-June dominance of Chlorophytes was considerably stronger than in the controls, making up about 80% of the total biomass versus 40% in the controls and the lake. This was largely due to a massive increase in the ultraplankton (<10 μm in their maximum linear dimension, MLD) and a significant increase in the presence of small, gelatinous, colonial green algal forms like S. schroeteri, G. planktonica and Palmella mucosa (Keutzing). The filamentous green Ulothrix cylindricum (Prescott), although not present in large numbers, (10^3 filaments/liter), contributed significantly to the early June total biomass in enclosure 7.

2) Unlike in the controls and the lake, the cryptophycean algae underwent an observable increase in numbers in both littoral fertilized enclosures, beginning in mid July and ending in late August. The increase was largely due to a bloom of the species Cryptomonas erosa (Ehren.) and Cryptomonas ovata (Ehren.). Densities reached as high as 10^6 cells/liter (vs.10^4 cells/liter in the controls).
3) The late summer dominance of Cyanophytes which occurred in both the controls and the lake did not manifest itself in the littoral fertilized enclosures. Instead, there was a dominance of small green algae resulting from a bloom of *Ankistrodesmus falcatus* (Corda). Secondary dominants included *S. schroeteri*, *G. planktonica*, and some small coccoid greens (probably fractured colonies).

4) Blue-green algae were generally much lower in the littoral fertilized enclosures when compared to controls and the lake, over the entire summer.

In the limnetic fertilized enclosures, all of the genera of algae indigenous to the lake and common to the control enclosures and the littoral fertilized enclosures, were present at all times, albeit sometimes in very low numbers (especially late in the summer). No new species appeared in the algal assemblage in these enclosures, however, some of the forms that were rare in the lake, such as, *Botryococcus sudeticus* (Lemmerman) and *Gloeocystis major* (Gerneck) appeared to benefit greatly from the added nutrients (See Appendix 2). The late summer species composition in the limnetic fertilized enclosures (Figure 22) was not overwhelmingly different from the littoral fertilized enclosures, however, the mid summer species composition in these enclosures was quite different from the littoral fertilized enclosures, the controls and the lake.
Except for a short period in mid-July in limnetic fertilized enclosure 4, small chlorophytes were the dominant algae over the entire summer in the limnetic fertilized enclosures. More than eighty percent of the early summer biomass consisted of the same dominants and subdominants that occurred in the littoral fertilized enclosures and the controls.

As in the controls, the early summer chlorophyte dominance began to wane by mid-July in limnetic fertilized enclosure 4. Larger chlorophytes such as *B. sudeticus* and *G. major*, which were previously very low in abundance, reached greater proportions in the biomass in this enclosure. *Sphaerocystis schroeteri* also increased in abundance in both limnetic fertilized enclosures at this time (to $10^5$ cells/liter).

Within 2 weeks of their appearance (mid-July, Figure 22), the large colonial gelatinous greens had virtually disappeared from the algal assemblage in both limnetic enclosures and the grazeable fraction rebounded dramatically, yielding a population dominated almost exclusively by the small green algae *Ankistrodesmus falcatus* (Corda) and *A. f. var. tumidus* (West and West). The smaller forms of gelatinous greens were also greatly reduced in number ($10^3$ cells/liter).

Small chlorophytes were always the dominant algae in enclosure 8. This enclosure developed a bloom of *Ankistrodesmus* approximately 2 weeks earlier than the one that occurred in enclosure 4. *Ankistrodesmus* spp. were present in the controls and the lake in fairly low numbers ($10^3$ cells/liter) beginning in early July, but they never became a significant component of
the algal biomass. Densities in the limnetic fertilized enclosures, however, reached $10^8$ cells/liter during peak abundance (Figure 23).

Blue-green algae were virtually non-existent in the limnetic fertilized enclosures in the latter part of the summer. They were present, however, in small amounts during early summer.

3.3.3 Size composition

(1) Effects of Enclosure

The summer algal assemblages in Placid Lake and the control enclosures in 1982 were numerically dominated by the ultraplankton (Figure 23), algae <10 um in their maximum linear dimension (Wetzel, 1975). Appendix 3 contains figures which summarize the seasonal density profiles of all of the various size classes of algae discussed below.

Densities of algae <2 um ranged from mid-summer (July - August) lows of around $5.0 \times 10^6$ cells/liter to early (June) and late summer (September - October) highs of 50-80 $\times 10^6$ cells/liter (not shown). Algae in the 2-6 um range were the small chlamydomonads and chlorococcoids. They exhibited the same seasonal abundance patterns of mid summer lows and early and late summer highs ranging in density from 1-3 $\times 10^6$ to 5-10 $\times 10^6$ cells/liter, respectively (Appendix 3). Abundances of algae in the 6 - 10 um size range were more evenly distributed over the summer with densities ranging between 2 $\times 10^6$ and 10 $\times$
Figure 23. Cumulative densities of algae in selected size class. Note the change in scale of the Y-axis on the plots for the limnetic fertilized enclosures.
10^6 cells/liter.

Densities of the nanoflagellates and other small algae in the size range most heavily grazed by Placid Lake zooplankton (ca. 10-20 um MLD; Krause, 1984), were quite low compared to the ultraplankton, being on the order of 5-30 X 10^4 cells/liter. Densities of these cells did not show pronounced seasonal variation, although periodic maxima were recorded during mid summer when populations of the larger cladocerans reached their lowest levels. Of the 10-20 um algae, densities of those in the 10-14 um size class were the lowest, on the order of 4-10 X 10^3 cells/liter. The bulk of the 10-20 um size range was made up of cells in the 14-20 um size class.

Maximum densities of the larger algae in the system (> 20 um MLD), which included the "net" plankton (50-100 um MLD), occurred in mid summer and were on the order of 1.0 X 10^5 cells/liter. Of these larger algae, colonial chrysophytes such as Chrysophaella longispina, Synura uvella, S. sphagnicola and Dinobryon spp. constituted the "net" plankton and dominated the biomass in July and August. Large (20-50 um MLD) colonial cyanophytes, such as Merismopedia spp. and Chroococcus prescottii dominated the late summer biomass with densities reaching 5-8 x 10^4 cells/liter.

Though the numerical dominance of the ultraplankton persisted throughout the summer in the controls and lake (Figure 23), this size fraction was dominant (> 30 %, Hutchinson, 1967) in the total biomass of the algae only in the early part of the summer (Figure 24), becoming insignificant by late July. By
Figure 24. Percent composition of algal biomass by detailed size classes
Legend:

- < 2 um
- 2 - 5 um
- 5 - 10 um
- 10 - 20 um
- 20 - 30 um
- > 30 um

Lake composition over time for different enclosures:

**Enclosure 1** (littoral control)

**Enclosure 3** (littoral fertilized)

**Enclosure 2** (limnetic control)

**Enclosure 4** (limnetic fertilized)

**Enclosure 5** (littoral control)

**Enclosure 7** (littoral fertilized)

**Enclosure 6** (limnetic control)

**Enclosure 8** (limnetic fertilized)
then, at least 80% of the total phytoplankton biomass was made up of cells > 20 um in their maximum linear dimension, and at least 60% of that was "net" plankton (50-100 um). Less than 20% of the total algal biomass was made up of those cells that are selectively fed upon (6-20 um MLD) by the dominant herbivorous zooplankton in this system. The controls had lower total zooplankton biomass levels than the lake in late summer, and fewer large cladocerans. As a result 20 to 30% of the late summer biomass was made up of cells in the 6-20 um size range, compared to only 10-20% in the lake.

The size composition of the algal assemblage in limnetic enclosure 2 differed from that in all of the other controls and the lake. The mid summer phytoplankton of this enclosure was dominated by algae in the 10-20 um size range, however, 50 - 80% of the biomass during that time was made up of the inedible cyanophyte *Merismopedia* (Figure 22) (Arnold, 1971; Ferrante, 1975; Krause, 1984).

(2) Effects of Fertilization

The ultraplankton did not numerically dominate the algal assemblages of the fertilized enclosures for the entire summer as they did in the controls. Fertilization had greatly enhanced the algae in the 10 - 20 um size fraction by the middle of August in most of the fertilized enclosures (Figure 23).

The initial response of the phytoplankton to nutrient addition in the littoral fertilized enclosures was a rapid increase in the ultraplankton, to concentrations 3-4 times
higher than in controls and the lake, reaching densities of about $2 \times 10^7$ cells/liter. This increase was short in duration, with concentrations returning to levels similar to those in controls and the lake within one week, and remaining at those levels for the duration of the study.

Significant increases in numerical abundances of part of the grazable fraction of the algae were first evident in littoral fertilized enclosure 3 in late July. There was a short-term bloom of the cryptomonad Cryptomonas ovata, which was apparently rapidly suppressed by grazers. Greater increases of longer duration occurred in late August in both littoral fertilized enclosures. These latter increases were the result of blooms of the green algae Ankistrodesmus falcatus, an algal form which induces excellent growth and survival rates in D. lus (Arnold, 1971). Concentrations of these cells reached a maximum of $2 \times 10^7$ cells/liter, 2-3 orders of magnitude higher than the concentrations of all of the algae in this size range (10-20 um MLD) in the controls and the lake at that time (Appendix 3).

Densities of the larger, less grazable, algae (> 20 um MLD) in the littoral fertilized enclosures were largely unchanged from densities in the controls and the lake. Maximum concentrations of $1-2 \times 10^5$ cells/liter occurred in early August (Appendix 3).

Early and late summer densities of ultraplankton in the limnetic fertilized enclosures closely approximated those found in the controls and the lake, on the order of $5-10 \times 10^6$
cells/liter. Unlike in the littoral fertilized enclosures, there were no immediate large increases in the abundance of these cells, however, blooms of ultraplankton did occur in the limnetic fertilized enclosures in August (Figure 23).

The bloom in limnetic fertilized enclosure 8 (2 x 10⁷ cells/liter, compared to 1-3 x 10⁶ cells/liter in controls) subsided within one week, but the bloom in limnetic fertilized enclosure 4 lasted about 5 weeks and reached maximum concentrations of 8.5 x 10⁷ cells/liter.

Fertilization strongly favoured the mid to late summer production of algae in the 10 - 20 um size ranges (Figure 23). Densities of the grazable algae reached as high as 1 x 10⁸ cells/liter and consisted almost exclusively of the highly nutritious (Arnold, 1971) alga *Ankistrodesmus falcatus*.

Fertilization did not radically alter the early summer size composition of the total algal biomass in either the littoral or limnetic fertilized enclosures (Figure 24) when compared with controls. Mid-summer algal size compositions in the littoral fertilized enclosures, as in the controls, were dominated by algae > 20 um and "net" plankton (Figure 24). The predominant algal forms in this size category were the same as in the controls, namely, large chrysophytes.

Occurrences of "net" plankton in the limnetic fertilized enclosures (Figures 24) were, by contrast, less frequent and consisted primarily of large, colonial, gelatinous greens. These forms tend to become abundant in systems that are heavily grazed by zooplankton (Porter, 1973). The large chrysophytes
that made up the "net" plankton in all of the other enclosures and the lake, comprised a relatively insignificant proportion of the total biomass of the limnetic fertilized enclosures.

The proportion of algal biomass in the 20 – 30 um size range in the fertilized enclosures during mid-summer was greater than in the controls. In the controls this size fraction was dominated by the inedible blue-green algae *Merismopedia* and *Chroococcus*. In the fertilized enclosures, it was dominated almost exclusively by the edible algae *Cryptomonas erosa* and *C. Ovata* (McQueen, 1969). This suggests that a greater proportion of the mid summer algal biomass in the fertilized enclosures though quite large, was palatable and of a manageable size for some Placid Lake zooplankton.

As in the controls, the biomass of algae in the 6-20 um size range in the fertilized enclosures dropped below 20 % of the total biomass during mid-summer. However, rather than remaining low for the balance of the summer as occurred in the controls, by late August, 60 – 80 % of the total algal biomass in the littoral fertilized enclosures and almost 100 % of the biomass in the limnetic fertilized enclosures was made up of algae <20 um in size, the bulk of which was in the 10 – 20 um size fraction. This size composition was maintained through to fall overturn in October.
3.3.4 Summary of Phytoplankton Results

Phytoplankton standing crop in the control enclosures was not significantly different from that in the lake.

Phytoplankton standing crop increased 3-fold and 7-fold over control values in the littoral and limnetic fertilized enclosures, respectively, following nutrient addition.

Changes in the percentage of live chlorophyll a with depth show that, in the control enclosures and the lake, the highest concentration of algal biomass (at 4-6 m) contained the lowest percentages of live chlorophyll a. The highest percentages of live chlorophyll a in the fertilized enclosures occurred in the 0-2 m depth stratum where the algal biomass was greatest.

Seasonal changes in the phyletic composition of the algae were similar in the control enclosures and the lake. The species composition of algae in enclosure 2 was noticeably different, but because all of the measured physical and chemical regimes in enclosure 2 were similar to all other controls and the lake, it is difficult to isolate the cause of this change.

Frequent doses of high N:P ratio fertilizer resulted in a larger proportion of the early summer algal community being composed of Chlorophyceae. The littoral fertilized communities were similar to the controls in that they also exhibited a mid-summer chrysophycean bloom. The late summer cyanophyte community, distinctive of the lake and all controls, was replaced by a chlorophycean bloom composed almost exclusively of the highly nutritious green alga *Ankistrodesmus*. Chlorophyte species dominated the algal community all summer long in the
limnetic fertilized enclosures. Chrysophyceae were essentially non-existent. A short, (2 week) period occurred during which a dominant component of the algal community consisted of large, gelatinous green algae, which were normally quite rare in the lake and did not occur in the controls. This episode was followed by a massive increase in the abundance and biomass of Ankistrodesmus.

Only 20-30 % and 10-20 % of the mid- and late summer biomass in the controls and the lake, respectively, was made up of algal cells in the grazable 6-20 um size fraction. Conversely, 60-80 % and virtually 100 % of the mid to late summer algal biomass in the littoral and limnetic fertilized enclosures fell within this size fraction.

Cyanophyceae were greatly reduced in abundance in all of the fertilized enclosures. They were virtually eliminated from the plankton in the limnetic fertilized enclosures.

3.4 Zooplankton Standing Crop, Species Composition and Community Structure

3.4.1 Standing Crop and Species Composition

(1) In The Lake

Under natural conditions, the biomass of zooplankton in Placid Lake, and all the lakes of the U.B.C. Research forest, was very low (ca. 50-100 ug/liter dry weight) (Figure 25). Table 3 summarizes the species of zooplankton which are commonly
Figure 25. Zooplankton biomass. Note the log-scale.
Zoo plankton Biomass

Enclosure 1
(Littoral Control)

Enclosure 2
(Limnetic Control)

Enclosure 3
(Littoral Fertilized)

Enclosure 4
(Limnetic Fertilized)

Enclosure 5
(Littoral Control)

Enclosure 6
(Limnetic Control)

Enclosure 7
(Littoral Fertilized)

Enclosure 8
(Limnetic Fertilized)
found in the lake.

Nearly all of the zooplankton species were concentrated in the upper 4 m of the lake, but there is some evidence of different species being depth segregated. Both *Daphnia rosea* and *Diaphanosoma brachyurum* attained maximum densities in the upper 4 m of the water column during June and July, but during August and September, *Daphnia* were most abundant in the 2-4 m depth zone, while *Diaphanosoma* maintained maximum densities in the 0-2 m stratum. *Holopedium gibberum* was found throughout the water column (0-6 m) during late June but moved into deeper water (4-6 m) as the summer progressed. *Polyphemus* and *Bosmina*, which are both rare in the lake, are near surface forms. *Ceriodaphnia* inhabited only deep water (4-6 m). *Diaptomus oregonensis* occupied the upper four meters for most of the summer, but moved to deeper water (4-6 m) around the middle of September. *Diacyclops thomasi*, the most abundant copepod, attained highest densities in the mid to deep water zone (4-6 m). Finally, *Diaptomus kenai*, which was present in the water column only in spring and early summer, was found near surface and near bottom, respectively in those seasons.

(2) Effects of Enclosure

Seasonal fluctuations in total zooplankton biomass in the controls were similar to those occurring in the lake to the degree that maximum biomass levels were reached in mid to late July and decreased steadily as the summer progressed (Figure 25). However, three major differences between the control
enclosures and the lake are immediately noticeable.

First, biomass levels in the enclosures were lower at the commencement of sampling on June 16. However, they quickly recovered to meet or exceed lake values within one week. The most likely reason for lower starting biomass levels in the control enclosures is that the lake zooplankton avoided the area in and around the enclosures while they were being installed and insufficient time was provided to allow full recruitment of the area before the enclosure sides were dropped and full enclosure effected.

The second major difference between the enclosures and the lake is that biomass levels in the controls declined much more rapidly after peak levels were reached than they did in the lake. I attribute this to fish predation being more intense inside the enclosures than in the lake. This will be discussed later.

Finally, the late summer zooplankton biomass levels in the controls were maintained at levels substantially lower than lake values. (This may have been mediated by the intense level of fish predation postulated above). Overall mean zooplankton biomass levels in the control enclosures were accordingly lower than in the lake (Table 9).

The major effects of enclosure on the species composition of zooplankton, determined by comparing enclosure zooplankton populations (Figures 26-28) with lake populations were; (1) a rapid decline in the numbers of *Holopedium gibberum* in all enclosures, (2) a significant reduction in the densities of
Table 9. Results of one way analysis of variance on total biomass of zooplankton (± SE ug/liter) at all depths averaged over the entire experiment. Numbers in brackets are probabilities of no significant treatment effect (F, for lake vs control grand mean comparisons, F, for control vs fertilized grand mean comparisons, F, for control vs fertilized depth means, F, for all other grand mean comparisons, and F, for all other depth mean comparisons.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment arithmetic means ± SE (ug/liter)</th>
<th></th>
<th></th>
<th></th>
<th></th>
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<tr>
<td></td>
<td>Depth (m)</td>
<td>Lake</td>
<td>Littoral Controls</td>
<td>Limnetic Controls</td>
<td>Littoral Fertilized</td>
</tr>
<tr>
<td>Zooplankton</td>
<td>0-2</td>
<td>67.85 ± 5.62</td>
<td>60.83 ± 9.97</td>
<td>35.05 ± 4.88</td>
<td>305.00 ± 41.38</td>
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<tr>
<td>Biomass (ug/liter)</td>
<td>2-4</td>
<td>53.10 ± 5.27</td>
<td>47.04 ± 4.50</td>
<td>44.76 ± 3.00</td>
<td>126.52 ± 18.95</td>
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<tr>
<td></td>
<td>4-6</td>
<td>24.02 ± 4.76</td>
<td>18.51 ± 2.61</td>
<td>34.37 ± 4.34</td>
<td>34.57 ± 5.87</td>
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<td></td>
<td>ALL</td>
<td>49.38 ± 4.00</td>
<td>42.42 ± 4.12</td>
<td>38.17 ± 2.41</td>
<td>159.48 ± 19.58</td>
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</table>

<table>
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<th>Depth (m)</th>
<th>Lake vs Control vs Littoral Control vs Limnetic Control vs Littoral Fertilized vs Limnetic Fertilized</th>
</tr>
</thead>
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<tr>
<td></td>
<td>0-2</td>
<td>L (0.003) F (0.000) Litt (0.006) ns (0.222)** F (0.000) F (0.000)</td>
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<tr>
<td></td>
<td>2-4</td>
<td>ns (0.195) F (0.000) ns (0.690) Lim (0.002) F (0.000) F (0.000)</td>
</tr>
<tr>
<td></td>
<td>4-6</td>
<td>ns (0.921) F (0.000) Lim (0.000) Lim (0.038) F (0.013) ns (0.108)</td>
</tr>
<tr>
<td></td>
<td>ALL</td>
<td>L (0.026) F (0.000) ns (0.513) Lim (0.011) F (0.000) F (0.000)</td>
</tr>
</tbody>
</table>

ns = not significant at α = 0.05
F, Litt, Lim, C or L = interaction significant at α = 0.05
** = variance heterogeneous at α = 0.05
Figure 26. Percent composition of zooplankton biomass by species in the 0-2 meter depth stratum
Figure 27. Percent composition of zooplankton biomass by species in the 2-4 meter depth stratum
Figure 28. Percent composition of zooplankton biomass by species in the 4-6 meter depth stratum
Diaphanosoma brachyurum in the limnetic enclosures, and (3) a significant increase in the densities of Diaptomus oregonensis in the limnetic enclosures compared to the littoral enclosures and the lake.

(3) Effects of Fertilization

Fertilization greatly enhanced the biomass of zooplankton in all of the fertilized enclosures (Figure 25, Table 9). Mean zooplankton biomass over the entire summer was significantly higher in the fertilized enclosures than in the controls (Table 9). Biomass levels in the littoral fertilized enclosures increased approximately 3-4 fold over littoral control values, whereas biomass levels in the limnetic fertilized enclosures increased approximately 7-fold over limnetic control values.

