Factors regulating phytoplankton populations at Churchill, Manitoba.

Isobelle McGregor Gray

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FACTORS REGULATING PHYTOPLANKTON POPULATIONS AT
CHURCHILL, MANITOBA

by

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A Thesis
submitted to the Faculty of Graduate Studies
through the Department of Biology in
Partial Fulfillment of the requirements for the degree of
Master of Science at
The University of Windsor
Windsor, Ontario, Canada

1987
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ABSTRACT

Non-density dependent factors tended to regulate the phytoplankton populations in ponds from various habitats in the Churchill, Manitoba area. The Churchill area experiences a variable environment in temperature, net radiation and precipitation. Yet the phytoplankton populations of all the ponds were similar in composition and had little dominance by any one species. No seasonal trend in phytoplankton class was observed for any of the ponds.

Differences in evaporation rates contributed to differences in chemical composition between the years 1980 and 1981. Total dissolved and soluble reactive phosphorus and calcium concentrations were higher in 1981. Calcium precipitation, observed in the tundra and experimental area ponds reduced phosphorus availability within the ponds. Differences in nutrient composition between ponds did not seem to affect the phytoplankton composition and biomass. Saline conditions, however, contributed to the presence of Brachiononas Westiana in the rock bluff ponds and Amphipora alata in the Goose Creek ponds.

Temporal and spatial variability in phytoplankton abundance and composition operated on microscales of minutes and centimeters. Variability was not due to zooplankton grazing or species specific differences but rather to non-density dependent variables, such as wind stress, since the temporal and spatial scales were too small for the
physiological response of the phytoplankton to the changing environment.

- The tundra ponds were regulated by non-density dependent factors which could only be uncoupled if nutrient additions were added on a regular basis rather than as a single nutrient pulse. A single addition of phosphorus (2.0 gm.m\(^{-2}\)) in both 1980 and 1981 did not produce an increase in either phytoplankton biomass or productivity. With multiple additions of phosphorus (10x 0.2 gm.m\(^{-2}\)) phytoplankton productivity significantly increased (t-test= 2.056, p<0.05). The addition of phosphorus to the surface of the ponds immediately increased the total dissolved and soluble reactive phosphorus concentrations. Within minutes the phosphorus was incorporated into the particulate fraction possibly as a result of the scavaging effect of calcium.

Silica, nitrogen, phosphorus and carbon were added to phytoplankton samples from tundra ponds and enclosed in plastic bags. Combined additions of phosphorus and nitrogen produced the maximum biomass increase of all nutrient combinations. Generally Bacillariophyceae increased the most in percent total biomass following nutrient additions with the cell size diameter of all populations generally remaining below 30 um before and after nutrient additions.
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and my friends and families who always cared to ask "and how's the thesis?".

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GENERAL INTRODUCTION

In aquatic systems many phytoplankton species coexist making up a highly heterogenous population which varies over time and space. Hutchinson (1961) wondered why so many species were encountered in the phytoplankton community assuming that the epilimnion was homogenous. In reality, the aquatic system is in constant disequilibrium. The variability of the system in turn produces temporary niches which favor opportunistic species. Such niches are frequently being broken down and reformed (Richerson et al. 1970). The rate at which the environment changes and the rate at which the phytoplankton can respond and track the changes ultimately determines the phytoplankton composition and abundance.

Growth of the phytoplankton is controlled by a host of factors all acting together. Factors operating without respect to phytoplankton density include temperature, light and nutrient availability. Factors which depend upon the population density include light attenuation, anabolic rates of species and nutrient utilization by species. Factors which are operating at the time scales at which the physiological mechanism can no longer buffer the perturbation will have the most profound affect on the biomass and species composition (Harris 1980).

Which hierarchy of factors, density dependent and/or non-density dependent, ultimately regulates a freshwater
system is studied herein with respect to arctic pond phytoplankton populations. Density dependent factors have been well examined under steady-state conditions in the laboratory (Tilman and Kilham 1976; Senft 1978; Nalewajko and Lean 1980). Natural bodies of water are rarely in steady-state conditions owing to variabilities in non-density dependent factors. The objective of this thesis was to determine what factors regulate phytoplankton composition and abundance among and within natural phytoplankton communities of arctic ponds. Secondly, with the addition of a potential limiting density dependent resource, would density dependent factors override the effects of non-density dependent factors to produce an autogenic change in phytoplankton composition and biomass?