The major effect of fertilization on the species composition of the zooplankton (Figure 26-28) was a dramatic increase in the densities and biomass of Cladocera, especially Daphnia rosea and Diaphanosoma brachyurum. Densities of Ceriodaphnia quadrangula and Diacyclops thomasi increased significantly in the deep water zone (4-6 m) following nutrient enrichment, whereas in the lake large cladocerans like Daphnia and Holopedium dominated the biomass in this depth stratum. However, their absolute densities were lower there than in the fertilized enclosures.
3.4.2. Zooplankton Community Structure

Densities of the major herbivorous zooplankton in the lake, the controls and the fertilized enclosures were highest in the 0-2 m depth stratum for most of the summer (Figure 29). Densities of all of the species considered in this study, were often considerably higher in this stratum than their average densities for the entire water column (Figures 30-36). Also, the distributions of zooplankters, by species, appeared to be representative of the water column as a whole. Therefore, in order to be consistent with the analysis applied to the phytoplankton data, the results of the statistical analyses that follow were derived almost exclusively from the data from the 0-2 m stratum with the assumption that the organisms in this depth stratum were representative of all organisms of that type in the lake.

(1) In The Lake

When sampling began in June, the species of herbivorous zooplankton present in the lake were, in decreasing order of abundance: Holopedium gibberum, Diaptomus oregonensis, Daphnia rosea, Diaphanosoma brachyurum, Ceriodaphnia quadrangula, Bosmina longirostris (Figures 30-36) and Diaptomus kenai (not shown). D. kenai are only present in significant numbers in the water column in the spring. They are only rarely found in the summer. The predatory copepod, Diacyclops thomasi (Figure 36), was abundant only in July and largely concentrated in the 4-6
Figure 29. Cumulative densities of the dominant herbivorous zooplankton species in the 0-2 meter depth stratum
Figure 30. Densities of *Holopedium gibberum*
Holopedium gibberum

- Enclosure 1 (littoral control)
- Enclosure 2 (limnetic control)
- Enclosure 3 (littoral fertilized)
- Enclosure 4 (limnetic fertilized)
- Enclosure 5 (littoral control)
- Enclosure 6 (limnetic control)
- Enclosure 7 (littoral fertilized)
- Enclosure 8 (limnetic fertilized)
Figure 31. Densities of *Daphnia rosea*. Note the log-scale.
Daphnia rosea

- Enclosure 1 (littoral control)
- Enclosure 2 (limnetic control)
- Enclosure 3 (littoral fertilized)
- Enclosure 4 (limnetic fertilized)
- Enclosure 5 (littoral control)
- Enclosure 6 (limnetic control)
- Enclosure 7 (littoral fertilized)
- Enclosure 8 (limnetic fertilized)

Number/liter

JUN  JLY  AUG  SEP  OCT  NOV

LAKE
Figure 32. Densities of *Diaphanosoma brachyurum*. Note the log-scale.
Diaphanosoma brachyurum

[Graphs showing population dynamics of Diaphanosoma brachyurum in different enclosures throughout the year.]
Figure 33. Densities of *Diaptomus oregonensis*. Note that the juvenile category consists only of copepodites and does not include nauplii.
Figure 34. Densities of *Ceriodaphnia quadrangula*
Enclosure 1
(littoral control)

Enclosure 2
(limnetic control)

Enclosure 3
(littoral fertilized)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 6
(limnetic control)

Enclosure 7
(littoral fertilized)

Enclosure 8
(limnetic fertilized)
Figure 35. Densities of *Bosmina longirostris*. Note the log-scale.
Bosmina longirostris

LAKE

Enclosure 1
(littoral control)

Enclosure 3
(littoral fertilized)

Enclosure 2
(limnetic control)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 7
(littoral fertilized)

Enclosure 6
(limnetic control)

Enclosure 8
(limnetic fertilized)
Figure 36. Densities of *Diacyclops thomasi*
Diacyclops thomasi

Enclosure 1 (littoral control)

Enclosure 2 (limnetic control)

Enclosure 3 (littoral fertilized)

Enclosure 4 (limnetic fertilized)

Enclosure 5 (littoral control)

Enclosure 6 (littoral fertilized)

Enclosure 7 (limnetic fertilized)

Enclosure 8 (limnetic fertilized)
meter depth stratum. As a result, these two species are not considered in statistical analyses comparing different treatments.

Other cladoceran zooplankton species were less commonly found in the lake and in the experimental enclosures. Their numbers were so low that they contributed little to the overall biomass. These included *Scaphaloberis kingii*, *Polyphemus pediculus* and *Chydoris sphaericus*. The primarily littoral cladoceran *Acantholeberis curvirostris* was encountered, but only very rarely in all of the littoral enclosures and the lake. A large species of cyclopoid copepod, possibly *Mesocyclops edax*, (Peacock, 1981) occurred in two littoral lake samples taken during a pre-experiment site survey in 1981, but was never found in 1982 samples.

All of the herbivorous zooplankters, with the exceptions of *Ceriodaphnia* (Figure 34) and *Bosmina* (Figure 35) (both of which appeared in mid-September in moderate numbers but were otherwise rare in the lake) dominated the zooplankton community, in terms of abundance and/or biomass, at some time during the summer. The sequence of shifts in species dominance was as follows: When the ice left the lake in late April, the copepods *Diaptomus kenai* and *Diaptomus oregonensis* dominated the zooplankton community (C.J. Walters, unpubl. data; Krause, 1984), while cladocerans were rare. By early June, *D. kenai* had almost disappeared from the zooplankton but *D. oregonensis* (Figure 33) remained unchanged in abundance. *Holopedium* (Figure 30) then became numerically dominant and remained so until July, at which
time the numbers of both Daphnia (Figure 31) and Diaphanosoma (Figure 32) began to increase while the population of Holopedium decreased. The population of D. oregonensis (Figure 33) did not decline as Daphnia and Diaphanosoma became abundant, but remained approximately the same. Daphnia reached maximum densities (8-10 individuals/liter in the 0-2 m stratum) in the last week of July, then declined rapidly while Diaphanosoma (Figure 32) increased to their summer maximum (10 - 12 individuals/liter in the 0-2 m stratum), achieving this level by early August. Diaphanosoma continued to dominate numerically until late August when the juvenile stages of D. oregonensis matured and the adult stage of that species (Figure 33) became the late summer dominant (6 - 7 individuals/liter in the 0-2 m stratum).

The mean body size of adult Holopedium in the lake dropped from a May - early June high of 1.4 mm. (max = 1.63 mm.) to a mid-June low of 1.2 mm. (min = 0.78 mm), and remained at this level for the duration of the study, increasing slightly in late October. Very few egg-bearing Holopedium were captured in the lake, and those too showed a similar trend towards a decrease in body size. The mean brood size of egg-bearing adults changed very little over the course of the summer, being around 1.0 eggs/female. Body sizes of juvenile Holopedium remained constant over the entire course of this study, at a mean size of 0.6 mm.

Mean body sizes of gravid and non-gravid adult Daphnia decreased from an average size of 1.3 mm. (max = 1.6mm.) at the
beginning of sampling in June, to about 1.0 mm. (min = 1.0 mm.) in mid-September (Figure 37). The mean brood size of gravid Daphnia also decreased from a spring-early summer high of about 1.6 eggs/female to a mid-summer low of 1.0 eggs/female (Figure 38). Juvenile Daphnia increased in size to a maximum of 1.0 mm. during mid summer (Figure 37).

The body sizes of Diaphanosoma (Figure 39) and D. oregonensis (Figure 40) did not change significantly over the study period. Too few gravid individuals of the these two species were collected to adequately determine changes in the mean brood sizes or body sizes of gravid females.

(2) Effects of Enclosure

The sequence of numerical dominance of the major herbivorous zooplankton species in the control enclosures was essentially the same as in the lake (Figs. 30-36), but there were some differences in the magnitude and timing of these changes.

Densities of Holopedium in the controls in June and July were considerably lower than in the lake (Fig. 30). Holopedium virtually disappeared from all of the control enclosures by early August. Statistical analysis showed that the seasonal mean densities in the controls were significantly lower than in the lake (Tables 10 and 11). However, mean brood sizes were not significantly different (Table 12). There was no significant difference in mean densities or mean brood sizes between littoral and limnetic controls.
Figure 37. Mean body sizes of adult, gravid female and juvenile *Daphnia rosea*
**Daphnia rosea**

**Mean Body Sizes (mm.)**

- **adults**
- **females/eggs**
- **juveniles**

**Enclosure 1**
(littoral control)

- **Seasonal Mean = 1.15**
- **Seasonal Mean = 0.89**

**Enclosure 2**
(limnetic control)

- **Seasonal Mean = 1.14**
- **Seasonal Mean = 0.82**

**Enclosure 3**
(littoral fertilized)

- **Seasonal Mean = 1.27**
- **Seasonal Mean = 0.86**

**Enclosure 4**
(limnetic fertilized)

- **Seasonal Mean = 1.30**
- **Seasonal Mean = 0.88**

**Enclosure 5**
(littoral control)

- **Seasonal Mean = 1.22**
- **Seasonal Mean = 0.82**

**Enclosure 6**
(limnetic control)

- **Seasonal Mean = 1.22**
- **Seasonal Mean = 0.83**

**Enclosure 7**
(littoral fertilized)

- **Seasonal Mean = 1.29**
- **Seasonal Mean = 0.84**

**Enclosure 8**
(limnetic fertilized)

- **Seasonal Mean = 1.37**
- **Seasonal Mean = 0.89**

**LAKE**

- **Seasonal Mean = 1.18**
- **Seasonal Mean = 0.83**
Figure 38. Mean brood sizes of Daphnia rosea
Mean brood sizes of Daphnia Rosea

Enclosure 1 (littoral control)

Enclosure 3 (littoral fertilized)

Enclosure 2 (limnetic control)

Enclosure 4 (limnetic fertilized)

Enclosure 5 (littoral control)

Enclosure 7 (littoral fertilized)

Enclosure 6 (limnetic control)

Enclosure 8 (limnetic fertilized)
Figure 39. Mean body sizes of adult *Diaphanosoma brachyurum*
Diaphanosoma Adults
Mean Body Sizes (mm.)

Enclosure 1
(littoral control)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.70

Enclosure 2
(limnetic control)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.69

Enclosure 3
(littoral fertilized)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.73

Enclosure 4
(limnetic fertilized)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.78

Enclosure 5
(littoral control)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.70

Enclosure 6
(limnetic control)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.71

Enclosure 7
(littoral fertilized)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.74

Enclosure 8
(limnetic fertilized)

JUN JLY AUG SEP OCT NOV

Seasonal Mean = 0.74
Figure 40. Mean body sizes of adult, gravid female and juvenile *Diaptomus oregonensis*
Diaptomus oregonensis
Mean Body Sizes (mm.)

Enclosure 1
(littoral control)

Seasonal Mean = 0.84

Enclosure 3
(littoral fertilized)

Seasonal Mean = 1.03

Enclosure 5
(littoral control)

Seasonal Mean = 0.84

Enclosure 7
(littoral fertilized)

Seasonal Mean = 0.88

Enclosure 6
(littoral control)

Seasonal Mean = 0.84

Enclosure 8
(littoral fertilized)

Seasonal Mean = 1.00

LAKE
Seasonal Mean = 0.87

JUN JLY AUG SEP OCT NOV

Mean Size (mm.)
Table 10. Mean densities (thousands/ cubic meter) of the dominant zooplankton species in the 0-2 m depth stratum.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment means (thousands/ cubic meter)</th>
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<tbody>
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<td></td>
<td>Lake</td>
</tr>
<tr>
<td>Daphnia rosea</td>
<td>4800</td>
</tr>
<tr>
<td>Diaphanosoma brachyurum</td>
<td>7400</td>
</tr>
<tr>
<td>Diaptomus oregonensis</td>
<td>8700</td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td>2000</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>5000</td>
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Table 11. Results of 3 way analysis of variance on log10 of the densities of the dominant zooplankton species in the 0-2 m depth stratum. Numbers in brackets are probabilities of no significant treatment effect ($F_{i,j}$ for lake vs control comparisons, $F_{i,j,k}$ for control vs fertilized comparisons, and $F_{i,j,k}$ for all other comparisons. The letters T and L indicate significant time or location within lake effects, respectively. The listed treatment is the one that is significantly higher (at $a = 0.05$).

<table>
<thead>
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<td></td>
<td>vs</td>
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<td>Control</td>
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<td>D. rosea</td>
<td>L (0.000)T</td>
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<td>D. brachyurum</td>
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<td>D. oregonensis</td>
<td>ns (0.457)T*</td>
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<tr>
<td>B. longirostris</td>
<td>C (0.024)L</td>
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<tr>
<td>H. gibberum</td>
<td>L (0.000)T</td>
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ns = not significant at $a = 0.05$
F, Litt, Lim, or C = interaction significant at $a = 0.05$
* = variance heterogeneous at $a = 0.05$
Table 12. Results of non-parametric one way analysis of variance (Kruskal-Wallis test) on the mean brood sizes of the dominant zooplankton species in the 0-2 m depth stratum. Numbers in brackets are the values of H adjusted for ties. If $H > x^* \ (df=2, \ a=0.05) = 3.841$, the listed treatment is the one that is significantly higher. The "***" indicates the sample size was small, but for all cases at the sample size tested, the results were not significantly different.

<table>
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<td></td>
<td>Littoral Fertilized vs</td>
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<td>Littoral Control vs</td>
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<td>D. rosea</td>
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<tr>
<td></td>
<td>ns (0.645) ns (0.306) F (23.060) vs</td>
</tr>
<tr>
<td></td>
<td>F (28.360)</td>
</tr>
<tr>
<td>D. brachyurum</td>
<td>ns (0.378) F (9.360) vs</td>
</tr>
<tr>
<td></td>
<td>ns (0.502) ns (1.557) ns (3.419) vs</td>
</tr>
<tr>
<td></td>
<td>ns (3.419)</td>
</tr>
<tr>
<td>D. oregonensis</td>
<td>ns (0.002) F (17.690) vs</td>
</tr>
<tr>
<td></td>
<td>ns (0.333) ns (4.522) F (9.491) vs</td>
</tr>
<tr>
<td></td>
<td>ns (1.490)</td>
</tr>
<tr>
<td>B. longirostris</td>
<td>C (4.629) F (81.130) vs</td>
</tr>
<tr>
<td></td>
<td>ns (2.836) ns (9.115) F (10.890) vs</td>
</tr>
<tr>
<td></td>
<td>F (21.900)</td>
</tr>
<tr>
<td>H. gibberum</td>
<td>ns (1.436) F (7.393) vs</td>
</tr>
<tr>
<td></td>
<td>ns (0.239) ns (0.004) ns (4.025) vs</td>
</tr>
<tr>
<td></td>
<td>ns (1.435)</td>
</tr>
<tr>
<td>C. quadrangula</td>
<td>ns (0.088) F (27.980) vs</td>
</tr>
<tr>
<td></td>
<td>ns (0.406) ns (1.435) F (4.025) vs</td>
</tr>
<tr>
<td></td>
<td>ns (1.435)</td>
</tr>
</tbody>
</table>

ns = not significant at $a = 0.05$

F, Litt, Lim, or C = interaction significant at $a = 0.05$
Densities of *Daphnia* in the control enclosures reached maximum levels about two weeks earlier than in the lake (Figure 31). With the exception of littoral control enclosure 1, maximum densities were slightly lower than in the lake at the time of peak abundance. The more rapid increase to maximum densities that occurred in the controls may have been facilitated by the exclusion of resident cutthroat trout from the enclosures. As in the lake, *Daphnia* populations in the control enclosures began to decline sharply in late July; however, these declines resulted in lower daphnid densities than in the lake, so that mean lake densities were significantly higher than in the controls (Tables 10 and 11). Mean brood sizes did not differ (Table 12) nor did mean body sizes (Table 13). Also, there were no significant differences in either parameter between littoral and limnetic controls.

*Diaphanosoma* populations in the littoral control enclosures responded in a similar fashion to lake populations except that the littoral control population levels were higher than in the lake (Figure 32). The average density in the limnetic controls was much lower than in the littoral enclosures and the lake (Tables 10 and 11). Statistical analysis showed that the pooled means of the densities of the littoral and limnetic populations were not significantly different from lake mean densities. However, mean littoral densities were only roughly similar (being slightly higher) to mean lake densities (ANOVA, $F_{(1,30)} = 3.60$, $p = 0.067$, $a = 0.05$), being slightly higher, and mean limnetic densities were significantly lower than mean lake
Table 13. Results of non-parametric one way analysis of variance (Kruskal-Wallis test) on the mean body sizes of 3 of the dominant zooplankton species in the 0-2 m depth stratum. Numbers in brackets are the values of $H$ adjusted for ties. If $H > x^2$ (df = 2, $a = 0.05$) = 3.841, the listed treatment is the one that is significantly higher.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment Comparison</th>
<th>Lake Control vs Littoral Control</th>
<th>Littoral Control vs Littoral Fertilized</th>
<th>Littoral Fertilized vs Limnetic Control</th>
<th>Limnetic Control vs Limnetic Fertilized</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>D. rosea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>ns (0.764)</td>
<td>F (20.480)</td>
<td>ns (0.332)</td>
<td>ns (3.241)</td>
<td>F (6.319)</td>
</tr>
<tr>
<td>Juvenile</td>
<td>ns (0.000)</td>
<td>ns (0.937)</td>
<td>ns (0.538)</td>
<td>ns (0.060)</td>
<td>ns (0.124)</td>
</tr>
<tr>
<td>Gravid females</td>
<td>ns (0.135)</td>
<td>F (25.580)</td>
<td>ns (0.198)</td>
<td>ns (2.045)</td>
<td>F (9.630)</td>
</tr>
<tr>
<td><strong>D. oregonensis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>ns (0.002)</td>
<td>F (49.290)</td>
<td>ns (0.501)</td>
<td>ns (3.399)</td>
<td>F (38.440)</td>
</tr>
<tr>
<td>Female</td>
<td>ns (2.890)</td>
<td>F (45.850)</td>
<td>ns (1.704)</td>
<td>ns (2.391)</td>
<td>F (22.740)</td>
</tr>
<tr>
<td>Copepodite</td>
<td>ns (0.003)</td>
<td>ns (0.323)</td>
<td>ns (0.824)</td>
<td>ns (0.489)</td>
<td>ns (0.291)</td>
</tr>
<tr>
<td><strong>D. brachyurum</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>ns (0.000)</td>
<td>F (24.510)</td>
<td>ns (0.006)</td>
<td>Lim (6.591)</td>
<td>F (15.760)</td>
</tr>
</tbody>
</table>

ns = not significant at $a = 0.05$
F, Litt, Lim, or C = interaction significant at $a = 0.05$
densities (ANOVA, $F_{(1, 32)} = 10.14, p < 0.05$). Mean brood sizes were similar in all three habitats (Table 12).

The enclosed populations of *D. oregonensis* exhibited seasonal trends that were similar to those occurring in the lake (Figure 33). The mean densities of *Diaptomus* in the 0-2 m depth stratum (Figure 29) of the enclosures were not significantly different from those in the lake or between littoral and limnetic enclosures (Tables 10 and 11). However, when the zooplankton data were examined over all depths, it became clear that *D. oregonensis* were more abundant at depths below 2m. When all counts of *D. oregonensis* over all depths were analyzed together, the results showed that the limnetic mean densities were not significantly different from the mean lake densities (ANOVA, $F_{(1, 50)} = 0.00, P = 1.0$) but the littoral mean densities were significantly lower (ANOVA, $F_{(1, 50)} = 8.96, p = 0.004, \alpha = 0.05$). Mean densities of *Diaptomus* in the littoral enclosures were also significantly lower than in the limnetic enclosures. Finally, with respect to *D. oregonensis* population dynamics, the mean brood sizes of animals in the control enclosures were not significantly different from lake animals or between enclosures (Table 12).

The life cycle of Placid Lake's *D. oregonensis* has never been fully documented, however, it appears to be similar to the life cycle of this species described by Lai and Carter (1970) and to the life cycle of *Diaptomus tyrelli*, its counterpart in other lakes of the U.B.C. Research forest (Oleneck, 1983; Marmorek, 1983). Samples were first taken in 1982 in May,
shortly after ice-out. At that time, the population of *D. oregonensis* appeared to consist mostly of adult copepods, and a few nauplii (D. Robinson, personal communication). This is similar to the pattern observed in previous years (Walters, unpubl. data). Thus, it appears that this species overwinters as adults in this lake. Less than 1% of the females at this time were gravid. The females became increasingly gravid (10-60% gravid) in June. This was followed by a pulse of nauplii (peak abundance approx. 10/liter) which peaked in mid June, the tail end of which can be seen in (Figure 41). This pulse of nauplii probably represented the first annual generation and probably arose from resting eggs as well as from adults. The structure of the population (ratio of copepodites:adults) remained relatively constant over the summer with minor fluctuations in density suggesting that there was little development beyond the copepodite stage. Very few females were gravid during the summer. Peaks of copepodite abundance appeared to follow small peaks in naupliar density which occurred throughout the summer. These small pulses of nauplii may have been the progeny of the adult copepods that remained from the May adult class, or they may have been hatched from resting eggs. Finally, by early September, the majority of copepodites matured into adults. However, this was not followed by a corresponding increase in nauplii production, despite the fact that many of the females were carrying eggs at this time. Cooley (1971) described subitaneous eggs of *D. oregonensis* as being green in colour, while Daunerier, or resting eggs, are
Figure 41. Densities of calanoid naupliii. Note the change in scale of the Y-axis on the plots for the fertilized enclosures.
Densities of Calanoid Nauplii

Enclosure 1
(littoral control)

Enclosure 3
(littoral fertilized)

Enclosure 2
(limnetic control)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 7
(littoral fertilized)

Enclosure 6
(limnetic control)

Enclosure 8
(limnetic fertilized)
reddish-brown. All of the eggs that I observed being carried by adult *D. Oregonensis* were of the latter colour. Thus, unless the egg type of these copepods, in this lake, is not distinguishable by colour, the late summer egg production by adult *D. oregonensis* appears to have consisted largely of resting eggs. If so, these eggs probably spawn much of the next year's spring hatch. It appears, then, that in 1982, *D. oregonensis* in this lake were bivoltine with an early summer (June-July) generation of young and a fall production of overwintering eggs.

*Ceriodaphnia* were rare in the lake but increased conspicuously in some of the control enclosures (Figure 34). Statistical analysis was not performed to determine whether control densities were significantly different from lake densities, however, it seems that this may have been the case in at least three of the four control enclosures. The mean brood sizes of *Ceriodaphnia* in the controls were not significantly different from those in the lake (Table 12).

*Bosmina longirostris*, which like *Ceriodaphnia* is rare in the lake (Neill, 1978), became quite numerous in the 0-2 m depth stratum in all of the controls (Figure 35). Densities (Tables 10 and 11) and mean brood sizes (Table 12) of *Bosmina* in the controls were significantly higher in the lake. Densities of *Bosmina* in littoral enclosures were significantly higher than in limnetic enclosures (Table 11) but mean brood sizes were not (Table 12).

*Diacyclops thomasi* was much more abundant throughout the
summer in the control enclosures than in the lake (Figure 36). Its increase must have resulted from an enhanced food supply. Two possible food items (Bosmina and Ceriodaphnia) were more abundant in the control enclosures than in the lake. McQueen (1969) has shown Diacyclops thomasi to prey upon Ceriodaphnia and Lynch (1979) reports predation by Cyclops vernalis, a very similar species, on both Ceriodaphnia and Bosmina.

(3) Effects of Fertilization

Effects of fertilization on zooplankton abundance (Figure 30-36) were particularly evident with respect to the Cladocera. The copepod D. oregonensis also increased significantly in density over the control populations, but not to the same extent as the cladocerans. The copepod Diacyclops thomasi decreased in response to nutrient addition.

The densities of D. rosea, D. brachyurum, C. quadrangula and B. longirostris increased significantly over those in the controls (Tables 10 and 11). Mean densities of D. rosea and D. brachyurum were not significantly different between littoral and limnetic enclosures. Mean densities of Bosmina were significantly higher in the limnetic fertilized enclosures than in the littoral enclosures, a result of an extremely large bloom of these animals in September - October in enclosure 4 (Figure 35). Densities of Holopedium were largely unaffected by nutrient addition, except that this species showed a brief resurgence following a major decline in Daphnia abundance in enclosure 4 in early July (Figure 31). Holopedium disappeared
rapidly from all of the other fertilized enclosures (within one week) after the initiation of fertilization (Figure 30).

The median brood sizes of all Cladocera were also significantly higher under fertilization than in controls (Table 12). Limnetic Daphnia, Bosmina and Ceriodaphnia all had larger brood sizes than their littoral counterparts, suggesting that limnetic animals had a better quality food base. Further, the mean body sizes of gravid Daphnia and non-gravid adult Daphnia and Diaphanosoma in the fertilized enclosures were larger than in controls (Table 13, Figures 37 and 39, respectively). There was no body size distinction between littoral and limnetic fertilized enclosures.

Analysis of variance on the mean densities of Diaptomus oregonensis in the 0-2 m depth stratum of the enclosures showed that the mean densities of these copepods in the fertilized enclosures (13.2 ± S.E.=1.85 individuals/liter) were not significantly different from those in the controls (7.0 ± S.E.=0.83 individuals/liter), nor were the densities in the limnetic fertilized enclosures (16.7 ± S.E.=3.3 individuals/liter) significantly different from the limnetic controls (8.7 ± S.E.=1.1 individuals/liter)(Tables 10 and 11). These same results were obtained with respect analysis of the densities of Diaptomus integrated over all depths but the plots of the density of the organisms (Figures 29 and 33) suggest that the above significance tests may be misleading. While the mean seasonal density in the limnetic fertilized enclosures was obviously higher than in the limnetic controls, the sample
variances were statistically very heterogeneous ($F_s = 4.37 > F_{(30,30)} (a = 0.05) = 2.07$). A t-test of equality of the means of two samples whose variances are found to be unequal (Sokal and Rohlf, 1981) determined that the two means were clearly significantly different ($t_s = 3.81 > t_{(30)} (a = 0.001) = 3.65$). Similarly, the overall mean densities of *Diaptomus* in the pooled fertilized enclosures were significantly higher than in the controls ($t_s = 24.26 >> t_{(60)} (a = 0.001) = 3.46$). Similar results were also obtained for the densities of *Diaptomus* integrated over all depths. The median brood sizes of *Diaptomus* in the fertilized enclosures were also significantly higher than in controls (Table 12). Littoral copepods had larger brood sizes than did limnetic copepods. Finally, the mean body sizes of male and female adult *D. oregonensis* were significantly larger under fertilization (Table 13).

Fertilization resulted in a slightly greater proportion of *D. oregonensis* population reaching adulthood (Figure 33). This may have contributed to the dramatic increase in the densities of nauplii that occurred in the fertilized enclosures (Figure 41). However, nauplii numbers in no way corresponded to the numbers of eggs being carried by gravid *D. oregonensis* females. There were so few gravid females in samples it precluded statistical analysis, yet numbers of nauplii increased enormously. I suspect that fertilization greatly enhanced the survival of nauplii hatching from resting eggs. The increase in naupliar density resulted in significantly greater numbers of copepodites, but only in the limnetic fertilized enclosures.
The greater densities of copepodites in the two limnetic fertilized enclosures, in August, did not result in significantly higher densities of adult *D. oregonensis* in September and October than occurred in the controls or the lake. Finally, as in the controls, the late summer appearance of adults of this species, did not result in a further increase in naupliar densities.

The predaceous *Diacyclops thomasi* exhibited a negative response to nutrient addition compared to the control populations (Figure 36). This decrease may have been due to the more pronounced anaerobic conditions that occurred in the hypolimnia of the fertilized enclosures in the latter part of the summer (Figure 6). This possibility will be discussed later.

Fertilization did not affect the sequence of shifts in numerical dominance of the major herbivorous zooplankton, but as in the controls, there were some enclosure-specific differences in the magnitude and timing of these shifts.

Densities of *Holopedium* in the fertilized enclosures did not increase in abundance shortly after enclosure as they did in the controls. Instead, the few individuals that were present rapidly declined in numbers (Figure 30). This response may have been due to some form of competitive interaction with the *Daphnia*, whose populations were rapidly increasing (Figure 31).

Densities of *Daphnia* began increasing very shortly after fertilization began, at a rate which persisted (in two enclosures - 3 and 8), with minor fluctuations until late July.
Densities in the fertilized enclosures were approximately 5X higher than in their respective controls at this time. Then the populations began to decline, as they did in the controls, but in a much less abrupt fashion and to minimum mid summer densities 10-20 times higher than in the controls. Populations remained "low" until early September, then began increasing again at a rate similar to that in June-July.

Clearly, *Daphnia rosea* dominated the zooplankton community in the fertilized enclosures in terms of abundance and biomass for most of the season. Maximum densities of *Daphnia* at the times of peak abundance in all fertilized enclosures, in the 0-2 m depth stratum where densities were greatest (Figure 29), exceeded 100 individuals/liter compared to maximum densities of about 10 individuals/liter in the controls. Also, densities peaked in a bimodal fashion reaching maximum levels in July and again in September (Figure 31). Densities of *Daphnia* in the controls and the lake peaked only once in July and were at their lowest in the latter part of the summer. The autumnal peaks in abundance in the littoral fertilized enclosures were much reduced compared to those in the limnetic fertilized enclosures.

Significantly higher densities of *Bosmina* were associated with the limnetic fertilized enclosures (Tables 10 and 11). This was due to an enormous "bloom" of this species in enclosure 4 in late summer (Figure 35). Densities of *Bosmina* of this magnitude were not apparent in any other enclosure.

With one exception (enclosure 7 in early July) the populations of *Diaphanosoma* in the fertilized enclosures
achieved numerical dominance at the same time as the control and lake populations, declining abruptly in late August - early September (Figure 32). Densities in enclosure 4 in late July - early August reached a maximum of 127 individuals/liter, higher than for any other species examined.

Densities of Ceriodaphnia in the fertilized enclosures were on average 3-5 times higher than in the controls during peak abundance periods in September (Figure 34). Densities were highest in enclosure 3. The Ceriodaphnia population in this enclosure began to increase more rapidly than the populations in the other fertilized enclosures starting in mid-August.

Coincident with this rapid rise in Ceriodaphnia abundance was a dramatic decrease in the abundance of Cyclops its chief predator (Figure 36).

One final note of interest is that the proportion of daphnids in the total Daphnia population that were adults, based on the body size of the smallest gravid individuals (ca. 1.1 mm), was greater in the limnetic fertilized enclosures than in their respective controls (Figure 42). This is important in that if the objective of an exercise is to increase the biomass of food for fish, it would be also beneficial to increase the size of the fish food to the extent that the fish will utilize it. Since it has been shown above that the apparent minimum body size of zooplankton eaten by fish in Placid Lake is 1.0 mm (Northcote and Clarotto, 1975), it is clear that this objective has been met, at least in the limnetic fertilized enclosures. The proportion of adult daphnids in the littoral fertilized
Figure 42. Proportion of adult *Daphnia rosea* in the lake, and control and fertilized enclosures.
Proportion of Daphnia That Are Adults

LAKE

Enclosure 1
(littoral control)

Enclosure 3
(littoral fertilized)

Enclosure 2
(limnetic control)

Enclosure 4
(limnetic fertilized)

Enclosure 5
(littoral control)

Enclosure 7
(littoral fertilized)

Enclosure 6
(limnetic control)

Enclosure 8
(limnetic fertilized)
enclosures remained the same as in the controls and the lake.

3.4.3 Summary of Zooplankton Results

Total zooplankton biomass after the July maximum was significantly lower in the control enclosures than in the lake. Zooplankton biomass did not differ significantly between littoral and limnetic controls.

Zooplankton biomass in the fertilized enclosures increased 4-fold and 7-fold over controls in the littoral and limnetic fertilized enclosures respectively. Zooplankton biomass in the limnetic fertilized enclosures was significantly higher than in the littoral fertilized enclosures.

Qualitative changes in zooplankton community structure in the control enclosures, as compared to the lake included, a reduction in numbers of large cladocerans, an increase in numbers of small cladocerans and an increase in numbers of the major predator on the small cladocerans, *Diacyclops thomasi*. Littoral populations of the copepod *D. oregonensis* were significantly smaller than limnetic populations. Limnetic populations of the littoral cladoceran *D. brachyurum* were significantly smaller than littoral populations. Mean body sizes and mean brood of all zooplankters except *Bosmina*, whose mean brood size increased, were the same as for lake animals.

Qualitative changes in the zooplankton community structure in the fertilized enclosures compared to controls included a massive increase in the numbers of the cladocerans *Daphnia rosea* and *D. brachyurum* and moderate increases in all other
zooplankters, except Holopedium. *Daphnia rosea*, which was only numerically dominant in the controls and the lake in July, also became numerically dominant in the latter part of summer in the fertilized enclosures. All of the other species became numerically dominant in the same chronological sequence that occurred in the controls and lake, although their peak densities were about 5X higher than in controls. The body sizes and mean brood sizes of all of the zooplankters were significantly higher under fertilization.

The mean percentage of adult, hence larger, *Daphnia* increased from 33.75% in the limnetic controls to 51.30% in the limnetic fertilized enclosures. Percentages of adult *Daphnia* in the littoral fertilized enclosures remained unchanged from controls.

### 3.5 EFFECTS OF FERTILIZATION ON CUTTHROAT TROUT DIETS

This section has two purposes. First, I wish to illustrate that it may be impractical to stock hatchery reared cutthroat trout fry (0.2 - 0.3 gm) into B.C.'s coastal mountain lakes in densities suggested by the British Columbia Fish and Wildlife's fish stocking formula. Second, I wish to demonstrate that the zooplankton biomass cultivated by nutrient additions in my experimental enclosures was extensively utilized by the trout indigenous to Placid Lake.

On June 14, 1982, 50 - 55 cutthroat trout fry (3600/hectare) were added to each enclosure (Table 14). The purpose of stocking the fish in the enclosures was to measure
Table 14. The average fork length (mm) and weight (grams) and numbers of cutthroat trout fry planted in each of the control and fertilized enclosures in June, 1982.

<table>
<thead>
<tr>
<th>Enclosure no.</th>
<th>Mean Size (mm)</th>
<th>Mean Weight (grams)</th>
<th>Number Planted</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>24.6</td>
<td>0.24</td>
<td>58</td>
</tr>
<tr>
<td>2</td>
<td>25.0</td>
<td>0.29</td>
<td>53</td>
</tr>
<tr>
<td>3</td>
<td>24.2</td>
<td>0.26</td>
<td>53</td>
</tr>
<tr>
<td>4</td>
<td>26.2</td>
<td>0.29</td>
<td>53</td>
</tr>
<tr>
<td>5</td>
<td>23.9</td>
<td>0.27</td>
<td>53</td>
</tr>
<tr>
<td>6</td>
<td>25.4</td>
<td>0.28</td>
<td>53</td>
</tr>
<tr>
<td>7</td>
<td>25.4</td>
<td>0.30</td>
<td>53</td>
</tr>
<tr>
<td>8</td>
<td>24.9</td>
<td>0.28</td>
<td>53</td>
</tr>
</tbody>
</table>
and compare the relative survival and growth of the fry under low (control), high (fertilized), littoral and limnetic food levels. Stocking densities were determined using a lake stocking formula developed and employed by the British Columbia Fish and Wildlife branch (Stringer et al. 1980) for the stocking of rainbow trout in the Kamloops-Okanagan region of British Columbia.

Unfortunately, all of the stocked fish disappeared from all of the enclosures within two weeks. It is doubtful that they escaped since daily inspections of the enclosures were made to ensure that there were no holes or rents through which they could escape. However, I cannot be certain that they did not find some way out. I could find no sign of them inside the enclosure or elsewhere in the lake; they were either eaten by predators, or moved into protective refuges (under the Sphagnum mat or, if they escaped to the lake, in the inlet or outlet streams, etc.). The only conclusion I could draw from the disappearance of the planted trout fry, was that fry survival was not enhanced despite protecting them from predation by indigenous adult fish through enclosure, and despite increased food levels in the fertilized enclosures.

Beginning in mid July, however, several groups of adult fish were observed cruising and feeding within the enclosures, and, at times, fish were seen jumping over the enclosure perimeters, into and out of the enclosures. All of the enclosures were being invaded by extraneous fish from the lake. Since I had lost the opportunity to measure changes in growth
and survival of juvenile cutthroat trout, I felt that any concerted effort to remove and exclude extraneous trout from the enclosures would have been too difficult, too costly and too time consuming. Besides, the invader fish provided an excellent opportunity to see whether these particular fish would exploit an enhanced food base in the form of crustacean zooplankton, since these fish have been shown to be consistent planktivores in other studies (Andrusak and Northcote, 1971; Shepherd, 1973; Northcote and Clarotto, 1975).

The results of fish stomach analysis on fish netted (with gill nets) in the enclosures show that the trout utilized the enhanced zooplankton standing crop, particularly Daphnia (Table 15). Mean numbers of Daphnia in the stomachs of fish netted in the fertilized enclosures were, on average, 27 times higher than in the controls or the lake.

D. rosea was an important prey item over the whole summer in the fertilized enclosures. Fish in the control enclosures and the lake appeared to feed extensively on the Daphnia and Holopedium in the early summer but began to rely more heavily on terrestrial flying insects, ephemeropteran and zygopteran larvae, chironomid larvae and Chaoborus as crustacean zooplankton became less abundant, in August. Fish in the fertilized enclosures rarely took terrestrial flying insects or insect larvae. Two out of the three fish caught in the littoral fertilized enclosures in August were found to have eaten many terrestrial insects. Very few zooplankton were in their guts which leads me to believe that these two fish were only recent
Table 15. Mean numbers of prey items in the stomachs of cutthroat trout captured in Placid Lake, and in the control and experimentally fertilized enclosures in 1982. A dash indicates that those species were not present in the gut.

<table>
<thead>
<tr>
<th>Prey Species</th>
<th>July</th>
<th>Aug</th>
<th>Sep</th>
<th>July</th>
<th>Aug</th>
<th>Sep</th>
<th>July</th>
<th>Aug</th>
<th>Sep</th>
<th>July</th>
<th>Aug</th>
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<th>Aug</th>
<th>Sep</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LAKE</td>
<td>Littoral Controls</td>
<td>Limnetic Controls</td>
<td>Littoral Fertilized</td>
<td>Limnetic Fertilized</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holopedium</td>
<td>988</td>
<td>36</td>
<td>7</td>
<td>43</td>
<td>1</td>
<td>-</td>
<td>51</td>
<td>-</td>
<td>0.5</td>
<td>0.7</td>
<td>392</td>
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immigrants to the enclosures.

Holopedium and Diaptomus kenai were found in a few cutthroat trout stomachs at times when those species were not recorded or appeared in very low densities in plankton samples taken at the same time (c.f. D. Kenai in August in the fertilized enclosures, Table 15). Perhaps these species were concentrated near the bottom of the lake where the sampling gear could not be used effectively. If so, trout feeding on these zooplankters would have occurred below 5m, a full 2m below the maximum depth sampled. These trout tend to move into deeper waters (4-6 m) as the summer progresses (Andrusak and Northcote, 1971). This would explain the low numbers of fish captured in 3m nets in August and September (Table 15).
4.0 DISCUSSION

4.1 Effects of Enclosure

Isolation of the water column within plastic or wooden enclosures (limnocorals) for the purpose of simulating natural lake conditions is a method that has been employed by limnologists for various investigations since the early 1960's (Goldman, 1962; Freshwater Biological Association, 1963). Limnocorals allow the investigator to perform several short-term experiments in a lake simultaneously. Further, controls can easily be established to judge the effects of biotic or abiotic manipulations on the chemical environment or on phytoplankton or zooplankton community ecology.

With small (1-2 m diameter) enclosures it is difficult to maintain natural phytoplankton or zooplankton populations for long enough periods to evaluate seasonal changes in biocenoses. Over long periods, plankton communities in small enclosures come to resemble pond or lake littoral communities. In response to this problem, limnologists (Lund, 1972; Reynolds, 1979) began to investigate the use of large (approx. 100 m²) enclosures with the hope that they would better represent the study lake's physical, chemical and biological environs.

To date, few studies have documented whether long-term impoundment of natural lake waters inside large limnocorals in any way alters the physical, chemical or biological environment. In many limnocorral investigations, the abiotic or biotic parameters measured in the control enclosures are seldom
compared to those in the parent lake. Since the value of an experiment, where the results are to be applied to the lake or lakes as a whole, depends on the behaviour of the dynamics of the control enclosures resembling those in the lake, this is a relevant concern.

4.1.1 On Physical Conditions and Water Chemistry

My results show that the physical and chemical environment inside large enclosures generally remained unaltered from ambient conditions in this small, shallow polymictic lake for 5 months in the summer of 1982. Moreover, the chemical environments in enclosed littoral regions were qualitatively similar to those in enclosed limnetic regions.

There was only one anomalous chemical result. That occurred in littoral control enclosure 1 and it is doubtful that this result was due to enclosure. Mid to late summer epilimnetic pH values in this enclosure rose to much higher levels (pH = 8.0) than in all other treatment enclosures, including the fertilized ones (Figure 15). The pH exceeded 7.0 for most of the latter part of the summer, declining to normal levels at fall overturn.