Nutrients often play a leading role in regulating the composition and abundance of phytoplankton in temperate lakes. Phytoplankton composition and biomass change in response to nutrient gradients and reflect those populations that are best fitted or adapted to exploit the nutrient resource (Tilman and Kilham 1976; Reynolds 1984). Dugdale (1967) applied the Monod equation, describing Michaelis-Menton enzyme kinetics, to the rate of uptake of a limiting nutrient by phytoplankton. The plot of rate of specific increase in cell biomass per unit time against nutrient concentration was a positive hyperbolic relationship. Different interspecific growth rates indicated that competition along resource-ratio gradients can occur.
Competition for common resources enhanced coexistence of species and influenced composition and dominance of phytoplankton assemblages (Kilham and Kilham 1980).

Droop's (1973) formulation of the relationship between growth rate and nutrients available to the cell took into account the internal reserves of nutrients by phytoplankton. Internal reserves were considered along with external concentrations such that the reserves were accumulated in excess of immediate demands as long as the external concentrations were sufficient.

The two models of Dugdale (1967) and Droop (1973) are based on steady-state conditions. It must be emphasized, however, that rarely are bodies of water under equilibrium conditions. When steady-state conditions exist, the Michaelis-Menton kinetics describe the relationship between growth rate and nutrient concentration because the half-saturation constants for uptake and growth are similar. Under disequilibrium conditions growth of algae and uptake can be altered. The half-saturation concentrations for growth are generally lowered (Tilman and Kilham 1976).

Nutrient limitation is often implied based on external concentrations without taking into account whether the nutrient is available to be utilized by the phytoplankton. Low external concentrations of a dissolved nutrient does not mean that a nutrient is limiting the cells' growth. Luxury uptake of a nutrient and utilization of various forms of a nutrient are adaptive physiological characteristics of
phytoplankton to retard the effects of nutrient limitation. The nutrient may be unavailable because of chemical complexing or because of local variations in nutrient uptake as a result of spatial and temporal heterogeneities in the distribution of phytoplankton.

Arctic ponds are useful systems in which to study factors regulating phytoplankton composition and abundance. The arctic tundra is strewn with thousands of small ponds less than one meter in depth. This provides an opportunity to test whether there is heterogeneity in phytoplankton composition and abundance among the ponds. The ponds freeze completely to the sediments during the winter months and thus there are no fish resulting in a simple natural system. A warm but short summer of 3-4 months enables the study of phytoplankton communities throughout their active growing period. As fish are absent, zooplankton communities also have a well defined seasonal cycle during the summer months (Hobbie 1980).

The fragility of the arctic ecosystem has been questioned by Dunbar (1972). The resilience of the arctic ecosystems possibly is a function of their highly variable spatial and temporal scales. Based upon the many expanses of freshwater in the subarctic and the high growth rates of phytoplankton during a short growing period, the arctic ecosystem with respect to phytoplankton might be resilient to perturbations. Conversely, aquatic ecosystems might be susceptible to minor perturbations because of low annual
productivity and slow decomposition rates. Also the lack of population diversity might enhance vulnerability to perturbation.

Tundra ponds are unique freshwater systems in that they are very shallow, reveal little tendency to stratify, are well oxygenated and are usually oligotrophic (Hobbie 1980). Although an arctic lake was found to be eutrophic as a result of sewage pollution (Kalff and Welch 1974; Schindler et al. 1974), naturally eutrophic arctic lakes are usually rare although they have been reported (Sheath and Munawar 1974). Increased phytoplankton standing crop and alterations in phytoplankton species composition are characteristic of fertilized ponds (Kalff 1965; Prentki et al. 1980). Phosphorus has been judged to be the key nutrient in the eutrophication of these ponds if either sediments were present or if nitrogen was supplied (Prentki et al. 1980).

It was the object of this study to 1) study the composition and similarity of phytoplankton communities in arctic ponds and 2) to experimentally fertilize a subarctic aquatic system with phosphorus to observe the response of the phytoplankton populations in order to gain more insight into nutrient-phytoplankton interactions in subarctic aquatic systems.