One mechanism which may explain such an increase in pH is an occurrence of a phytoplankton or epibenthic algal bloom taking up significant quantities of CO₂ (causing a shift in the carbonate-bicarbonate equilibrium towards carbonate), resulting in an overall decrease in hydrogen ion content of the water. The data give no indication that a phytoplankton bloom occurred.
Though I have no direct evidence to rule out a bloom of epibenthic algae, there were no visible signs that such a bloom might have occurred (personal observation). Welch (1952, page 122) reported that epilimnetic waters in lakes having a sphagnum dominated littoral region can exhibit strikingly different pH levels in areas in close proximity to each other, however, no examples or causal mechanisms were given.

In the next few paragraphs, I will attempt to resolve why the nutrient concentrations in the littoral control enclosures were the same as in the limnetic control enclosures.

Littoral macrophytes are important in the cycling of nutrients, functioning as both a source (Rigler, 1964; McRoy, 1972; Wallsten, 1979) and a sink (Coffin et al., 1949; Hayes and Coffin, 1951; McRoy, 1972) for inorganic reactive phosphorous. However, Rigler (1964) showed that return of reactive phosphorous from the littoral to the epilimnion during the summer in small lakes was 20% greater than loss. The littoral is also a major site of nitrogen flux. Internal sources of nitrogen to the water column are largely from the sediments (Keeney, 1973). Mixing of surficial sediments by water movements, activities of benthic organisms and gas bubbles, and simple diffusion processes will all contribute to the N supply of overlying waters. These processes would have a more profound impact on littoral epilimnetic nitrogen concentrations than the same processes occurring in deeper hypolimnetic waters would have on limnetic epilimnion concentrations. Translocation of nutrients from the littoral zone to the epilimnion of lakes has
been well documented (Schroder, 1975; Lie, 1977). This, one could argue, could lead to higher nutrient concentrations in epilimnetic waters in littoral enclosures than in limnetic enclosures, since nutrient transport to the limnetic zone was obstructed by an impermeable barrier and the volume of the epilimnion was smaller in the littoral than in the limnetic enclosures. I found, in fact, that in the control enclosures, the littoral epilimnion had roughly the same nutrient concentrations as in the limnetic zone.

The dominant littoral macrophyte in all of the littoral enclosures was Sphagnum spp. We know from work done in mires and peatlands (Moore and Bellamy, 1974) and in bog lakes (Coffin et al., 1949; Hayes and Coffin, 1951; Rigler, 1956) that Sphagnum can function as a nutrient trap. Thus, it may be that both N and P released from littoral macrophytes and sediments in Placid Lake were bound up in the peat rather than cycled into the epilimnion. P absorption by Sphagnum has been documented in studies done in bog lakes (Coffin et al., 1949; Hayes and Coffin, 1951; Rigler, 1956). Also, Sphagnum mats are major sites of cation flux in lakes (Gorham, 1956; Clymo, 1963; Craigie and Mass, 1966). Since the main inorganic form of nitrogen released by sediments is the cation ammonium (Keeney, 1973), it too was probably taken up by Sphagnum.

Thus, it is not surprising that the littoral control enclosures did not develop higher concentrations of inorganic nutrients in their epilimnetic waters. It appears that under natural conditions the concentrations of inorganic nutrients in
Placid Lake, may be maintained at an equilibrium level where the rate of supply is balanced by the rate of loss. If so, one should not expect a net increase in inorganic nutrient concentrations in the water column unless the water receives a significant amount of nutrient.

In lakes not affected by direct human activities, nutrient increments occur in the form of precipitation, runoff and stream discharge. These processes are also the major allochthonous sources of free nutrients to Placid Lake. That precipitation is a major nutrient source is clearly illustrated by the conspicuous increases in nutrient levels in the water column during the only two major pluvial events that occurred in the summer of 1982, in August and September (Figures 8-15). The nutrient pulses are also evident even in the limnetic enclosures which would receive no surface runoff or stream carried nutrients, only those that are rain borne. However, this input rarely occurred over the summer and it was rapidly depleted by algal assimilation and/or a probable net flux into the sediments.

Since there were no obvious differences in the nutrient regimes of the littoral and limnetic enclosures and allochthonous nutrient sources were minimal, it is likely that autochthonous nutrient recycling mechanisms like zooplankton assimilation and excretion (Hargrave and Geen, 1968; Richey, 1979; Taylor, 1984) and sediment desorption and diffusion or resuspension and diffusion processes (Syers et al., 1973; Keeney, 1973; Lijklema et al., 1983; Twinch and Peters, 1984)
supplied almost all of the nutrients available for biological production during the summer months. Nutrient remineralization by zooplankton does not provide inorganic nutrients at rates comparable to rates of supply of nutrients from allochthonous sources during winter months (Lehman, 1980). However, the rate of supply of nutrients from the former process is sufficient to supply a sizable fraction of the daily N and P requirements of the phytoplankton during summer months when external sources are at a minimum (Lehman, 1980). Krause (1984) has shown that the zooplankton in Placid Lake are important in this regard in years when allochthonous nutrient sources are minimal.

The water temperature profile for Placid Lake (Figure 5) shows that thermal stratification in 1982 was weak and no definite stable epilimnion existed. Also, only 17% of the total lake volume lies below 4 m (Table 1), the depth at which a weak density gradient appeared to exist. This leads me to believe that the epilimnion depth for 1982 was essentially the entire depth of the lake. Thus, vertical flux of released inorganic nutrients from sediments may also have been an important internal nutrient source. Because the lake is sheltered from strong winds, it is doubtful that enough wind energy can be generated to result in significant nutrient fluxes by direct entrainment of the mixed waters over the sediments (Stauffer and Armstrong, 1984). Therefore, I surmise that diffusion of nutrients into the epilimnion from sediment pore waters was a more likely source of free inorganic nutrients.
4.1.2 On Phytoplankton

Since the physical and chemical regimes in the enclosures were close replicates of each other and the lake, it is not surprising that the vertical and seasonal distributions of chlorophyll a in all control enclosures were similar to those in the lake. However, significantly higher concentrations of phaeophytin occurred in all control enclosures at 2-4 m. I suggest that this may have been due to sedimentation of seston on the weak density gradient that existed at 4 m. Thus, one consequence of enclosure may be that metalimnetic entrainment of the water column may have been impeded, preventing the resuspension of the accumulated dead and dying plankton. This is possible since the circulation inducing action of the wind would have been impeded by the flotation gear at the sides of the enclosures.

The difference in the mid summer phyletic composition of the algae between limnetic enclosure 2, which was dominated by the blue-green alga *Merismopedia*, and all of the other controls and the lake is puzzling since gross physical and chemical characteristics were the same for all cases. One reason for this difference may be that calanoid copepods rather than cladocerans dominated the mid summer zooplankton assemblages of the limnetic controls. They also occurred in much higher densities than in the other controls or the lake. Calanoid copepods have a much greater capability than do cladocerans for selecting food based on size (Richman et al. 1980; Alcaraz et al. 1980), taste (Poulet and Marsot, 1978,1980) and shape
(McNaught et al. 1980). Given this, it is possible that D. oregonensis can avoid even small amounts of toxic or unmanageable blue-green algae in the heterogeneous mixture of food particles that makes up their environment. Selective feeding by D. oregonensis may have resulted in a larger pool of free nutrients being made available to the ungrazed blue-greens and subsequently resulted in their dominance of the algal community. This argument assumes that the more passively feeding Cladocera cannot or do not avoid ingesting toxic algae that appear in low abundance relative to non-toxic forms; there is evidence to support this assumption (Porter, 1977). A similar, but less pronounced dominance of blue-green algae occurred in limnetic enclosure 6 (Figure 22). Enclosure 6 had significantly higher numbers of Diaphanosoma (5-6/liter) than enclosure 2 (2-3/liter) during mid summer, so there may have been a significant grazing pressure exerted on the blue-greens in this enclosure negating the effect of selective feeding by the copepods.

4.1.3 On Zooplankton

There was a rapid extinction of Holopedium from all of the limnocorral within two weeks after enclosure. Holopedium has always disappeared from smaller enclosures in other experiments even where fish were excluded (Oleneck, 1983; Marmorek, 1983; Neill, pers. comm.). I do not believe that the disappearance of Holopedium from my large bags was due to enclosure since the enclosures resembled the lake in all measured aspects of
nutrients and food; rather, it may have been due predation on zooplankton by cutthroat trout, which invaded all treatment enclosures and were probably more dense in the enclosures than in the lake (discussed below). This may also explain why densities of Daphnia during late summer were significantly lower in all control enclosures compared to the lake.

Densities of Diaphanosoma were significantly lower in the limnetic controls than in the littoral controls or the lake (Table 11). This is not surprising since D. brachyurum is most commonly found in the littoral margins of lakes and is limnetic only in small lakes (Brooks, 1959). D. brachyurum in Placid Lake had unfettered access to the limnetic region of the lake and may have had constant recruitment from larger littoral populations. Thus, they were relatively abundant at the limnetic lake sampling sites. However, the populations of Diaphanosoma in the limnetic controls arose from organisms that were "enclosed" when the species' densities were low, in early June, and there was no recruitment from the littoral zone, so the population remained small. Less than 10% of the population consisted of gravid females which suggests that their level of reproduction may have been too low to allow the population to do more than maintain it's numbers.

In contrast, densities of Diaphanosoma were significantly higher in the littoral enclosures than in both the limnetic enclosures and the lake. There are 2 possible explanations for this aside from the fact that Diaphanosoma is, generally, a littoral cladoceran (Brooks, 1959) and would be expected to
occur in greater densities there. First, the littoral population was "enclosed" and could not disperse, so there was no dilution of population numbers. Second, reduced overall abundances of *Holopedium* and *Daphnia* in the enclosures, compared to lake numbers, may have alleviated some form of competitive interaction acting to hold down *Diaphanosoma* numbers in the lake.

While observed densities of *D. oregonensis* were significantly lower in the littoral controls than in limnetic controls and the lake (Figure 33), it is possible that the actual densities of *D. oregonensis* in the littoral enclosures were as high as in the lake and the limnetic enclosures. Pelagic crustaceans are known to exhibit a behaviour pattern known as "Uferflucht" or "avoidance of shore" in response to changing light regimes (Siebert, 1980). This pattern of movement occurs as shadows cast by shoreline features lengthen during the day. The copepods migrate out of the shaded areas. If *D. oregonensis* exhibits such a behaviour, most of the copepods in the littoral enclosures would migrate towards the enclosure wall separating the littoral from the limnetic zone (that would occur in the enclosures on the south side of the lake), or towards the side of the enclosure least likely to cause shading (the north side of the enclosures on the northwest side of the lake). This migration might have occurred, since the afternoon sun was almost always partially blocked by mountains and trees lining the lake's southern and southwestern shore. This blockage of the sun resulted in shadows falling on
littoral enclosures 1 and 3 over most of the summer. Such "avoidance" migrations, if they occurred, would lead to biased estimates of population size because the animals would be removed from the "open water" of these enclosures (the area that was sampled). The fact that densities of *D. oregonensis* in littoral enclosure 5 were significantly higher than in littoral enclosure 1 (ANOVA, $F_{(1,3)} = 7.95, p = 0.008$) makes this surmise seem probable since animals in enclosure 5, because of its location, could not be affected by shadows.

4.1.4 On Intensity of Trout Predation on Zooplankton

I argued above that fish predation was likely to be much more intense in the enclosures than in the lake, resulting in some profound changes in the densities of *Holopedium* and *Daphnia* that could not be attributed to other features of the enclosures. This section presents the basis for that argument.

As noted earlier, in mid to late July several adult cutthroat trout were observed several times over the summer (observations made from surface) inside all of the enclosures. As many as 5-10 fish were observed at any given time. Based on a surface area of approximately 0.015 hectare, I conservatively estimate fish abundance was on the order of 300-600 fish/hectare inside the enclosures. The only available population estimate for fish in the lake was made by Shepherd (1973). He estimated the population to be around 300 fish or 160 fish/hectare (based on a surface area of 1.87 hectares). One could argue that the fish population in Placid Lake in 1982 was not the same as in
1973, or that the original estimate may have been too low, but there are no data to support these objections. Thus, based on available estimates, it appears that fish abundance inside the enclosures may have been from 2-6 times higher than in the lake.

The data are consistent with the hypothesis that fish predation was more intense in the enclosures. Densities of *Holopedium* and *Daphnia* in all of the control enclosures declined to much lower levels than in the lake, to the extent that adults of both species were undetectable (or nearly so) in the enclosures by late August (Figures 30 and 31). Also, the body sizes of all adult (and egg-bearing) daphnids in the control enclosures, which ranged between 1.3 and 1.6 mm in length before fish invasion, decreased sharply to around 1.0-1.1 mm within 1-2 weeks after the fish were first detected (Figure 37). Since the majority of the trout in Placid Lake are usually found near the lake's south shore (Shepherd, 1973), the probability of more fish encounters occurring within the south side enclosures (1 and 2, Figure 3) may explain why *Daphnia* body sizes declined more rapidly in those enclosures than in the control enclosures situated on the northwest side of the lake (enclosures 5 and 6, Figure 3). *Daphnia* juveniles also exhibited a slight decrease in body size as the summer progressed (Figure 37). Similar reductions in the sizes of *Daphnia* also occurred in the lake, however, a mean body size of between 1.0-1.1 mm was not realized until mid-September, more than one month later than in the enclosures (Figure 37). Other workers (Green, 1967; Wells, 1970; Warshaw, 1972; Northcote and Clarotto, 1975) have observed
similar reductions in offspring and adult size in zooplankton species exposed to fish predation.

Overshadowing the assumption that fish predation was responsible for the reduced body sizes of daphnids in the controls and the lake, are reports that food quantity (Hall, 1964; Brombilla, 1980), food quality (Taub and Dollar, 1969) and water temperature (Culver, 1980) have all been implicated in the control of body size in Daphnia. However, with respect to changes in the body sizes of daphnids in this study, these 3 factors can be ruled out. There is no evidence that the food quantity (Appendix 3) or food quality (Figures 22 and 24) changed in the controls compared to the lake, particularly over the time that the sizes of daphnids in the control enclosures dropped most rapidly (late July - early August). During this time the density of grazable algae in all controls and the lake were similar. Also, there were no major differences in the species composition of the algae in the controls and the lake. If temperature was a factor controlling daphnid body size in this system, then daphnid sizes in the fall should have returned to early summer levels in response to decreasing water temperatures (Culver, 1980). This did not occur.

Thus, fish predation is the most likely mechanism controlling the abundance and body sizes of the two major prey species in Placid Lake. This is reinforced by the observation that during late summer, when predation on zooplankton by the trout is most intense (Northcote and Clarotto, 1975; Neill, 1978), the body sizes of the daphnids declined to their lowest
levels (1.0-1.2 mm). This suggests that 1.0 mm may be the minimum body size of zooplankters upon which the cutthroat trout feed. Indeed, the body sizes of *Diaphanosoma* (Figure 39) and *D. oregonensis* (Figure 40), two species which are only rarely eaten by the trout, seldom exceed this "threshold" size limit.

As noted earlier, smaller cladocerans were much more abundant in the control enclosures than in the lake. This observed shift from a population dominated numerically by larger cladocerans (in this case *Holopedium*, *Daphnia* and *Diaphanosoma*) to one dominated by smaller cladocerans is characteristic of zooplankton communities subjected to intense predation by visually feeding predators (Lynch, 1978, 1980; Zaret, 1980). Since the algal food resources in the control enclosures were not significantly different in terms of quality and quantity from those in the lake, differences in food were not likely a causal factor in the observed species shift.

The almost complete eradication of *Holopedium* from all of the control enclosures is also suggestive of more intense fish predation occurring within the enclosures. The seasonal decline in this species that occurred in both the lake and the controls is similar to declines noted by Stenson (1973) for lakes in Sweden. He found very significant negative correlations between increased fish activity, abundance and numbers of fish fry and *Holopedium* density. Not one of several physical or chemical variables tested were correlated with declines in *Holopedium*. 
4.2 Effects of Fertilization

The principal purpose of this section is to establish the effects of frequent additions of inorganic nutrients containing N and P in an atomic ratio of 40:1 (21:1 by weight) on the abiotic and biotic characteristics of Placid Lake.

4.2.1 On Water Chemistry

From the data in Section 3.2.2 it is quite apparent that the concentrations of all of the nutrient species examined increased in the fertilized enclosures compared to the controls. Some of the observed changes were very interesting, particularly with respect to inorganic N and P.

(1) Phosphorous

\((\text{NH}_4)_2\text{HPO}_4\) was added in three equal doses (3.3 ugP/liter of epilimnion) each week for 16 weeks to the fertilized enclosures so as to raise the allochthonous phosphate input by 10 ugP/liter of epilimnion per week. Additions of this magnitude and frequency resulted in detectable levels of ortho-P occurring in all of the fertilized enclosures, at all depths, until early August (Figure 8). Early summer concentrations of ortho-P in these enclosures reached as high as 10 ug/liter, the amount of P being added on a weekly basis. This is in direct contrast to observations made in other lake fertilization studies (Coffin et al., 1949; Rigler, 1956; Schindler et al., 1971, 1973; Stockner et al., 1980), where similar or higher phosphate loading rates
were applied to whole lakes but epilimnetic concentrations of ortho-P were found to be undetectable within 1-2 hours after fertilization. Why did such rapid depletion of the added phosphate not occur in my enclosures?

I propose 4 possible mechanisms which may have interacted to produce this apparent lack of P utilization. There may be others, but I feel these are the most important.

1) The first few fertilization events may have saturated the cell phosphate quota requirement of the existing phytoplankton such that frequent subsequent additions may not have been taken up so rapidly as if the phytoplankton had been in a P-starved state.

2) The growth of the phytoplankton in Placid Lake may not have been limited by phosphorous therefore, phosphorous demand was low.

3) Until late summer, biomass of larger (and perhaps not grazer limited) algal forms was low and grazer limited smaller forms might have been unable to take up all of the added nutrient.

4) The added phosphorous may have been rapidly assimilated by the phytoplankton but zooplankton grazing pressure could have been so intense that all of the ensuing phytoplankton production could be cropped and the
nutrients recycled by the zooplankton at a rate equal to or greater than phytoplankton uptake rates.

I will discuss each possibility in the order presented above.

The nutrient addition experiments cited above involved either one-time additions of phosphate (Coffin et al. 1949; Rigler, 1956) or once weekly additions of N and P over 15-20 weeks during the summer (Schindler et al., 1971, 1973; Stockner et al., 1980) to phosphorous-limited phytoplankton communities.

P-uptake by phosphorous starved algae is rapid and is a function of both internal and external substrate concentrations (Rhee, 1980). When the internal concentration of P is low, uptake rate is high and vice versa. Therefore, phosphorous starved algae will have extremely rapid P-uptake rates. Jeanjean et al. (1970, cited in Halman and Stiller, 1974) reported maximum P-uptake rates, for very dense populations of P-starved algae, of $2.17 \times 10^6$ ug/liter/hour. More conservative estimates of P-uptake by phosphorous starved lake phytoplankton populations range from 0-30 ug/liter/hour (Halman and Stiller, 1974; Lean and Pick, 1981) at external P concentrations ranging from 0-50 ug/liter P (for algal biomasses of 5000 ug/liter in the first study and 300 ug/liter in the latter).

Virtually all measurements of P-uptake by phytoplankton arise from studies of the response of P-starved algae to a single dose of nutrient. I have not found one report that addresses the question of how phytoplankton would respond to subsequent, repeated additions of P. However, it is possible to
visualize a scenario in which one dose of phosphate may be enough to saturate the P-debt (nutrient requirement) of a phosphorous deficient algal community, thereby reducing the demand for, and the rate of uptake of, that nutrient, to the degree that subsequent additions of that nutrient would be taken up very slowly or not at all (Paul J. Harrison, personal communication). Because photosynthesis and cell growth are suppressed when algae are replenishing nutrient stores (Lean and Pick, 1981), cell division may not occur for several days (Gerhart and Likens, 1975). Since I fertilized every 48 hours, in the time following a nutrient addition, algal P-debts may have been saturated (assuming they were deficient in phosphate to begin with) and algal biomass may not have yet begun to increase. Therefore, additional phosphate would have been more or less surplus to algal requirements. Weekly fertilizations give algae more time to assimilate the added nutrient and return a P-starved state, so that the next nutrient pulse would be more likely to be assimilated immediately after it was made available.

It could be argued that in the studies of Schindler et al. (1971, 1973) and Stockner et al. (1980) phytoplankton biomass levels were higher so there were more algae available to take up the added nutrients, but this was not the case. Total chlorophyll values (uncorrected for phaeophytin) in the SEP lakes prior to fertilization, averaged 0.88 ug/liter (Stephens and Stockner, 1983). Levels in Lake 227 were slightly higher, 1-5 ug/liter (Schindler, 1973). These values are very close to
the values observed in Placid Lake in 1982 (0.96 ug/liter, this study, Table 6). It should be pointed out that in both of these studies, the nutrients, per addition, were added in amounts 3 times (10 ug/liter P) greater than I added to my enclosures at any one time (3.3 ug/liter P), yet the phosphate was still depleted within one hour.

Above, I alluded to the possibility that the growth rate of algae in Placid Lake may not have been limited at all by phosphorus, hence the demand for this nutrient was low and the added nutrient was not being rapidly assimilated. I will now address this further. Nutrient limitation can be inferred from nitrogen:phosphorous ratios in phytoplankton. Healey (1975) and Healey and Hendzel (1980) suggested that N:P ratios > 10 imply phosphorous limitation. The average summer N:P ratio of the algae in Placid Lake, in 1982, was 9, which is indicative of nitrogen rather than phosphorous limitation (Healey and Hendzel, 1980). Since the rate of P-uptake is a saturating function of both internal and external substrate concentrations (Healey, 1973; Rhee, 1980), this means that P-uptake rates by algae with low N:P ratios will be slower than if the algae were phosphorous limited (N:P > 10), and growth rate will be unaffected by external P concentration.

Biomasses of algae similar to those found in the fertilized enclosures in the early summer (200-300 ug/liter dry weight), in a system where P was known to be the limiting nutrient (Kooteney Lake, B.C), were found to take up phosphate at a rate of 0.20 ug/liter/hr at an external P concentration of around 3 ug/liter
(Lean and Pick, 1981), the concentration I was adding at each addition. If these conditions prevailed in my enclosures, this level of algal biomass, if it was P-limited, should have depleted at least 1.0 ug of the added P within 5 hrs. In fact, the concentrations of inorganic phosphorous in my fertilized enclosures showed no apparent decline up to 6 hours after the nutrient was added. Phosphate concentrations were found to be much higher (6-10 ug/liter) after addition than what was being added (3.3 ug/liter), suggesting that even very little P from the previous nutrient addition had been taken up. This is consistent with the above suggestion that phosphate was not in great demand in this system.

It appears then, that the low standing stock of algae in Placid Lake may not be a result of a lack of phosphate as we have believed. Rather, there may be enough phosphate available to support maximum growth rates of the algae at existing, or even slightly higher biomass levels. There is evidence to support this hypothesis. Zooplankton removal experiments, performed in enclosures in Placid Lake, revealed that algal biomass increased by as much as 50 % in enclosures without zooplankton over those with zooplankton (Krause, 1984). (It should be mentioned that these enclosures were dosed with small quantities of fertilizer but they were only sufficient to replace the phosphate that would normally be recycled by the zooplankton).

The latter point, that zooplankton removal experiments resulted in increased algal biomass, suggests a third mechanism,
zooplankton grazing, which may partially explain the apparent lack of P-uptake by the algae. The phytoplankton that dominated the algal biomass at the onset of fertilization were small (<20 um), edible algal forms, making up as much as 70-90% of the biomass, depending on the enclosure (Figure 26). Large, ungrazable algae were relatively scarce. These small algae must have been growing and dividing rapidly following fertilization as evidenced by the exponential increase in the numbers of *Daphnia rosea*, the juveniles and adults of which feed on algae <20 um in size (Burns, 1968a; Neill, 1975; Krause, 1984). The ensuing grazing rate must have been such that 100% of the new algae produced, was being cropped, since neither algal biomass, nor the percent composition of these small algal forms in the total biomass, increased. Thus, zooplankton appeared to be removing any new cells which would otherwise be taking up the added P. It may be then, that the small biomass of algae remaining in the system was unable to take up all of the added P. There is a weakness to this argument however. If the algae were not P-limited, as suggested by N:P ratios, then adding P should have had no effect on algal growth rates. Therefore, in order to increase cell division rates under these conditions, some other nutrient in the fertilizer must have been limiting cell division rates. The N:P ratios suggest that nitrogen was the limiting nutrient. This will be discussed later.

Perhaps zooplankton grazing and their subsequent recycling of nutrient in tandem were responsible for the observed phosphate pool. There is no doubt that zooplankton
remineralization of P would contribute some of the P that was measured. However, it does not seem likely, given published zooplankton remineralization rates, that the amount of P measured in the fertilized enclosures could be wholly attributed to zooplankton excretion. Peters and Rigler (1973) determined that only an estimated 14.8% of the total P of the trophogenic zone of eutrophic Heart Lake, Ontario, was regenerated daily, directly or indirectly, by zooplankton grazers. The greatest portion of the ingested P was converted into zooplankton biomass.

I calculated zooplankton excretion rates for the animals in the fertilized enclosures using the equation for excretion rate \( E \) (ug/liter/hour) derived by Peters and Rigler (1973). The equation is

\[
E = 0.0286 \times e^{(0.0378T + 0.00001C - 3.34P)} \times W^{-0.383} \tag{1}
\]

where \( T \) is temperature in degrees Celsius, \( C \) is food concentration in cells/ml, \( P \) is phosphorous concentration in the food in ug/ml and \( W \) is dry weight of zooplankton in mg. This equation was derived for excretion by \textit{Daphnia} and is valid in this case because \textit{Daphnia} made up the greatest proportion of the biomass in the fertilized enclosures at this time.

The mean surface temperature for July, 1982 in Placid Lake was 18.5 °C. The average concentration of food in the epilimnion of the fertilized enclosures was not easy to determine because zooplankton grazing was very intense, but a
conservative measure would be $1 \times 10^4$ cells/ml. Particulate P measurements in the epilimnion of the enclosures averaged 9-15 ug/liter. Not all of this was phytoplankton, but to be conservative, I chose a value of 10 ug/liter P (0.01 ug/ml P). The average dry weight of zooplankton in the enclosures was around 0.250 mg/liter. Using these values, $E = 0.105$ ug/liter/hour, which was remarkably close to the rate of phosphate regeneration by *Daphnia rosea* (0.08 ug/liter/hour), measured by Peters and Lean (1973), and by a natural lake zooplankton community (0.076 - 0.49 ug/liter/hour) measured by Lehman (1980). My value may have been slightly overestimated because I was liberal in my determinations of food availability and its P content.

The P-uptake rate of 0.20 ug/liter/hour for the P-starved Kooteney Lake phytoplankton biomass levels (mentioned above), suggests that, at that level of biomass, the algae in my enclosures could be taking up P at more than twice the rate than it could be supplied by the zooplankton. Thus, while the zooplankton in my fertilized enclosures may have contributed a significant proportion of the P made available for phytoplankton growth, it may have been taken up immediately thereby making it undetectable in the water column. Therefore, it is unlikely that zooplankton were responsible for the detectable phosphate pool in the fertilized enclosures except in so far as they limited phytoplankton biomass increases and hence the algal biomass available to take up and hold P in particulate form.

The evidence provided thus far suggests that, at the
biomass levels of algae present in Placid Lake in early summer, phosphorous was not imposing major limitations on algal growth rates or abundance. Added phosphate was not used up as quickly as would be expected for a P-starved algal community. Could it be that the spring-early summer growth of phytoplankton in this lake is limited more by the availability of nitrogen rather than phosphorous? The low ratios of TN:TP suggest that this may be so.

(2) Nitrogen and Possible Nitrogen Limitations on Phytoplankton Growth

There is circumstantial evidence that inorganic nitrogen may be in short supply during the spring and early summer in one of the other U.B.C. research forest lakes. Dickman (1968) found that the addition of nitrate nitrogen to enclosures in Marion Lake induced significantly higher spring and early summer primary production values than did phosphate. Further, added nitrogen disappeared 4 times faster (20 ug/liter/day) than phosphate (5 ug/liter/day) (Dickman, 1968 - Figure 4). This suggests that inorganic nitrogen may have been in greater demand.

Inorganic nitrogen in the form of NH₄⁺ and NO₃⁻ did not disappear rapidly from my enclosures following addition (Figures 11 and 12), except in the littoral fertilized enclosures. Concentrations of both NH₄⁺ and NO₃⁻ were as high (or higher, in the case of NO₃⁻) 4-6 hrs after fertilization as the concentration of nutrient added. This does not mean that
nitrogen was not in demand. Maximum NH$_4^+$ and NO$_3^-$ uptake rates for phytoplankton (in both freshwater oligotrophic-N-limited and eutrophic-N-sufficient systems, and in the sea), are commonly below 0.2 ug/liter/hour (Dugdale and Goering, 1967; Toetz et al., 1973; Murphy, 1980; Berman et al., 1984). At these rates, it would be impossible to measure any great declines in nutrient additions that measured 75 and 60 ug/liter (NH$_4^+$ and NO$_3^-$, respectively) in the 4-6 hours after fertilization when nutrient samples were taken. It would have taken 5 hours for the phytoplankton to deplete only 1 ug of the added nutrient, assuming maximum uptake was occurring. This slow rate of N-uptake, which occurs as a saturating function of N concentration, may explain the apparent lag periods in algal biomass increases following combined N and P additions in the waters of U.B.C. Research forest lakes (Dickman, 1968; Walters et al., in press; this study) and in the apparent lack of response of algae to additions of only N in short term enclosure studies in the same waters (W.E. Neill, personal communication).

If the growth of an algal population was limited by the availability of inorganic nitrogen and the uptake of added nitrogen was very slow despite its increased availability, then one would expect algal biomass to increase only after sufficient N had been taken up so as to allow for growth and division. Moreover, the N:P ratio at which optimal cellular growth occurs appears to be species specific (Rhee and Gotham, 1980). Thus, in the same nutrient environment, the growth of some species may
be more rapid than for others. Assuming that the extracellular N:P ratios favoured maximum growth of a species that was initially found in very low numbers in the phytoplankton soup, then rapid algal biomass increases might not occur until this (or these) species reached numbers sufficient to generate a "bloom".

Thus, while I do not have measurements of the kinetics of nitrogen uptake in my system, the low concentrations of inorganic N, the apparent slow rate of P-uptake, evidence that addition of nitrate stimulated greater primary productivity than the addition of only phosphate in a nearby lake (Dickman, 1968) and the low ratios of cellular N:P (PN:PP), all suggest that in the early summer, the primary productivity of Placid Lake may be restricted by nitrogen deficiency.

How would N rather than P limitation arise in a lake in a limnological region in which the average TN:TP ratio of lakes is 89:1 (Stockner and Shortreed, 1985), a clear indication of P limitation? The TN:TP ratio of nearby Gwendoline Lake, only 500 m to the northwest averages 30:1 (W.E. Neill, personal communication). I believe that the answer lies in the fact that Sphagnum peat mats dominate the littoral vegetation of Placid Lake.

In light of the high cation exchange capacity of Sphagnum (Clymo, 1963), the ammonium cation (NH₄⁺) should have a propensity towards being incorporated into the peat. The ionic composition of the waters in the vicinity of the Sphagnum mats then, should be one that is low in NH₄⁺. This loss factor was
evident in the littoral fertilized enclosures, where \( \text{NH}_4^+ \) concentrations were 3-5 times lower than in the limnetic fertilized enclosures (Figure 12), which did not have a water–Sphagnum interface. There may also have been greater net loss processes of \( \text{NH}_4^+ \) flux to the epilimnetic sediment-water interface in the littoral fertilized enclosures since ammonia is known to be strongly sorbed to particulate and colloidal particles (Wetzel, 1975) and to clays and organic colloids in sediments (Toetz, 1970; Brezonik, 1972; Keeney et al., 1973; Rosenfeld, 1979) and this sorption can be rapid (Brooks, 1969).

Bacteria involved in the nitrogen cycle, both aerobic nitrogen fixing and nitrifying bacteria are virtually absent from peat because of extreme physical conditions of high \( \text{pH} \) and low \( \text{O}_2 \) (Moore and Bellamy, 1974). This is of considerable importance because any \( \text{NH}_4^+ \) present in or around the peat is unlikely to be recycled as \( \text{NO}_3^- \) in the absence of nitrifying bacteria. Thus, such nutrients are effectively removed from circulation. Any nitrate produced under these conditions is probably utilized as rapidly as it is produced. This would explain why \( [\text{NO}_3^-] \) was below the limit of detection (<20 \text{ ug/liter}) at all times in the lake (Figure 11). This might also explain the lower epilimnetic \( \text{NO}_3^- \) concentrations in the littoral compared to the limnetic fertilized enclosures. An absence of nitrifying bacteria due to the presence of the Sphagnum would mean that much of the added ammonium would not be oxidized to nitrate. Conversely, the lack of a water–Sphagnum interface in the limnetic fertilized enclosures means that
nitrifying bacteria may have been more abundant in the open water, converting much of the added $NH_4^+$ to $NO_3^-$, hence, the apparent accumulation of $NO_3^-$ (Figure 11).

(3) pH change and Ammonium Nitrate-Ammonium Phosphate Additions

The lack of a significant change in the hydrogen ion content of the epilimnetic waters in the fertilized enclosures compared to the controls (Figure 15) is interesting and unexpected. Nelson and Edmondson (1955), Smith (1967) and Schindler et al. (1971, 1973) all noted significant increases in epilimnetic pH values following fertilization. In all of these studies, biologically mediated photosynthetic utilization of $CO_2$ was implicated in the observed pH changes. Primary production levels (10 - 50 ug/liter Chl a) at which the highest pH levels (9.0, up from 7.0) occurred following the fertilization of Lake 227 (Schindler et al., 1971, 1973), were similar to those obtained in my limnetic fertilized enclosures (10 - 40 ug/liter Chl a, Figure 16) without noticeable increases in pH.

High levels of ammonium ion added to my fertilized enclosures may be, in part, responsible for the observed lack of change in pH. Ammonium induced suppression of algal assimilation of nitrate and may have contributed sufficient $H^+$ ions through its own subsequent assimilation so as to buffer increases in pH caused by $CO_2$ depletion. Ammonium was not added in the studies cited above, only nitrate. The assimilation of the added nitrate would have compounded increases in pH due to
CO₂ utilization, by increasing the hydroxyl ion concentration as shown by the following equation for the assimilation of nitrate by algae (Brewer and Goldman, 1976);

$$106(CO₂) + 130(H₂O) + 16NO₃⁻ → (CH₂O)106(NH₃)16 + 160H⁺ + 106O₂ (3)$$

Most species of algae show a preference for utilizing NH₄⁺ over NO₃⁻ when both are present (MacIsaac and Dugdale, 1968, 1972; Brezonik, 1972; Eppley et al., 1979; Syrett, 1981). In fact, the addition of NH₄⁺ can lead to a rapid cessation of nitrate utilization in batch culture (Syrett, 1981). McCarthy et al. (1977) showed that this inhibition of nitrate assimilation by ammonium can also occur in natural phytoplankton populations and that the extent of the inhibition was dependent on the NH₄⁺ concentration. Concentrations of NH₄⁺ in excess of 15-30 ug/liter almost totally suppressed NO₃⁻ utilization by Chesapeake Bay phytoplankton. Since I was adding approximately 70 ug NH₄-N/liter three times weekly for 16 weeks, it seems reasonable to assume that NO₃⁻ assimilation in the fertilized enclosures would be severely inhibited and the algae would be preferentially assimilating NH₄⁺.

Assimilation of NH₄⁺ by algae could supply hydrogen ions to compensate for losses resulting from CO₂ depletion, as suggested above. The equation describing this process is as follows (Brewer and Goldman, 1976);

$$106(CO₂) + 106(H₂O) + 16NH₄⁺ → (CH₂O)106(NH₃)16 + 16H⁺ + 106O₂$$
This shows that each molecule of NH$_4^+$ assimilated by algae generates one equivalent of strong acid. However, for each molecule of CO$_2$ consumed, one hydrogen ion is removed from the system due to shifts in the carbonate-bicarbonate equilibrium (Schindler, 1973). Therefore, 6 times as many hydrogen ions are still being lost for each one produced by the assimilation of NH$_4^+$.

This imbalance may be partially offset by the synchronously occurring process of NH$_4^+$ oxidation by nitrifying bacteria. The overall nitrification reaction (Wetzel, 1975) produces 2 molecules of H$^+$ ion for every molecule of NH$_4^+$ consumed:

\[
\text{NH}_4^+ + 2\text{O}_2 \rightarrow \text{NO}_3^- + \text{H}_2\text{O} + 2\text{H}^+ (5)
\]

Unfortunately, I did not quantify the extent to which nitrification occurred in the fertilized enclosures. Furthermore, few data are available in the literature to enable one to make reasonable assumptions about probable rates of nitrification based on trophic levels or physical-chemical conditions of the waters in question. Despite the paucity of information regarding nitrification processes in the water column of lakes, many believe that nitrification can significantly reduce the quantity of ammonium (Brezonik, 1972; Hall et al., 1978; Christofi, 1981; Stewart et al., 1982) and the pH (Gerletti and Provini, 1977) in the water column during
summer stratification. In the latter study, it was found that the nitrification of ammonium led to the acidification of Lake Orta. This is evidence that nitrification can contribute substantial amounts of hydrogen ion to the water column.

Further, active cation exchange processes occurring in the walls of Sphagnum moss and free organic acids secreted by Sphagnum may be responsible for the acidity in many bog systems (Clymo, 1964, 1966), but Clymo (1966) has shown that the contribution of the latter to the overall acidity of bog waters is relatively low (< 30 % of H⁺). However, due to the nature of the construction of the enclosures, both of these processes would have only been important in the littoral fertilized enclosures. Finally, the diffusion of CO₂ into lake water from the atmosphere may compensate for losses due to algal assimilation, but this is dependent on many abiotic factors (Emerson et al., 1973).

4.2.2 On Phytoplankton

From the data in Section 3.3.1, it is quite apparent that phytoplankton production increased in the fertilized enclosures at all depths compared to the controls. Nutrient enrichment resulted in a 7-fold increase in total phytoplankton biomass in the limnetic fertilized enclosures compared to controls. The littoral fertilized enclosures responded with only a 3-fold increase in total biomass compared to their controls. This result arose despite the same concentrations of nutrient added to both littoral and limnetic habitats. The differences in the
magnitudes of the responses of the enhanced phytoplankton communities reflect the differences, discussed above, in the availability of free inorganic nutrients.

(1) Shifts in Species Composition

An interesting change in the primary producers resulting from fertilization is the shift from an algal assemblage dominated by inedible blue-green algae and large hard-to-handle (from the perspective of the zooplankton) chrysophytes towards one dominated by small, highly nutritious, edible green algae. This change was predicted to occur under the fertilization regime employed and was expected to greatly benefit the larger cladoceran zooplankton.

The species composition of the algal assemblages in the fertilized enclosures differed between the littoral and limnetic zones (Figure 22). Chrysophytes dominated the algal assemblage in the littoral fertilized enclosures from late July to late August whereas chrysophytes were largely absent from all limnetic enclosures, including the unfertilized ones. The mechanism responsible for this difference was probably related to the hydromechanical properties of the littoral zone rather than the differences in nutrient availability (discussed above) since free inorganic nutrients were available in the same relative proportions in both fertilized habitats. They differed only in the overall concentration. Turbulent mixing of the epilimnetic waters in the littoral zone would result in agitation and resuspension of littoral sediments, a condition
which would not occur in the limnetic zone. This might result in the resuspension of vegetative spores or propagules of algal species which would otherwise be confined to the sediments.

Many chrysophytes including, *Dinobryon*, *Synura*, *Mallomonas*, and *Uroglena* (all except the latter are present in Placid Lake) form persistent, siliceous cysts (Reynolds, 1982). Cysts are passive particles that can settle to sediments to seed recurrent blooms and can be resuspended from bottom sediments into environments favourable for germination. Reynolds (1982) related the poor development of *Ceratium* (a dinoflagellate) populations in Lund tubes compared to the surrounding waters, to a very low inoculation of cysts because the tubes were hydrologically isolated at the time the cysts were resuspended from sediments. An analogous situation may have existed in my limnetic enclosures in that once chrysophytes were lost to the hypolimnion through sinking, they would not be replaced by resuspended encysted forms.

The resuspension of cysts could conceivably have occurred the whole summer long in the littoral zone of the lake allowing the littoral enclosures to maintain large chrysophyte populations. Isolation of the limnetic waters by enclosure would have eliminated the "seeding" phenomenon thereby changing the successional progression of the algae. In the case of the limnetic controls, blue-green algae became dominants. In the limnetic fertilized enclosures, green algal species which were normally rare in the system were favoured.
(2) Delayed Biomass Increase

Another particularly striking feature of the response of the algal population to nutrient addition is that the total phytoplankton biomass did not increase significantly in any of the fertilized enclosures, over control levels, until 6-8 weeks after fertilization commenced. This is shown by changes in Secchi depth (Figure 7), phytoplankton cell volumes (Figure 16) and chlorophyll a (Figure 17). Similar delays in detectable increases in phytoplankton biomass have been reported following nutrient addition studies in two other U.B.C. research forest lakes (Dickman, 1968; Walters et al., in prep). I hypothesize that this result was due to the massive increase in the abundances of cladoceran zooplankton, in particular *Daphnia rosea* and *Diaphanosoma brachyurum*, that occurred immediately after fertilization began (Figures 29). The supervening grazing pressures appear to have been intense enough to result in the cropping of almost 100% of the enhanced algal production, since algal biomass increased very slowly or not at all (Figure 16) until this grazing pressure was alleviated. This did not occur until the populations of *Daphnia* declined significantly in late June or early August, depending on the enclosure examined (Figures 29).