While Moore (1978) sampled community structures of some temporary ponds north of Manitoba there have been no comprehensive phycological studies of such habitats in northern Manitoba. Several studies have been made to

Churchill, Manitoba was chosen as an ideal location for experimental manipulation of natural phytoplankton systems. Churchill, Manitoba is of interest because it lies between the tundra and the coniferous forest defined by Bluthgen (1970) as a subarctic zone. Near Churchill one has access to a large number of small ponds with similar morphometry. Similarity in chemistry and in phytoplankton composition was initially tested for in this thesis. Hydrology of the region was such that inputs to the ponds occurred primarily during spring thaw. While overflow from one pond to the other was probable during spring thaw, added nutrients would remain within the ponds during the summer season. Also important to the study was the absence of human interference. This supported field experimentation with control conditions which would have been impractical in a more populated area.
CHAPTER ONE

PHYTOPLANKTON SURVEY OF PONDS IN CHURCHILL, MANITOBA
INTRODUCTION

A. Hypothesis

The occurrence of so many common freshwater phytoplankton species throughout the world is indicative of their ease of dispersal through air-borne distribution, transportation of water and/or sediment from one location to another by animals, humans and boats, excretion of viable algal cells by animals and overflow from one lake to another (Round 1984). Superimposed on the dispersal pattern are environmentally imposed constraints on phytoplankton composition: temperature, light and chemical composition. While these non-density dependent factors will set limits on the types of phytoplankton able to grow within resource ranges it is generally considered that it is the physiological responses of the phytoplankton to the available resources which will ultimately determine its growth and dominance.

Growth of species is enhanced provided the species remain in suspension, are able to obtain and utilize macronutrients and micronutrients and can carry out photosynthesis. It is hypothesized that phytoplankton composition and biomass in Churchill area ponds is regulated by density dependent factors, of which variations in nutrient concentrations have the greatest affect. To test this a wide variety of ponds were sampled in 1980 and 1981 to examine if there was a relationship between the type of
pond and the resident algal community.

B. Land and Geology

Churchill, Manitoba is located at 85°45'N, 94°04'W in northern Manitoba where the Churchill River meets Hudson Bay. Churchill lies between the treeless tundra which follows the outcropping of the Precambrian Shield from the Northwest Territories to just north of Churchill and a coniferous forest which extends from Churchill south along the Paleozoic limestone bedrock (MNR 1980).

The entire coastal region is underlain by ancient Precambrian bedrock. This bedrock is composed of quartzite, dolomite and limestone. The bedrock is overlain by Palaeozoic shallow flat-lying sediments. Limestone makes up about 55 per cent of the sediment, siltstone about 35 per cent, sandstone 6 per cent and gypsum 2 per cent. The tundra region is characterized by humus, nano-podsol and peaty soils. Leaching caused by rainfall is usually very low and waterlogging in the lowlands is very common as permafrost is commonly found one meter or more below the surface (MNR 1980).

C. Climate

The climate of Churchill is characterized by short, warm summers and long cold winters, with almost no transitional periods (Bluthgen 1970). Beginning late May the mean daily temperatures increased rapidly and the net
radiation became sufficient to stimulate primary productivity (Table 1.1). By June daily temperatures were above zero and the ponds were largely ice-free. The highest values of net radiation usually occurred in June and July even despite increased cloudiness and fog. The greatest amount of fog is recorded in June with an average of 7.3 days of heavy fog (Environment Canada 1970-1981). Precipitation is considered moderate in the Churchill area (Beals 1968). The mean annual precipitation for Churchill is 407 mm of which 38% falls during June, July and August (Tables 1.1 and 1.2). By September minimum temperatures are falling below zero. And by October the mean daily temperature is below freezing and the ponds in the Churchill area are becoming frozen (Environment Canada 1970-1981).

The weather of Churchill, Manitoba is primarily dependent on changes in the state of the water surface of Hudson Bay (Beals 1968). Persistent winds off the frozen bay retard spring thawing until late May or even early June. Northerly winds result in increased fog during the summer months and frequent snowstorms in early fall. The Churchill area is relatively windy during the summer months with a mean wind speed of approximately 18 km hr⁻¹ for July. The most frequent wind direction during the summer is from the north or northwest.