*Daphnia* and other cladocerans usually account for 80% of the total zooplankton community grazing rate in mesotrophic and eutrophic natural lakes (Porter, 1977). Maximum community grazing rates as high as 114% (the entire volume of water) during one day have been reported for oligotrophic and bog lakes
whose dominant zooplankton were *Daphnia* (Haney, 1973). Major peaks in grazing activity were correlated with increases in the population density of the zooplankton.

I estimated zooplankton community filtering rates for my enclosures by applying the maximum zooplankton community filtering rate (3 ml/ug zooplankton/day) estimated for Placid Lake zooplankton by Buckingham (1968) to the mean (Table 9) and maximum (Figure 25) zooplankton biomass levels in my enclosures. In my control enclosures and the lake, cladocerans dominated the zooplankton community for much of the summer, however, the mean zooplankton community grazing rate (% of total water column per day) averaged only 15 % over the summer with maxima reaching about 30 % at peak biomass periods. In contrast, *Daphnia* numbers exploded in the fertilized enclosures resulting in higher overall biomasses. Total zooplankton community grazing rates increased accordingly to an average for the summer of 48 % in the littoral fertilized enclosures and 80 % in the limnetic fertilized enclosures. Maximum rates reached as high as 140 % at peak biomass periods. The filtering rates estimated by Buckingham (1968) are higher than the equivalent mean filtering rate (0.5 ml/ug zooplankton/day, assuming a mean zooplankter weight of 5 ug) that I estimated for the zooplankton species in Drowned Bog Lake (Haney, 1973, Table 4), upon which this comparison is based. Regardless, the figures show that grazers can exert significant effects on phytoplankton abundance.

Thus, increasing the abundance of cladocerans through fertilization increases the overall zooplankton grazing
pressure. This may explain why phytoplankton biomass did not increase during the first 6-8 weeks following fertilization (Figure 16) as one might expect. Zooplankton were apparently able to suppress algal biomass increases. This suppression of algal biomass appears to have been alleviated by declines in the numbers of zooplankton (Figure 25) which may have resulted from such factors as species succession of the phytoplankton (Porter, 1977; Gliwicz, 1980), overgrazing of the edible algae (discussed later), fish predation (also discussed later) or some other environmental perturbation.

The rate of phytoplankton renewal in the fertilized enclosures during the early summer zooplankton bloom appeared to match losses due to grazing. The fact that phytoplankton biomass in the fertilized enclosures increased slightly rather than decreased in response to increased grazing activity strongly suggests that fertilization enabled the phytoplankton to renew 100% or more of the algal standing crop per day. This is in accordance with the observation that phytoplankton renewal rates in most natural lakes of intermediate to extreme eutrophy are commonly around 100% (Haney, 1973). The grazing rate of the zooplankton reached maxima approaching 140% of the water column per day on several occasions, yet no observable depression in the biomass (Figure 24) or density (Appendix 3) of grazable algae occurred.
(3) Size Fraction of Enhanced Algae

It is clear from Figure 23 that fertilization favoured the production of algal species <20 um in their maximum linear dimension (MLD) starting in late August in all of the fertilized enclosures, but it is not clear what size range of particles was enhanced in early summer. This is because virtually all of the enhanced phytoplankton production was grazed by zooplankton. Further, the particle size distribution of the algal biomass was no different from that in the controls or the lake during this period (Figure 24). However, since it appears that virtually all of the early summer algal biomass enhanced by fertilization was grazed away by the zooplankton, it is possible, knowing the size range of algae that would be grazed by the zooplankton assemblage, to determine the size ranges of the algal particles that were enhanced by fertilization at this time.

There are several reports in the literature that document the size spectrum of food particles selectively fed upon by particular zooplankton species. Krause (1984) presents a review of the available data relating to the herbivorous zooplankton of Placid Lake. Together with this and with the results of her species specific grazing experiments, she concluded that all of the important grazers in Placid lake feed selectively on algal cells (of Placid Lake spp.) with a maximum linear dimension ranging from 2-20 um (Krause, 1984).

These data suggest that the huge increases in the D. rosea and D. brachyurum populations that occurred in my fertilized enclosures shortly after fertilization commenced, in June, must
have been fueled by increases in the phytoplankton within the preferred size ranges (6-20 um MLD) for these species. Also, these large cladoceran population increases imply high juvenile survival. Neill (1975) has shown that the juvenile survival of the microcrustaceans is especially sensitive to food concentration. Neill (1981) confirms this for Daphnia rosea in Placid Lake waters. Daphnia juveniles were found to exploit food particles in the 2-10 um size range. Therefore, in order for the juvenile cladocerans in my system to attain better survival, there must have been an enhancement of algal forms in the 2-10 um size range as well.

With the exception of D. oregonensis (Richman et al., 1980), none of the important grazers found in Placid Lake have been reported to feed upon food particles > 20 um MLD with any degree of selectivity or efficiency. While Richman et al. (1980) found that D. oregonensis from Lake Winnebago, Wisconsin, fed selectively on food particles within a size range of 25-30 um, Krause (1984) found that D. oregonensis in Placid lake restricted their food intake to particles in the 14-20 um size range. This is important because if none of the grazers in the fertilized enclosures fed on particles >20 um MLD, and if these particles were being enhanced by fertilization, one would expect to see a significant increase in their density. This did not occur.

There were slight increases in the densities of algal particles in the 20-30 um size range during July and August in littoral fertilized enclosures 3 and 7 and limnetic fertilized
enclosure 4 (Appendix 3), but the increases were not statistically significant. Furthermore, where small increases in this size fraction did occur, they were composed almost exclusively of the cryptophytes *Cryptomonas ovata* and *Cryptomonas erosa*, both of which, though relatively large, are readily consumed by *Daphnia* (Infante and Abella, 1985) and *D. oregonensis* (McQueen, 1967). In contrast the 20-30 um size fraction in the controls was dominated by the inedible blue-green algae *Merismopedia* and *Chroococcus* over the entire summer (Figures 22 and 24).

The observed increases in the densities of particles >20 um that occurred in littoral fertilized enclosure 7 and limnetic fertilized enclosure 8 in October (Appendix 3) were primarily due to a bloom of *Dinobryon*. My reported densities are biased upward in that these numbers represent counts of single loricas rather than complete colonies which were larger and less abundant. A major increase in the density of algae >30 um was also recorded for a single date, in June, in littoral fertilized enclosure 3 (Appendix 3). This too is artifact. The sample was contaminated by large diatoms which had probably been resuspended from littoral sediments by SCUBA divers who had been working inside that enclosure earlier in the day.

Thus, it appears that only those algal food particles in the overall size range of 2-20 um were the most likely beneficiaries of the adopted fertilization regime; small, frequent doses of inorganic nitrogen and phosphorous at a high N:P ratio.
In conclusion, fertilizer was added at a high N:P ratio (40:1 atomic, 21:1 by weight) to isolated sections of the littoral and limnetic zones of the lake. The objective was to promote increases in algal biomass, while promoting a shift in a phytoplankton assemblage from one which has been dominated in past years (Krause, 1984) by large (> 20 um), inedible blue-green algae and large, ungrazed chrysophytes, towards one that favoured dominance by small, edible algal forms in the size ranges selectively fed upon by the zooplankton in the lake. The results show clearly that there was a definite shift in the species composition of the algal assemblage. Blue-green algae comprised less than 5% of the total algal biomass in the fertilized enclosures. They were replaced by chlorophytes and cryptophytes. Large chrysophytes were virtually eliminated from the limnetic fertilized enclosures but maintained a presence in the littoral fertilized enclosures. The disappearance of the chrysophytes from all limnetic enclosures and their persistence in the littoral enclosures was probably mediated by differences in littoral-limnetic hydrodynamic processes. Fertilization did not enhance their abundance where they did occur. A dramatic increase in the abundance and biomass of cladoceran zooplankton which feed selectively on algae in the 2-20 um size range strongly suggests that this was the particle size range enhanced by fertilization in the early part of the summer. Less than 20% and more than 80% of the late summer algal biomass consisted
of particles < 20 um in size in the control and the fertilized enclosures, respectively.

4.2.3 On Zooplankton Community Structure

The primary effects of fertilization, as reflected in the zooplankton, included significant increases in the total biomass of all of the treated enclosures, compared to controls, and increases in the density (except for Holopedium gibberum) and egg production of all of the important grazers. The body sizes of adult Daphnia rosea, Diaptomus oregonensis and Diaphanosoma brachyurum were also increased under fertilization. Juvenile body sizes of these species did not increase.

Biomass in the limnetic fertilized enclosures increased 7-fold over limnetic controls while biomass in the littoral fertilized enclosures increased only 3-fold over littoral controls. Daphnia rosea consistently accounted for >50% of the total biomass for the entire season in all of the treated enclosures. The differences in biomass between littoral and limnetic enclosures can be attributed entirely to the effects of nutrient addition on the phytoplankton, as demonstrated in the previous section. The differential magnitudes of the increases between littoral and limnetic biomasses were proportional to the magnitudes of the increases in phytoplankton biomass in the respective lake zones.

The performance of the individual zooplankton species in the nutrient enriched enclosures differed in some respects between littoral and limnetic habitats. Also, there were some
enclosure specific responses peculiar to some of the species examined which may have been related to factors other than fertilization, such as predation or interspecific competition. In order to deal with each result effectively, I will discuss each species separately and attempt to identify whether food availability, competition, predation, temporal or spatial idiomorphisms or some combination of these factors were responsible for its observed pattern of abundance.

(1) Holopedium gibberum

It was surprising to find that Holopedium fared worse under fertilization than it did in control enclosures. In the controls, Holopedium densities, which were lower than lake values at the onset of enclosure, increased in abundance (to near-lake levels) shortly after the experiment began. In the fertilized enclosures, the few Holopedium that were present at the onset of fertilization, declined rapidly in numbers despite increased levels of food availability.

That food was available in abundance during this early decline is evidenced by the fact that the few Holopedium present before the decline showed dramatically increased levels of egg production. Some of the gravid individuals that were sampled were found to be carrying as many as 30-40 eggs. The maximum number of eggs in any Holopedium in the controls was 8, found in only one individual. This strongly suggests that Holopedium in the fertilized enclosures benefitted from enhanced levels of food production but some other factor acted to prevent them from
capitalizing on the resource.

One such factor may have been fish predation. However, the early demise of the Holopedium could not have been due to fish predation since fish had not yet invaded the enclosures. Also, predation on Holopedium by the juvenile cutthroat trout that were stocked in the enclosures can be ruled out as a factor since the same densities of fish were stocked in the control enclosures with no likewise effect. This is not to say that Holopedium were not affected by the fish that invaded the enclosures later, in July, as was suggested for control populations (see above). Predation by the invading adult cutthroat trout may explain why Holopedium were almost completely eradicated from all of the enclosures, both control and fertilized. The presence of Holopedium in the guts of fish captured in the enclosures, at all times over the summer (Table 15) support this assumption.

Another factor which may have prevented Holopedium from capitalizing on the enhanced food resource, is interspecific competition with Daphnia rosea, which increased dramatically in number, almost instantaneously, following fertilization. In support of this are the observations that Holopedium decreased in numbers almost as rapidly as the daphnids increased, and, that the density of Holopedium exploded in limnetic fertilized enclosure 4 following a rapid decline in the numbers of Daphnia, which fell from over 100 individuals/liter to less than 10/liter in less than two weeks. Also, the feeding rates of D. rosea, under the conditions of food concentration (ca. 300-500
ug/liter dry weight) and temperature (16 °C to 20 °C) present in the enclosures during the early part of the experiment, may have been 3-4 times higher than for Holopedium (0.1 vs 0.03 ug/ug zooplankton/hr, respectively, Buckingham, 1978), which might have given the Daphnia a competitive advantage.

(2) Daphnia rosea

Large cladocerans like Daphnia are an important food for fish in lakes. Since one of the main objectives of this study was to enhance the food for fish in trout lakes by a fertilization scheme favouring the growth of Daphnia food, I will discuss the responses of this species in some detail.

Densities of Daphnia rosea increased dramatically following nutrient addition. They persisted as the biomass dominant for the entire summer while Daphnia in unfertilized enclosures and the lake declined by late July. None of the other zooplankton species exhibited such a dramatic prolongation of their normal seasonal cycles.

In 3 enclosures out of 4, the curve representing the population size of D. rosea in the fertilized enclosures was somewhat bimodal, with high densities in the early summer and fall, and lower densities (but still higher than in the controls) in the mid-summer months. In the fourth case, that of enclosure 8, densities of Daphnia increased rapidly initially, remained stable through mid-summer, then increased again in the fall. There was no observable decline in either densities of Daphnia (Figure 31) or total zooplankton biomass (Figure 25).
The pattern of population growth, described for the other three fertilized enclosures, is often interpreted as a reflection of a food-limited system where zooplankton increase in numbers with the spring phytoplankton bloom until nutrient depletion of epilimnetic waters results in decreased levels of phytoplankton production and the food supply is overgrazed. Overgrazing results in a decline in zooplankton numbers which is maintained by low rates of algal production and a dominance of large net phytoplankton characteristic of summer algal assemblages. Nutrient recharge to the epilimnion from hypolimnetic waters at fall overturn results in increased phytoplankton production and subsequent increases in zooplankton numbers.

Why did the numbers of *Daphnia* decline in the fertilized enclosures during the mid-summer despite continued fertilization to keep food levels high? Was it a result of *Daphnia* demographics or simple predator-prey oscillations (Murdoch and McCauley, 1985), fish predation, overgrazing of the grazeable algae, interference during blooms of net phytoplankton, or a combination of these factors? I will address each of these concerns in the order I have presented them.

Murdoch and McCauley (1985) indicate that *Daphnia* populations raised in the laboratory under conditions of constant food and temperature, can exhibit regular cyclic fluctuations in density with a period of 20-40 days. Such oscillations are deemed to be a property of *Daphnia* demography and have nothing to do with predator-prey oscillations. Demography refers to the dynamic balance of a population with
regard to density and capacity for expansion or decline (i.e. growth rates, distribution, fecundity, mortality) If the fluctuations in daphnid density that occurred in my enclosures were a result of demographical changes in population size, should they not have been more regular in their pattern of rise and fall? The daphnid declines all occurred rapidly, over one sampling period (1 week). Recovery was generally very slow and took several weeks. These rapid declines suggest that some mechanism other than \textit{Daphnia} demographics was occurring. Moreover, in two (enclosures 4 and 7) out of the 3 enclosures with major declines leading to low mid-summer densities, the drop occurred at the same time as in the lake and control populations. In one of the cases (enclosure 4), the resulting recovery followed the class \textit{1} dynamics described by Murdoch and McCauley (1985). In the other (enclosure 7), the daphnid population remained low for the duration of the experiment with one brief resurgence in numbers (which could have been a random sampling error) occurring in the fall.

With respect to predator-prey oscillations, none are really evident. Densities of grazable algae do increase following declines in the numbers of \textit{Daphnia} (Appendix 3), but the increases are more suggestive of an algal species obtaining optimal growth conditions and growing so fast that the daphnid grazing could not hold them in check, resulting in an algal bloom.

Thus, the results do not clearly fit any of the dynamic patterns of \textit{Daphnia} populations described by Murdoch and
McCauley (1985). There must have been some other, less clear explanations for the Daphnia dynamics I observed.

Were the Daphnia populations in the fertilized enclosures food-limited during the mid-summer despite continuous nutrient additions to keep food levels high, or was some other factor responsible for the low mid-summer daphnid densities?

My results suggest that Daphnia in fertilized enclosures during mid-summer were not food-limited. If the lower mid-summer densities were a result of food limitation, one would expect that little energy would be allotted for the production of eggs. Hall (1964) suggested that the average brood size of an equilibrium population of Daphnia (one that has reached the carrying capacity of the environment in terms of food supply) should be 1.0 eggs/adult or less (Hall, 1964). In fact, during the months of July, August and September, in my system, the average brood sizes of the Daphnia in the littoral and limnetic fertilized enclosures ranged between 1.5 and 6.0 eggs/adult (Figure 38). Moreover, the proportion of gravid adult daphnids ranged from 50-90 % of the population over the same period. These data are hardly suggestive of populations in equilibrium.

I suggest that the mid-summer Daphnia population sizes in the fertilized enclosures were maintained by predation rather than low food supply. The predator was probably cutthroat trout. Fish predation on zooplankton in this system was discussed in some detail with respect to changes in the zooplankton community structure of the control enclosures compared to that of the lake, therefore, I will deal with it
briefly here. Evidence for fish predation causing these reduced mid-summer densities of daphnids in the fertilized enclosures is sparse but, I believe, substantive.

Recall that the primary zooplankton prey of Placid Lake cutthroat trout are *Holopedium gibberum* and *Daphnia rosea* (Northcote and Clarotto, 1975). They are also selective in their choice of food based on size, with their planktivory largely restricted to *Holopedium* and *Daphnia* over 1.0 mm long (Northcote and Clarotto, 1975). The mean body sizes of the adult daphnids declined sharply to a maximum of 1.1 mm from 1.3 to 1.6 mm in July when fish presence was first noted. Also, the densities of *Daphnia* fell to lower levels after the fish invasion than at any other time during the summer, except perhaps, at the beginning of the experiment. Finally, *Daphnia* were found in abundance in the stomachs of fish captured within the fertilized enclosures. Daphnids in the guts of these fish numbered in the thousands (max = 7194 for one age 2+ fish) in July through September. In contrast, daphnids in the guts of fish captured within the control enclosures numbered in the hundreds (max = 160 for one unmeasured adult) in July, falling to only tens (max = 88) through August and September. These observations argue for a significant role of fish predation in structuring the *Daphnia* populations in the fertilized enclosures. While the numbers of daphnids/liter were on average only 5X higher than control values at any given time during the experiment, the numbers of daphnids consumed by fish increased by a factor of 100 - 1000.
Major short-term (1-2 weeks) declines in the population sizes of *Daphnia*, which were not apparent in any of the other fertilized enclosures or the controls, occurred in enclosures 4 and 7 in July (Figure 31). (The declines are not as evident for enclosure 7 in Figure 31 because of the log-scale axis.) These declines were paralleled by very sharp decreases in the average brood size (Figure 38) and, in enclosure 7 only, by a decrease in the proportion of gravid females. This led me to believe that there may have been enclosure specific incidences of overgrazing of the food supply due to extremely rapid increases in the numbers of *Daphnia*. Since the phytoplankton data gave no clear indication that the food resource in these enclosures had been overgrazed, I decided to test whether the standing stock of zooplankton, preceding these declines, would have been capable of decimating the available food supply.

Peak zooplankton biomasses preceding the declines averaged 450 ug/liter (Figure 25). Buckingham (1978) estimated maximum filtering rates for Placid Lake *D. rosea* to be around 1-1.5 ml/ug zooplankton/day for zooplankters exposed to food concentrations in the range of 100-500 ug/liter dry weight. These filtering rates are appropriate to use in estimating the total community filtering rates in my enclosures during these biomass peaks since 70-90% of the zooplankton biomass at these times was made up of *Daphnia*. Also, this range of grazing rates is comparable to the range of filtering rates reported for 1.3 - 1.6 mm *Daphnia pulex* (roughly the size range of *D. rosea* in my enclosures) by Haney (1985, his figures 1 and 2). If one
assumes that the average weight of a 1.3-1.6 D. pulex to be around 10 ug (derived from my biomass estimate of 450 ug/liter of a xenic monoculture of Daphnia divided by the maximum number of individuals per liter, 45, see Figure 31) then Haney's filtering rates are 1.0-1.5 ml/ ug zooplankton/ day.

Assuming these filtering rates are realistic estimates of the grazing pressure exerted in my enclosures at peak biomass times, then the grazers were only taking 45-70 % of the phytoplankton biomass per day. I have already shown above that phytoplankton renewal rates in the fertilized enclosures appear to be sufficient to result in more than 100 % of the standing stock in one day. In support of this, examination of a short burst of algal biomass over 2 weeks in enclosure 8 in August (Figure 17) suggests that the net daily growth rate of phytoplankton biomass in the fertilized enclosures could be as high as 0.6 per day. This was high enough to permit a bloom to occur, since zooplankton were removing only about 45-70 % of the algal biomass daily.

Thus, it appears that the sharp declines in daphnid densities in enclosures 4 and 7, in July, may not have been due to overgrazing of the food supply. In accordance with this, large populations of other herbivorous zooplankton like Holopedium (in enclosure 4), Diaphanosoma and D. oregonensis, all species which appear to feed on the same size spectrum of food as Daphnia, almost instantaneously increased in number to replace Daphnia as the community dominants. This suggests that the availability of food was not likely to have been a factor
associated with these observed Daphnia declines.

Is there then some other factor related to food supply other than food quantity that may have reduced the competitive advantage of D. rosea thereby allowing Diaphanosoma or Diaptomus oregonensis to outcompete the daphnids? There is evidence in the literature that the quality of food may be an important factor in the temporal dynamics of large cladocerans such as Daphnia.

Gliwicz (1980) found that summer blooms of net phytoplankton ( > 50 um) were responsible for decreases in the effective filtering rate, fecundity and densities of the "spring" cladoceran Daphnia cucullata. The decline in daphnids was accompanied by increases in Diaphanosoma brachyurum and Chydomus sphaericus which were postulated by Gliwicz (1980) to be less affected by the presence of large algae that might interfere with filtration. This implies that while the quantity of grazable algae may not be limiting, the Daphnia were not able to harvest it effectively and were excluded by species which were more efficient filter feeders in a low quality food environment.

Similar findings were reported by Richman and Dodson (1983) for cladoceran-copepod interactions. These workers found that even at a high food abundance, Daphnia pulex was excluded by Diaptomus siciloides in a competition experiment when the proportion of net plankton (as number of cells) in the test medium exceeded 40 %. The reason given for the competitive advantage of the copepod over the cladoceran was that the
selective feeding ability of copepods allows them to feed more efficiently in a low-quality food environment by selecting edible forms and avoiding inedible species. The cladocerans on the other hand, expend much of their energy rejecting collected food when net phytoplankton are found in abundance. Thus the copepod has a greater energetic efficiency than the cladoceran which allows it to outcompete the cladoceran when food quality is poor.

Net phytoplankton were abundant in enclosures 4 and 7 in July when the afore-mentioned periods of *Daphnia* decline occurred. In enclosure 4 and 7, net phytoplankton constituted 65 and 50-70 % of the phytoplankton biomass, respectively at these times (Figure 24). Both daphnid density and brood size decreased in accordance with the observations of Gliwicz (1980). Therefore, net phytoplankton interference can explain these enclosure-specific sharp declines in *D. rosea* abundance.

In conclusion, *Daphnia rosea* greatly benefited from the algal enhancement brought on by nutrient addition. Periodic increases in the net phytoplankton in some of the enclosures appear to have had devastating effects on the performance of the daphnids. This is important in that it suggests that to achieve maximum production of *Daphnia* as zooplanktonic fish food, attempts must be made to keep net phytoplankton to a minimum. Fertilization with high N:P ratio fertilizers may be one way to control net phytoplankton by enhancing small chlorococcoids and flagellates that are more characteristic of phosphorous limited, generally oligotrophic lakes as is shown in this study.
Occurrences of net phytoplankton were greatly minimized over those that appeared in controls, however, it appears that their presence is not totally suppressed by this method of fertilization.

(3) *Diaphanosoma brachyurum*

*Diaphanosoma* are a major component of the summer zooplankton assemblage in the U.B.C. Research Forest lakes. Densities of this species are higher in Placid Lake than in most of the other lakes in the research forest (Northcote and Clarotto, 1975). Maximum densities in Placid Lake seldom exceed 10 individuals/liter (Northcote and Clarotto, 1975; Krause, 1984; this study).

Typically, abundances of *Diaphanosoma* are low during the spring, begin to increase in early July reaching maximum densities by early August, and decline sharply in September (Krause, 1984; this study). This seasonal cycle of rise and fall was not disrupted following fertilization. However, a dramatic numerical response, that was highly variable from one enclosure to another, occurred as a result of fertilization. Maximum densities in two of the four fertilized enclosures exceeded 100 individuals/liter. Maximum densities in the other two fertilized enclosures ranged between 40 and 60 individuals/liter. These maxima were attained at different times during the summer.

The variability in the numerical response of the *Diaphanosoma* between the fertilized enclosures appears to have
been strongly influenced by the presence of Daphnia rosea. The greatest increases in abundances of Diaphanosoma occurred in conjunction with major declines in the daphnids. This was also true for Diaphanosoma populations in the lake and controls. Diaphanosoma appeared to perform much better in the fertilized enclosures where daphnid abundances dropped below 20 individuals/liter. This was particularly noticeable during the early summer crashes of the daphnid populations in enclosures 4 and 7. In enclosures 3 and 8, where early and mid-summer daphnid densities always exceeded 20 individuals/liter, Diaphanosoma numbers remained below about 30-40 individuals/liter. Only when daphnid densities in enclosure 3 declined precipitously in late August, probably as a result of intensive predation pressure by fishes, did Diaphanosoma increase to maximum densities for that enclosure. The interaction between these two cladocerans suggests the existence of some form of exploitation competition.

The suggestion that Daphnia rosea and Diaphanosoma brachyurum compete is not a new one. Marmorek (1983) concluded that increases in densities of Diaphanosoma in Eunice Lake enclosures that were subjected to combined treatments of acidification and nutrient enrichment, were largely due to acidification induced declines of D. rosea. Further, Neill (1984) found that D. rosea removal from fertilized enclosures resulted in substantial increases in the densities of D. brachyurum. Competition between these two species was not inferred by Neill (1984), though his data support the
hypothesis.

Despite increased densities of *Diaphanosoma* in the fertilized enclosures (> 100/liter in enclosures 4 and 7), *Diaphanosoma* were never found in the stomachs of any of 28 fish captured in those enclosures, nor in any of the stomachs of 30 fish netted in the control enclosures and the lake over the summer. Northcote and Clarotto (1975) found that *Diaphanosoma* was very rarely eaten by Placid Lake cutthroat. Possibly their small size (<0.8 mm) and transparent bodies or their cryptic swimming behaviour (Brooks, 1968) explain their absence from fish stomachs.

(4) *Bosmina longirostris*

*Bosmina longirostris* is a panmictic cladoceran which can tolerate all extremes relating to lake morphometry, temperature and water chemistry (Patalas, 1971; Carter et al., 1980). It is often a dominant member of the zooplankton community in bog lakes (Haney, 1973), however, it appears that its dominance is restricted to lakes where all other cladocerans are poorly represented (Patalas, 1971, table 1; Patalas and Salki, 1973, table 2), or, if they are present at all, they are small in size (i.e. *Daphnia catawba*, *Daphnia retrocurva*, and *Diaphanosoma brachyurum*).

Since the zooplankton assemblage in Placid Lake is numerically dominated by larger cladocerans like *Daphnia rosea* and *Holopedium gibberum* for most of the summer, it is not surprising that *B. longirostris* is found only in very low
numbers (<1/liter). *B. longirostris* did appear in significantly greater densities in the fall in the lake when the densities of all of the other cladocerans were at their lowest levels of the summer and in early August in the control enclosures when densities of *D. rosea* and *Holopedium* were sharply reduced.

Despite its occurrence in lakes of all types, *Bosmina longirostris* has been taken to be an animal indicator of eutrophication (Brooks, 1969). This accord is based solely on the fact that this bosminid is often the only one found in eutrophic lakes, having replaced all other species of *Bosmina* that previously occurred in the lakes prior to eutrophication. However, it is not clear why *Bosmina longirostris* actually becomes a community dominant in lakes following eutrophication. Its performance may be directly influenced by chemical enrichment processes or alterations in the populations of planktivorous fish following eutrophication (Brooks, 1969).

Some reports in the literature suggest that *Bosmina longirostris* may not be enhanced as a direct result of nutrient enrichment. Edmondson and Litt (1982) found that *Bosmina longirostris* actually became more abundant in Lake Washington after sewage diversion resulted in a reversal of the eutrophication process. Also, McNaught *et al.* (1983) found that the proportion of *B. longirostris* in the zooplankton community of Saginaw Bay, Lake Huron, remained constant following nutrient diversion and an improvement in water quality.

My study shows that *Bosmina longirostris* may not be an
indicator of eutrophication if it has historically been the only bosminid in the lake being investigated. My results show that increases in the abundance of *B. longirostris* following nutrient enrichment were confined to only one enclosure, limnetic fertilized enclosure 4, even though all of the fertilized enclosures were subjected to the same fertilization regime. The density of bosminids in enclosure 4 exceeded 1000/liter in October. Densities in all of the other fertilized enclosures were below 10/liter.

The unusually high density reported for only one sampling date in October may have been a sampling artifact. I may have encountered a *Bosmina* "swarm" during sampling. *Bosmina* swarming has been reported to occur in other bog lakes. Haney (1973) reports that one sample from Drowned Bog Lake near Dorset, Ontario contained in excess of 20,000 bosminids/liter. Normal lake densities ranged between 1000-3000 bosminids/liter. Also, Jarnefelt (1956) reported occurrences of dense clouds of bosminids in several bog lakes in Finland.

Regardless of the possibility of a swarm contributing to the unusually high density recorded in October, it is clear that *B. longirostris* in enclosure 4 derived some benefit from fertilization. This is supported by the fact that the bosminids in this enclosure progressively increased in density starting in late August. The question is, why did fertilization only benefit *B. longirostris* in only one of the fertilized enclosures? I believe that the improved performance of the bosminids in enclosure 4 was a result of two factors: a larger
increase in the quantity of small algal cells induced by fertilization than occurred in all of the other fertilized enclosures, and a reduction in competitive limitation of *B. longirostris* by *D. rosea* induced by intensive fish predation exerted upon the latter.

With regard to the first hypothesis, the phytoplankton that bloomed (80-90 % of the total biomass) in enclosure 4 in late August were very small forms of *Ankistrodesmus*. The average maximum linear dimension for these cells (14.3 um) was much smaller than the average for the same species in all of the other fertilized enclosures (19.8 um) which developed significant concentrations of *Ankistrodesmus* but not *Bosmina*. Also, the maximum density of these algal cells in enclosure 4 (1.1 X 10^8 cells/liter) was significantly higher than in its replicate, enclosure 8 (7.5 X 10^7 cells/liter) or in the littoral enclosures (1-2 X 10^7 cells/liter).

Burns (1968a) found that the maximum size of particles that can be ingested by *B. longirostris* was very close to 20 um. The average size of the most abundant algal particles in enclosure 4 at the time of the *Bosmina* outbreak fell well short of this maximum, while in all of the other fertilized enclosures, the average particle size was closer to the maximum size ingestible. Therefore, much more food of manageable size was available to the bosminids in enclosure 4 than to those in the other fertilized enclosures.

With respect to competitive interactions with *D. rosea*, there is evidence in the literature that these two cladocerans
do compete. Neill (1983) found that removal of *D. rosea* from nutrient enriched enclosures resulted in dramatic increases in *B. longirostris*. Marmorek (1983) found that when *D. rosea* died out during combined acidification and nutrient enrichment experiments, *B. longirostris* developed a more dramatic and sustained numerical response than in enclosure that received only nutrient additions but retained their *Daphnia* populations. Finally, Lynch (1978) found that in a series of competition experiments in enclosures in nutrient-rich Pleasant Pond, *Bosmina* was consistently out-competed by *Daphnia*.

The extent of the competitive interactions between these two species is greatly regulated by resource availability (Kerfoot and DeMott, 1980) and size-specific predation (Brooks, 1969). The former workers showed that the level of competitive interaction between *Daphnia* and *Bosmina* was particularly intense under laboratory conditions where both species were forced to share a single limiting resource, small algal particles. Under natural lake conditions which supplied a more diverse spectrum of food particles, *Daphnia* and *Bosmina* could coexist.

The food resource in enclosure 4 in late August consisted almost exclusively of a single resource, small *Ankistrodesmus*, but the amount of food available suggests that it may have been sufficient to maintain a coexisting population of *Daphnia* and *Bosmina* provided that the *Daphnia* population was prevented in some way from increasing in abundance. Intense size-specific predation exerted on the *Daphnia* could have suppressed *Daphnia* production to a level where the smaller *Bosmina* could have
escaped from probable conditions of food limitation. Indeed, abundances of *Daphnia* in enclosure 4, before the *Bosmina* increase, were much lower than could be accounted for by the quality and quantity of the available food supply; a food supply that could be efficiently harvested by the bosminids. Had there not been fish predation exerted in enclosure 4, it is quite likely that the *Bosmina* would not have reached such high densities because they would have been out-competed by the *Daphnia*.

In conclusion, nutrient enrichment alone did not result in an increase in the densities of *Bosmina* in the fertilized enclosures. Where the bosminids did appear to benefit from fertilization, a large reduction in the numbers of one of its chief competitors (the daphnids), through size-selective predation, seems to have been necessary.

(5) *Ceriodaphnia quadrangula*

As with the unique bosminid, *C. quadrangula* is a historically rare component of the Placid Lake zooplankton community which sometimes appears in moderate numbers in the hypolimnion of the lake (W.E. Neill, personal communication). Densities of this animal never exceeded 1 per liter (averaged over the entire water column) in 1982. The species' seasonal abundance profile was monocyclic, with maximum densities occurring in the fall.

Both enclosure and fertilization resulted in enhanced levels of *Ceriodaphnia* production, however, except for its
performance in littoral fertilized enclosure 3, increases in the abundances of this species were insignificant compared to those of the other herbivores in the system. Baseline increases of Ceriodaphnia in both the control and fertilized treatments, i.e. the enclosure effect, were probably food related.

The preferred food of Ceriodaphnia quadrangula is bacteria (Gophen et al., 1974; Smyly, 1975; DeMott, 1985). Densities of C. quadrangula were always highest in all treatment enclosures in the 4-6 m depth stratum. Given their preference for microbial matter, these animals were probably grazing on decomposing detritus that had settled out from the epilimnetic waters.

Decreased entrainment of the metalimnetic waters in the control enclosures (a previously discussed effect of enclosure) may have resulted in a higher than usual accumulation of microbial matter in the the thermally induced density gradient at around 4m. If this is true, then the increased densities of Ceriodaphnia in the controls compared to the lake may have been due to this unexpected, non-nutrient induced, food enrichment. Higher densities of detrital matter (leading to increased microbial production) in the fertilized enclosures, resulting directly from increased algal production induced by nutrient enrichment, would account for the higher densities of Ceriodaphnia in the fertilized treatments.

The performance of Ceriodaphnia in all of the enclosures may have been further enhanced by predation-induced or seasonally induced depressions in the numbers of all of the
other filter-feeding cladocerans that occurred during the latter part of the summer. This may have alleviated some form of competitive interaction that may have restrained *Ceriodaphnia* population growth. As the densities of the other major cladocerans, the *Daphnia* and the *Diaphanosoma*, declined in the latter part of the summer, the *Ceriodaphnia* appeared in greater numbers in the epilimnetic waters. This suggests that the *Ceriodaphnia* may have been competitively excluded from the epilimnion by the larger, more efficient filter-feeders.

There is also some circumstantial evidence that suggests that the *Ceriodaphnia* seasonal abundance cycle may be controlled by copepod predation. The cyclopoid copepod *Diacyclops thomasi* is the numerically dominant copepod throughout the early and mid-summer months in Placid Lake. This copepod is known to be an obligate carnivore and it is also known to actively feed on *Ceriodaphnia* (McQueen, 1969). Densities of *Ceriodaphnia* in all of the enclosures attained seasonal maxima only after a late summer decline in the densities of *Diacyclops*. This was particularly evident in littoral fertilized enclosure 3. Densities of *Diacyclops* declined much earlier and much more sharply in this enclosure than in all of the other enclosures. This decline was paralleled by a dramatic increase in the numbers of *Ceriodaphnia*. 
Diaptomus oregonensis

A numerical response by D. oregonensis to nutrient addition was only really evident in the limnetic fertilized enclosures, although fertilization significantly increased D. oregonensis egg production and mean body size in both the littoral and limnetic fertilized enclosures. This differential response may be a sampling artifact. If the phenomenon of "avoidance of shore" that I discussed previously, is exhibited by these copepods, then it may have been that a major portion of the copepod production in the littoral fertilized enclosures was not being sampled. Despite this possible bias, it is clear that the copepods responded less dramatically to fertilization that the cladocerans.

The onset of fertilization, in June, coincided with what appeared to be a production of a new generation of D. oregonensis nauplii. Thus, one would have expected that if fertilization benefitted this species, there would have been a large increase in the numbers of diaptomids later in the year. In fact, numbers of the copepods increased only modestly, compared to the cladocerans, and compared to the numbers of nauplii present in the water column in July. Further, only a small proportion of the copepodites in these enclosures matured into adults. The lack of an overall numerical response in these copepods can probably be attributed to poor juvenile (nauplii to early copepodite) survival while the lack of survival and development of the late summer copepodites may have been due to competitive interactions with the abundant cladocerans.
Mortality of *D. oregonensis* nauplii must have been high in my fertilized enclosures. Naupliar densities reached as high as 80/liter in enclosure 4 in late July but this translated into a maximum of only 50 copepodites/liter by mid-August. Whether this high mortality was a result of competition between juvenile cladocerans and the nauplii or some other factor is a matter of speculation since I have no data to support either claim.

Competitive limitation of the copepods by the cladocerans, if it did exist, was probably most strongly expressed in the early summer when the nauplii were most abundant. The rapid increase in the numbers of juvenile cladocerans that occurred at this time may have resulted in greatly reduced survival rates for the copepod nauplii. This is assuming that both animals exploit the same food resource. Although the stage at which naupliar feeding on algae commences is unknown, Rigler and Cooley (1974) report that food must be supplied to second instar *D. oregonensis* if significant mortality is to be averted. The food added to their zooplankton cultures consisted of small forms of green algae such as *Chlorella* sp., *Selenastrum* sp. and *Chlamydomonas reinhardtii*, which range in size from 3-10 um (Prescott, 1962), the same size spectrum exploited by small daphnids (Neill, 1975). Since juvenile daphnids were present in great numbers and were increasing in numbers almost exponentially, it seems reasonable to assume some form of competitive interaction was occurring. Another factor which may have led to reduced survival, was that during the early part of summer the cyclopoid copepod *Diacyclops thomasi* were present in
large numbers. These copepods are known to be predatory on the nauplii of calanoid copepods and can significantly reduce the population of diaptomid nauplii in a matter of days (McQueen, 1967, 1968).

The apparently poor survival and development of *D. oregonensis* copepodites in August in the limnetic fertilized enclosures may be related to the fact that this species, in this lake, is thought to feed on the same size range of food particles that are selectively browsed by all of the more efficient cladoceran species (Krause, 1984). Because cladocerans have higher filtering rates (Wetzel, 1975) and can filter a wider range of particle sizes than copepods (Bogdan and McNaught, 1975), they were probably able to suppress copepod numbers, possibly through food limitation. Conversely, if this diaptomid in this lake exploits larger food particles than the cladocerans (ca. 25-35 um), as suggested for this species by McQueen (1969) and Richman *et al.* (1980), then these copepods may have been exploiting a particle size spectrum that was previously shown to have been only marginally enhanced by the chosen fertilization regime.

(7) *Diacyclops thomasi*

*Diacyclops thomasi* did not increase in response to fertilization; on the contrary, they appeared to suffer a decrease in numbers. Also, there was an earlier population decline than occurred in the control enclosures. This is surprising since one of *Diacyclops*' preferred food items,
Ceriodaphnia (McQueen, 1969), increased in abundance in the fertilized enclosures.

I believe this early decline of *D. thomasi* densities was a result of an increase in the thickness of the anoxic hypolimnetic water mass in the fertilized enclosures. The thickness of the anoxic zone (<1 mg/liter O₂) in the controls was miniscule and only evident in late September in the deepest waters (below 6m), whereas the anoxic zone in the fertilized enclosures extended to as much as 0.5 m above the sediments and, in some of the enclosures, was evident as early in the season as the beginning of August. This increase in the depth of the anoxic zone must surely have restricted hypolimnetic dwelling animals to a smaller volume of habitable water.

This hypothesis is supported by the observation that densities of *D. thomasi* in limnetic fertilized enclosure 4, during the period of most severe anoxia (late summer), were 2-3 times higher than in any of the other fertilized enclosures. Enclosure 4 had a maximum depth of 6m. All of the other fertilized enclosures had a maximum depth of only 5m. Thus, virtually the entire hypolimnion in all of these enclosures would have been almost totally anoxic. Enclosure 4 could have contained as much as 1.0-1.5 m of O₂-sufficient living space, even though the oxygen content of this water was relatively low. *Diacyclops thomasi* can survive in waters containing relatively low concentrations of dissolved oxygen (Stross et al., 1961). These workers found that practically the entire population of *Cyclops* in Peter-Paul Lake, a small bog lake in Gogebic County,
Michigan, was located in a two meter zone near the thermocline, which contained a dissolved oxygen concentration as low as 1.0 mg/liter.
5.0 PLACID LAKE CUTTHROAT TROUT

5.1 Life History Traits

The life history of the coastal cutthroat trout (*Salmo clarki* Richardson - Scott and Crossman, 1973) is extremely varied from stock to stock. There are two forms of this species in British Columbia, the interior form (*Salmo clarki lewisi*) and the coastal form (*Salmo clarki clarki*). The coastal form has both anadromous and non-anadromous stocks. Placid Lake cutthroat are of the latter type. Very little is known about the life history of the U.B.C. Research forest cutthroat stocks so I will outline some of the things I have learned about the Placid Lake stock.