D. Vegetation

Bog, forested organic terrain and terrain with almost
Table 1.1: Meteorological Data for Churchill, Manitoba 1970-1979

<table>
<thead>
<tr>
<th></th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Temperature (°C)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.89</td>
<td>7.30</td>
<td>11.00</td>
<td>9.66</td>
</tr>
<tr>
<td>Std. Dev.</td>
<td>3.73</td>
<td>3.15</td>
<td>2.12</td>
<td>4.27</td>
</tr>
<tr>
<td>Max.</td>
<td>4.87</td>
<td>12.27</td>
<td>15.97</td>
<td>14.14</td>
</tr>
<tr>
<td>Std. Dev.</td>
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<td>3.84</td>
<td>2.21</td>
<td>4.59</td>
</tr>
<tr>
<td>Min.</td>
<td>-3.24</td>
<td>2.31</td>
<td>5.98</td>
<td>5.13</td>
</tr>
<tr>
<td>Std. Dev.</td>
<td>3.47</td>
<td>2.72</td>
<td>2.20</td>
<td>4.01</td>
</tr>
<tr>
<td><strong>Precipitation (mm)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>29.39</td>
<td>42.93</td>
<td>53.11</td>
<td>56.97</td>
</tr>
<tr>
<td>Std. Dev.</td>
<td>35.21</td>
<td>22.94</td>
<td>23.64</td>
<td>23.52</td>
</tr>
<tr>
<td><strong>Net Radiation (megajoules m⁻²)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>8.36</td>
<td>10.51</td>
<td>9.22</td>
<td>6.88</td>
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<td>0.52</td>
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<tr>
<td><strong>Mean Wind Speed (km hr⁻¹)</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>19.23</td>
<td>19.17</td>
<td>17.99</td>
<td>18.63</td>
</tr>
<tr>
<td>Std. Dev.</td>
<td>2.11</td>
<td>2.26</td>
<td>1.58</td>
<td>1.72</td>
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</table>
### May-June-July-August 1981

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<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
</tr>
</thead>
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<td></td>
<td>-5.2</td>
<td>18.9</td>
<td>1.8</td>
</tr>
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<td></td>
<td>0.4</td>
<td>16.3</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>7.6</td>
<td>15.0</td>
<td>4.6</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Precipitation (mm)</th>
<th>Total</th>
</tr>
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<tbody>
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<table>
<thead>
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<th>Net Radiation</th>
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<td>57.0</td>
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<table>
<thead>
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<th>Mean Wind Speed</th>
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<td>8.75</td>
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</tbody>
</table>

<table>
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<th>Mean Wind Direction (km/hr)</th>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Prevailing Wind (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.8 16.3 15.3 16.6 18.4</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
no vegetation all occur within the Churchill, Manitoba area. The area of closest proximity to the bay is characterized by sedges (Carex spp., Eriophorum spp.), mosses and lichen (Sphagnum spp., Cladonia sp., Umbilicaria sp.) dominated by shrubby birch (Betula spp.) and willows (Salix spp.), blueberry (Vaccinium uliginosum), crowberry (Empetrum hermaphroditum) and labrador tea (Ledum palustre or L. groenlandica) (Energy, Mines and Resources 1980). To the west and south of the bay the area is characterized by moss and sedge covered floors and patches of white or black spruce (Picea glauca, P. mariana) dominated by sphagnum moss and sedges (Energy, Mines and Resources 1980).

E. Ponds

Four different types of habitats were chosen to analyse the phytoplankton population composition for differences among habitats. Five ponds were chosen within each habitat type to test for similarity of phytoplankton composition and biomass. All the ponds chosen had maximum depths less than two meters. The ponds froze to the sediments during the winter months and thus fish populations were absent.

Five ponds were chosen along Goose Creek Road (Fig. 1.1). Goose Creek Road ran parallel to the Churchill River which overflowed onto the surrounding area. Within a short distance from the town of Churchill, the river and the bay mixed producing waters with variable salinity. Stands of white spruce (Picea glauca) were found to grow in
Figure 1.1: Churchill, Manitoba

A. Goose Creek Road
B. Rock Bluff Area
C. Launch Road
D. Experimental Pond Area
association with marsh, shrubs (Betula spp., Salix spp.) and tamarack (Larix spp.) (Energy, Mines and Resources 1980).

Five ponds were chosen from the rock bluffs along the shores of Hudson Bay (Fig. 1.1). The ponds were exposed to salt spray and macrophyte accumulation from the bay. The outcrop ridges were interspersed with sparse vegetation of heath tundra (for example: Ledum palustre, Diapensia lapponica) and sedge meadow communities (Carex spp., Eriophorum spp.).

Ten ponds were chosen in tundra areas, five along the east to west of Launch Road. These ponds were on higher terrain, with widespread spruce (Picea mariana) islands suggesting that the ponds had been established for some time. Five other ponds, within an area off of Launch Road in which further experiments on ponds were occurring, were also sampled (Fig. 1.1). Peat deposits, lichen and moss muskeg (Sphagnum spp., Cladonia spp., Umbilicaria spp.) were characteristic of both tundra areas. All the experimental area ponds were located within a half mile radius whereas the tundra ponds were spread out along a 22 km east-west stretch between the town of Churchill and the NSERC rocket launch site.

The following study provides a detailed description of phytoplankton composition of the twenty ponds and discusses differences among and within the various habitats of phytoplankton composition and chemical composition. Factors regulating phytoplankton population composition and size
were determined and discussed.
MATERIAL AND METHODS

A. Physical and Meteorological Data

Surface area was approximated by measurements of length and width of the ponds. A maximum depth of each pond was obtained from depth measurements taken along transects following the length and the width of each pond. The depth measurements were conducted on a day in which neither phytoplankton nor chemical collections were taken since disturbances to the sediment would invalidate sampling.

Meteorological data was collected and reported by Environment Canada (1970-1981) and Atmospheric Environment Canada (1970-1981). Evaporation data was calculated using a mass transfer formulation (Derecki 1975). Mean wind speed and mean dewpoint temperature values used in the formulation were obtained from Atmospheric Environment Services (1970-1981).

B. Chemical Collection and Analysis

Water samples for chemical analyses were collected at similar sites to the algal samples at approximately 10 cm below the surface of each pond using both 1 L glass bottles. All samples were placed in covered boxes and transported to the laboratory for immediate analyses. Chemical analyses were preformed monthly during June, July and August of 1980 and 1981.

Dissolved oxygen was determined using the azide
modification of the Winkler method (A.P.H.A. 1976). Total alkalinity, calcium and magnesium values were obtained by the titration methods of Rainwater and Thatcher (1960). Duplicate samples were measured for total alkalinity, calcium and magnesium values in 1980 while triplicate samples were measured in 1981. The pH, temperature (°C), specific conductance (useimens) and salinity (‰) were determined in the field using portable probes.

Upon arrival in the laboratory, subsamples were filtered through Whatman GF/C (1 um sieve) glass fiber filters for analysis of nitrate-nitrogen, soluble reactive phosphorus and total dissolved phosphorus. Colorimetric observations were performed using 2 inch cuvettes (1.0 cm path length) in a Bausch and Lomb Spectronic 20 in 1980 and 4 cm tube in a Pye Unicam UV/VIS spectrophotometer in 1981.

Nitrate-nitrogen was determined colorimetrically at a wavelength of 410 nm by the salicylic acid method of Cataldo et al. (1975). The water sample was first concentrated by evaporation and then the nitrate-nitrogen was determined by nitration of salicylic acid combined with sulfuric acid.

Orthophosphorus is the form of phosphorus most readily utilized by phytoplankton (Wetzel 1975). Difficulties in measuring orthophosphorus arise from difficulties in separating orthophosphorus from other forms of dissolved phosphorus: polyphosphates and phosphorus adsorbed to colloids. The method used herein attempts to identify orthophosphorus by the reactivity of phosphorus with
molybdate. It is therefore more appropriate to use the term soluble reactive phosphorus rather than orthophosphorus.