Placid Lake cutthroat are spawned in gravelly portions of the downstream reaches of the lake's outflow stream. A few small redds, about 10-15 cm in diameter and 5-7 cm deep were found in loose gravel, riffled portions in areas of relatively flat relief, about 500 - 800 m downstream from the lake. There may have been some more farther down stream but I did not investigate this.

Thirty female cutthroat trout were taken from the lake in early October of 1981 to serve as brood stock for the following year's experiments. Of these, approximately one-third had already spawned, one-third contained ripe or nearly ripe eggs and one-third were not ready to spawn but were spawned in a hatchery setting the following January. Spawning thus evidently occurs over a long period of time, at least from September to
January. This is in accordance with the observations of DeWitt (1955) who reported that female cutthroat containing ripe or nearly ripe eggs had been taken from several coastal California streams from September to April. On the other hand, Dymond (1928) and Scott and Crossman (1973) report that spawning of cutthroat in British Columbia only occurs from February to May. This emphasizes the variability of the life history characteristics among the various stocks of this species.

Fecundity of mature females in Placid Lake is very low, averaging 120 eggs/female (average for 6 fish ranging in size from 17-21 cm fork length). Scott and Crossman (1973) report that average egg number per female for this species, disregarding size and location, should be 1100-1700. This suggests that Placid Lake cutthroat are probably severely affected by low food availability since very little energy is being converted into eggs.

Young of the year probably spend much of their early life in the stream environment. I have no evidence to support this but DeWitt (1955) and Scott and Crossman (1973) both observed that young of the year of this species commonly spent about 1 year in the stream environment before moving into their destination habitats as fingerling trout. I electro-fished the outlet stream to obtain young fish to replace the ones that had disappeared from my enclosures, and captured fifty-four small trout ranging in size from 2.5-14 cm fork length. Most of these fish were less than 8 cm long. Only one was 14 cm long. I also surveyed the lake using SCUBA and snorkeling gear to seek out
young fish. The smallest cutthroat I observed in the lake was around 5 cm in length. All sightings of juvenile fish occurred in the vicinity of the outlet stream. Perhaps these juvenile fish were just moving into the lake environment from the downstream rearing areas.

It is clear from my results and from those of Shepherd (1973), Andrusak and Northcote (1973) and Northcote and Clarotto (1975) that zooplankton, almost exclusively large cladocerans like Daphnia and Holopedium, insect larvae (predominantly dipteran pupae and trichopteran larvae) and flying aquatic dipterans are the main dietary components of Placid Lake cutthroat. Some of the larger individuals (> 200 mm) have been known to eat small fish (Andrusak and Northcote, 1973; Hume, 1978) which may partially explain the disappearance of the cutthroat trout fry I stocked in the enclosures.

There was a marked seasonality in the trout diets. Large cladoceran zooplankton were taken almost exclusively in the late spring and early summer when they were at their maximum densities in the water column. As the summer progressed, insect larvae and flying insects became the predominant prey types.

There was also evidence that individual fish preferred certain prey types (personal observation). The guts of some of the fish I analyzed contained Daphnia almost exclusively. Others contained only Holopedium and some Chaoborus larvae and still others contained a mixture of all prey types. One fish was found to have only Diaptomus kenai and several chironomid larvae in its gut. This was unusual in that D. kenai were not
present in the water column at the time (based on sample enumerations). However, the presence of chironomid larvae in the gut suggests that this fish was feeding near the bottom. This suggests that *D. kenai*, during the mid to late summer months, may be concentrated near the bottom in this lake, placing it out of reach of our traditional sampling gear, the bilge pump. We tend to avoid getting too close to the sediments because they are easily disturbed and will be sucked up by the pump, thereby contaminating the samples and making them difficult to enumerate. It would be interesting to determine whether *D. kenai* is feeding on episammic phytoplankters, such as diatoms at this time.

The varied diets of individual fish, i.e. some containing benthic prey types like *Chaoborus* and chironomid larvae, and differences in the colouration of fishes in the lake leads me to believe that there are two separate varieties of cutthroat in this lake. One type being predominantly littoral and benthic oriented and the other being a more limnetic variety. Littoral or benthic morphs of the fish exhibit a dark golden-green colour with very distinct parr marks and heavy spotting. Parr marks were evident even on some larger, obviously adult fish. Limnetic types are dark only on the dorsal side, distinctly lighter on the ventral side, have no parr marks and are less heavily spotted. This is a phenomenon worth future investigation. It may be that the darker coloured fish are simply in spawning colouration, but if this is so then almost one-half of the population is always in spawning condition.
5.2 Fertilization and The Diet of the Trout

It is clear from my results that the cutthroat trout in the fertilized enclosures benefited immensely from the enhancement of *Daphnia rosea*. Daphnids occurred in extremely large numbers in the stomachs of fish captured in these enclosures. In fact, the abundance and availability of the *Daphnia* appear to have elicited a shift in the diet of these fish. During the late summer when flying aquatic insects and their aquatic larvae formed the dominant component of the diet of fish in the controls and the lake, the fish in the fertilized enclosures gorged themselves on *Daphnia* and largely ignored insects and insect larvae.

Despite the fact that the densities of all of the major herbivorous zooplankton (except *Bosmina*) increased appreciably following fertilization, *Daphnia* were the only zooplankton taken in significant numbers by the fish. Does this mean that enhancement of the smaller zooplankton species was "wasted" in the sense that these smaller zooplankton will derive benefits from enhancement but not contribute to the growth of the target species, the cutthroat trout?

If the answer to the above question is "yes", then one could proceed with a plan for nutrient enrichment that does not have the maintenance of the existing species composition of the zooplankton as one of its goals, as is so often the case (Parsons et al., 1972; Stockner et al., 1980). Instead, one could give full attention to the problem of maximizing the production of only the large species of zooplankton on which the
fish will feed. The answer would be "yes" if it is only important to consider the adult trout in the lake. But what of the juveniles of this trout species? It may be that the juvenile trout would consume small zooplankton once they enter the lake until they reach a size that enables them to handle the larger cladocerans. The enhancement of small zooplankton would not be "empty" in this regard.

I could find only two published reports which detail the food of juvenile cutthroat trout. Hazzard and Madsen (1933) reported that fingerling (2-4 cm) interior cutthroat, *Salmo clarki lewisi* (Girard), taken from a tributary of Jackson Lake, Wyoming, fed almost exclusively on small immature forms of dipterans, mayflies, caddisflies and stoneflies. The two-winged flies, particularly the midges, were taken most frequently and in the largest numbers. No crustacean zooplankton were found, probably because zooplankton do not inhabit lotic waters. The question then arises, do fingerling cutthroat trout, once they move into the lake, feed on zooplankton, a food item with which they are completely unfamiliar? Calhoun (1944) found that the food of fingerling black-spotted trout, *Salmo clarkii henshawi*, in Blue Lake, Alpine Valley, California, still consisted largely of chironomid pupae and larvae, and land insects. Microcrustaceans made up only 5.8% of the volume of the food in their guts. Conversely, as much as 70% (by volume) of food in the guts of adult black-spotted trout consisted of microcrustaceans (*Daphnia* and copepods).

The ability of fingerling cutthroat to consume small
dipteran flies, which range in size from 2-40 mm (Johannsen, 1934; Unsinger, 1963), suggests that they should be capable of consuming the large zooplankters they will encounter in the lake. If so, they will probably avoid the smaller zooplankters if given the choice. Doble and Eggers (1978) found that the juvenile sockeye salmon in Lake Washington were extremely selective in their food choice, taking only the largest zooplankton available to them. Narver (1970) found that underyearling sockeye in Babine Lake, British Columbia preferentially consumed the larger zooplankters in the lake, namely *Daphnia longispina* (larger than our *D. rosea*) and *Heterocope septentrionalis*, a very large (3-4 mm) diaptomid copepod. Small zooplankton in both lakes were consumed only after the larger species had decreases in numbers. These data, although not specific to cutthroat trout, suggest that the fingerling trout would probably select for the largest zooplankton they could find, if they feed on them at all.

Interestingly, Hume (1978) found that the smallest cutthroat trout he captured (70 mm) in Eunice and Loon Lakes (in the U.B.C research forest) consumed far fewer zooplankton and far more surface prey (insects) than the medium (140-279 mm) and large (> 280 mm) sized fish. Perhaps feeding on zooplankton is a skill that must be learned by naive fish. Free swimming prey can avoid an encounter with a predator much easier than a prey item that is trapped in the surface film of the lake's surface. The juvenile trout would have to first learn the free swimmer's predator avoidance behaviour before it could become efficient at
feeding on them.

Thus, it seems that the augmentation of small zooplankters through fertilization may very well be "wasted" enhancement in terms of fish production. Unless one takes into account the possibility that these small animals may serve to increase the survival of larger predatory aquatic insect larvae which prey on small crustaceans and which, in turn, are preyed upon by the fish. But as a direct, immediate, rapidly reproducing food supply, they do not appear to be important. Detailed work on the feeding habits and dietary requirements of fingerling trout would be required before this idea can be confirmed.
6.0 CONCLUSIONS

1. The use of large enclosures for impounding the water column in shallow lakes in order to study the effects of experimentally induced perturbations, on the physical, chemical or biological components of the system, appears to be a viable experimental tool for limnologists. Since the use of large limnocorral does not appear to alter the above parameters in relation to the study lake, results from such experiments may be used to predict the effects of similar perturbations if applied to the study lake as a whole.

2. The effects of fertilization on the physical, chemical and biological dynamics of the lake waters were more evident in the limnetic zone of the lake than in the littoral zone.

3. Small frequent doses of fertilizer at high N:P ratios (40:1) resulted in changes in the lake's phytoplankton assemblage to the extent that deleterious blue-green algae were virtually eliminated from the algal community. This provides some support for the hypothesis that dominance of phytoplankton assemblages by blue-green algae is favoured by a deficiency in the availability of inorganic nitrogen in the water column.

4. The predominant species of algae in the fertilized enclosure over most of the summer consisted of small green algal
forms, which were in the size range that was grazable by the zooplankton in the lake. This was particularly true for the limnetic zone. Net phytoplankton showed no significant increase in density as a result of fertilization. This result provides some support for the hypothesis that small algal forms grow faster than large algae when conditions for growth are identical (Banse, 1976) and that natural phytoplankton assemblages can be manipulated to produce algal communities dominated by small cells (Turpin and Harrison, 1980).

5. Fertilizer induced changes at the primary trophic level did not result in significant changes in the seasonal sequence of shifts in numerical dominance of the major herbivorous zooplankton species, except for *Daphnia*. This is important in that it suggests that some mechanism other than food abundance or quality, or competition between co-existing species may drive the seasonal cycle of some zooplankton species in lakes. The food regime that is normally available to the species of herbivorous zooplankton in Placid Lake was drastically altered as a result of fertilization, yet the normal seasonal cycles of abundance in the zooplankton occurred.

6. The *Daphnia* were the zooplankton which derived the greatest benefit from this enhanced algal biomass. It appears that the chosen fertilization regime was successful
in generating the size range and species composition of algae that induced good growth in the *Daphnia* population over most of the summer. *Daphnia* dominated the zooplankton biomass in all of the fertilized enclosures for most of the summer instead of only during early summer as in the lake and controls.

7. The growth of cutthroat trout in this lake is apparently limited by food availability. However, it is quite clear that this fish species becomes highly planktivorous given that there is abundant zooplankton on which to feed. The data clearly show that *Daphnia* is the predominant zooplankter in the diets of these fish during the mid and late summer months.

8. It is likely that trout of fingerling or catchable size would obtain greater survival rates if planted in such an artificially enriched environment than if they were planted in the typical unproductive coastal mountain lake. However, it appears as though fertilization did not result in increased growth and survival of planted, hatchery reared, wild cutthroat trout fry. Avian predators took many of the planted fish, others may have been lost to adult fish which invaded the enclosures. This is important because it suggests that predation is more important than food in determining the survival rate of juvenile fish in aquatic systems.
9. Estimates of fish yield based on the summer chlorophyll a relationship derived by Oglesby (1977), suggest that the unfertilized lake waters would yield only 0.02 g dry weight of fish/m²/ year. If the lake was to be fertilized to the level obtained in this experiment, fish yield should rise to a respectable level of 0.5 g dry weight of fish/m²/ year, a 25 fold increase in production.

10. The results of this research have important implications for the overall management of lakes which are subject to cultural eutrophication through the discharge of wastewaters. Changes in the N:P ratios of lakes can be achieved by reduction of P at the point source, or by adjusting the N:P ratio of the discharge in some other way.
REFERENCES CITED


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APPENDIX 1
Table A1. List of common phytoplankton species encountered in the euplankton of Placid Lake.

**Chlorophytes**

Pyramimonas tetrarynchus (Schmarda)
Chlamydomonas polypyroideum (Prescott)
" pseudopertyi (Pascher)
" Dinobryoni (Smith)
" epiphytica (Smith)
" mucicola (Schmidle)
" sphagnicola (Fritsch @ Takeda)

Chlorella ellipsoida (Gerneck)

Palmellar stage of Chlamydomonas

**Nannochloris**

Oocystis lacustris (Chodat)
" Borgei (Snow)
" pusilla (Hansgirg)
" parva (West and West)

Botryococcus braunii (BS)

Chlorella vulgaris (Beijerinck)

Cosmarium sp.

Cosmocladium sp.

Sphaerocytis Schroeteri (Chodat)

Gloeocystis planktonica (West)

Palmella mucosa (Keutzing)

Gloeocystis major (Gerneck)

Botryococcus braunii (BS)
Westella linearis (Smith)

Ankistrodesmus falcatus (Corda)
  " f. var. acicularis (A. Braun)
  " f. var. mirabilis (West and West)
  " Braunii (Brunnthaler)

Ulothrix zonata (Keutzing)
  " cylindricum (Prescott)
  " subconstricta (West)

Scenedesmus perforatus (Lemmermann)
  " bijuga (Lagerheim)

Oedogonium spp.

Euglenoids

Euglena polymorpha (Dangeard)
  " minuta (Prescott)
  " elastica (Prescott)
  " convoluta (Korshnikov)
  " acus (Ehrenberg)

Astasia sp. (Dujardin)

Phacus birgei (Prescott)
  " longicauda (Dujardin)
  " Chloroplastes (Prescott)
  " anacoelus (Prescott)
  " caudatus (Heubner)
Cyanophytes

Anacystis sp.
Glacaeocapsa aeruginosa (Kutz)
Aphanocapsa sp.
Microcystis aeruginosa (Elenkin)
Merismopedia elegans (A. Braun)
   " glauca (Naegeli)
   " Meyen (Stein)
Chroococcus limneticus (Lemmermann)
   " l. var. distans (Smith)
   " minor (Naegeli)
   " Prescottii (Drouet & Daily)
Oscillatoria curviceps (Agardh)
   " tenuis (Agardh)
Lyngbya sp.
Coelosporium Naegelianum (Unger)
Anabaena lapponica (Borge)
   " constricta
Rhabdoderma sp.
Aphanothece sp.
Nostoc shaericum (Vaucher)
Dactylococcopsis sp.
Microcystis aeruginosa (Kuetz)

Chrysophytes

Ochromonas (Wyssotzki)
Dinobryon sertularia (Ehrenberg)
  " sociale (Ehrenberg)
  " stipitatum (Stein)
  " cylindricum v. palustre (Lemm.)

Synura uvella (Ehrenberg)
  " sphagnicola (Korshnikov)
  " petersonii (Korshnikov)

Chrysophaella longispina (Lauterborn)

Mallamonas alpina (Pascher @ Ruttner)

Trachelamonas lacustris (Drezepolski)
  " dubia (Swirenko)

Cryptophytes

Cryptomonad ovata (Ehrenberg)
  " erosa (Ehrenberg)

Chroomonas Nordstedtii (Hansgirg)

Bacillariophytes (rare in water column during summer but common in water column during spring and on bottom muds during summer.)

Cymbella sp.
Pinnularia sp.
Gomphonema sp.
Caloneis sp.
Amphora sp.
Stauroneis sp.
Navicula sp.
Diploneis sp.
Amphicampa sp.
Synedra sp.
Tabellaria sp.
Campylodiscus sp.
Actinella sp.
Meridion sp.
Asterionella sp.
Fragellaria sp.
Cocconeis sp.
Hantzscheia sp.
Frustulia sp.
Cyclotella sp.

Species that are rare in the limnoplankton (<5/ml)

The Desmids

Penium
Closteridium
Netrium
Cosmarium
Staurastrum
Xanthidium
Microasterias
Hyalothica
Phymatodocis
Cylindrocystis
Mesotaenium
Arthrodesmus

Bulbochaetae
Cruceqenia tetrapedia (West and West)
Spirogyra condensata (Keutzing)
Glaeotheca linearis (Naegeli)
Trebearia setigerum (Smith)
Schroederia setigera (Lemmermann)
Tetraedron hastatum (Hansgirg)
Tetraedron regulare (Keutzing)
Actinastrum Hantzchii (Lemmermann)
Micrasterius radiata (Hass)
Chara sejuncta (A. Braun)
Ophiocytium Naegeli
Ciliophora sp.
Schitzogonium sp.
Tetrallantes Lagerheimii (Teiling)
Groenbladia sp.
Chromulina sp.
Schitzochlamys gelatinosa (A. Braun)
Nephrocytium sp.
Geminella sp.
Spirulina laxa (Smith)
Spirogyra sp.
Genicularia sp.
Cylindrosporum sp.
Tribonema sp.
Kirchneriella lunaris (Smith)
Quadrigula closteroides (Bohlin)
Kentrosphaera gloeophila (Brunnth.)
Cladophora insignis (Kuetzing)
Cylindrocapsa sp.
Synechococcus aeruginosus (Naeg.)
Closteriopsis sp.
APPENDIX 2
Gloeocystis major, a large, planar form of algae (ca. 100 um MLD) was rarely found in the lake, controls and littoral F enclosures (<20 cells/liter) but this species reached densities as high as $10^4$ cells/liter in limnetic F enclosure 8 in late July and $10^5$ cells/liter in limnetic F enclosure 4 in late August (August 26 - September 2) and became a dominant member of the plankton assemblage, along with the smaller colonial greens.

Botryococcus sudeticus was found in all control enclosures and the lake as mid-sized colonies (up to 30 - 40 um MLD) and as single cells ranging from 6 - 20 um in diameter and in fairly low densities (< 100 cells/liter). Starting in the last week of July in limnetic F enclosure 8 and littoral F enclosure 7, for about one week, and in the second week of August in limnetic F enclosure 4 and littoral F enclosure 3 for about one week, this species formed large colonies containing 20 - 100 cells encased in a gelatinous matrix and occasionally appeared as a thin patina floating on the surface of the water. These blooms were the first visible sign of algal enhancement caused by fertilization, occurring even before changes in water colour or Secchi depth. No blooms ever appeared in the controls or on the lake. The layer was so thin there was no reduction in the Secchi disc visibility. The blooms drifted around the enclosures on the surface of the water often "piling up" at the edges of the enclosures and looking quite thick. Blooms in the littoral F enclosures were much lighter than in the limnetic F enclosures. The durations of appearance of these blooms were very short, their demise being caused by rain. The impact of
raindrops on the water's surface was sufficient to break up the patinae and cause the smaller non-cohered colonies to sink below the surface. Once they were pulverized by rain, they did not reappear, however the smaller (50 - 100 um MLD) colonies and/or single cells were interspersed throughout the epilimnion and formed one of the dominant species in terms of both biomass and abundance until the end of August.
Figure A1. Densities of algae in selected size classes in all of the enclosures and the lake. Y-axis is number/liter $\times 10^6$ unless indicated otherwise.
ENCLOSURE 1

2 - 6 um

6 - 10 um

10 - 14 um

10 - 20 um

20 - 30 um

> 30 um

Number/Litre

(J x 10^6)

(J x 10^6)

(J x 10^6)

(J x 10^6)

(J x 10^6)

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ENCLOSURE 2

2 - 6 um

6 - 10 um

10 - 14 um

14 - 20 um

20 - 30 um

> 30 um

Number/11.1m

(x 10^6) Um

(x 10^6) Um

(x 10^6) Um

(x 10^6) Um

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