Soluble reactive phosphorus was analysed by the Murphy and Riley (1962) method. Although Rigler (1968) suggested that this method exaggerated the concentration of soluble orthophosphate by 10-100 fold, Walton and Lee (1972) found no discrepancies between soluble reactive molybdenum blue phosphorus and additions of soluble orthophosphate using standardized bioassay procedures. Total dissolved phosphorus was determined by performing a persulfate digestion (Menzel and Corwin 1965) to measure total phosphorus of the filtered sample. Both soluble and total dissolved phosphorus were determined on a red phototube at wavelengths 690 nm and 880 nm.

Silica was determined colorimetrically at a wavelength of either 410 nm using a blue phototube or 815 nm using a red phototube by the ammonium molybdate method (A.P.H.A. 1976). This procedure omits the conversion step of unreactive silica to a reactive form and therefore what is really molybdate-reactive silica will be reported as silicate-silica. In reality, this provides a simple measurement of the immediate bio-available silica pool in the ponds as opposed to total silica.

Chlorophyll a corrected for phaeophytin was estimated by filtering 1.0 L of sample that had been maintained in the dark until filtering and extraction in 90% acetone made basic with magnesium carbonate (Golterman and Clymo 1969).
Absorbance of the extract was measured at 750 and 665 nm before and after acidifying the extract. To correct for turbidity the absorbance at 750 nm was subtracted from the other absorbance. The amount of pigment was calculated by the equation in Appendix I. Chlorophyll a values were obtained only in 1980. The most accurate method of determining biomass of phytoplankton is by direct microscopic enumeration. Measurements of chlorophyll a only gives an estimate of biochemical biomass. The amount of chlorophyll a per cell may vary with algal species (Gillbricht 1952) and physiological state of the phytoplankton population (Senft 1978). Therefore phytoplankton biomass was only determined by direct microscope enumeration.

All glassware was washed in phosphate-free detergent (Liquinox, Canlab), rinsed at least three times in distilled water and air dried.

C. Phytoplankton Collection and Analysis

The twenty ponds were sampled for phytoplankton monthly during the ice-free months of 1980 and 1981. Samples were obtained using a vertical hose sampler (2.0 cm. internal diameter, 1.0 m length) modified from Lund (1949). The sampler was lowered slowly into the water in front of oneself to collect a uniform sample of the water column to a depth approaching the sediment-water interface. A composite phytoplankton sample was obtained by taking five discrete
samples including the four corners and center of each pond. A mixed subsample was removed and then preserved with modified Lugol's solution (Nauwerck 1963; Vollenweider 1969) at a 1% v/v concentration. The phytoplankton were enumerated using the methods of Lund et al. (1958) which are based upon Utermöhl (1931) techniques. Aliquots of 2-5 mL were sedimented in modified sedimentation chambers (Evans 1972) and examined on a Nikon inverted phase microscope. From 400 to 1000 plankton cells (single cell, colonies or filaments) found within two or more transects across the chamber were identified and counted. The whole bottom of the chamber was scanned for larger plankton cells, colonies or filaments using a lower power objective, (200x). Representatives (<50) of each species counted in one sample were also measured. Units without visible cell content were not counted and were presumed moribund. Few such units were noted. An enumerated sample totalled 200-800 units in order to achieve an adequate counting efficiency (Lund et al. 1958).

The cell volume of each species was estimated from the average dimensions and the geometrical shape that most closely resembled the species form (Vollenweider 1969; Trevisan 1978; Appendix II). Total biomass was reported as \( \mu \text{m}^3 \text{mL}^{-1} \). The total biomass can be calculated as wet weight assuming a specific gravity of 1.0 gm.cc.\(^{-1}\) for algal cells. Most commonly used taxonomic works for the identification of phytoplankton included: Anton and Duthie (1981), Bourreelly (1966, 1968), Germain (1981), Huber-Pestalozzi (1938-1972),

Similarity between the algal communities of all the ponds was calculated quantitatively and qualitatively by using the percentage similarity index and the Jaccard index, respectively (Whittaker 1952; Appendix I). Cluster analysis was applied to the data by the weighted pair group method (Sokal and Sneath 1963). Samples enumerated from July of 1980 and 1981 were compared using the percent similarity index, while presence of species over the whole sampling season for 1980 and 1981 were used to calculate the Jaccard's index.
A. Meteorological

The year 1981 was an unusual year in monthly precipitation and net radiation as compared with the years 1970-1979 (Tables 1.1 and 1.2). Precipitation in May and June 1981 was only 14.3 and 18.2 mm compared with average precipitation values of 29.39 and 42.93 mm for May and June 1970-1979. Net radiation for the months of June and July were 12.22 and 10.22 megajoules.m\(^{-2}\) compared with the average net radiation values of 10.51 and 9.22 megajoules.m\(^{-2}\) during the years 1970-1979. The summer was therefore drier and net radiation was higher than in other years. A lower wind speed in the summer reduced the effect of the bay in lowering air temperature and increasing the amount of fog.

In 1980, from 26 April to 4 May the daily temperatures rose from below freezing to a record maximum of 28.2°C with a mean daily temperature of 9°C (Environment Canada 1980-1981). This precipitated an early thawing of the ponds but in late May when sampling commenced the ponds had refrozen and the rest of the summer progressed normally.

During June, July and August 1981 the monthly temperatures were 2.1% above 1980 values (Fig. 1.2) although the temperatures were not unusual from the ten year averages (Table 1.1). Temperatures increased to a summer high of 16.3°C in 1980 and 18.9°C in 1981. From May to September 1980 the
Figure 1.2: Air temperature (°C) of Churchill, Manitoba during the summer months of 1980 and 1981. (maximum temperature = ---, minimum temperature = ---)
Figure 1.3: Total precipitation (mm) of Churchill, Manitoba during the summer months of 1980 and 1981.
Figure 1.4: Total net radiation (megajoules m\(^{-2}\)) of Churchill, Manitoba during the summer months of 1980 and 1981.
total precipitation was 226.3 mm compared to 140.3 mm during the summer months in 1981 (Fig. 1.3). With reduced cloudiness in 1981 net radiation was higher than in 1980 particularly during June and August (Fig. 1.4).

B. Physical

Table 1.3 compares the surface area and depth for Goose Creek, rock bluff, experimental pond area and tundra ponds. The tundra ponds and the experimental pond area ponds had on average larger surface areas than either the Goose Creek or rock bluff ponds. Goose Creek ponds have greater depths than the other ponds. Depths of the experimental pond area and rock bluff ponds were very similar.
Table 1.3: Physical Characteristics of Ponds in Churchill, Manitoba

<table>
<thead>
<tr>
<th></th>
<th>Goose Creek</th>
<th>Rock Bluff</th>
<th>Tundra</th>
<th>Experimental Area</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Surface Area m²</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>24.8</td>
<td>11.4</td>
<td>14408.4</td>
<td>884.0</td>
</tr>
<tr>
<td>Std. Dev.</td>
<td>11.9</td>
<td>17.8</td>
<td>25770.7</td>
<td>435.4</td>
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<tr>
<td><strong>Depth cm</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Mean</td>
<td>60.4</td>
<td>23.8</td>
<td>34.8</td>
<td>25.6</td>
</tr>
<tr>
<td>Std. Dev.</td>
<td>/28.8</td>
<td>5.4</td>
<td>25.6</td>
<td>2.3</td>
</tr>
</tbody>
</table>
C. Chemistry

Average summer chemical composition of the twenty ponds is given in Table 1.4. Phosphorus and calcium concentration showed differences between the various groups of ponds. Total dissolved phosphorus and soluble reactive phosphorus varied significantly ($F = 23.614$, $F = 16.800$, $p < 0.001$) between the years of 1980 and 1981 (Table 1.5). All the ponds had greater phosphorus concentrations in 1981 (Table 1.4). The total dissolved phosphorus concentrations ranged from 0.002 to 0.178 mg.L$^{-1}$ in 1980 and from 0.038 to 0.940 mg.L$^{-1}$ in 1981. The highest concentrations occurred in the ponds situated along the rock bluffs. Soluble reactive phosphorus of all the ponds ranged from 0 to 0.098 mg.L$^{-1}$ in 1980 and from 0 to 0.103 mg.L$^{-1}$ in 1981.

The calcium concentrations measured as calcium and alkalinity varied between groups and years. Most of the ponds showed an increase in calcium concentrations over the summer. Calcium concentrations were generally higher in 1981 than 1980 as a result of less precipitation (Tables 1.2 and 1.6). The largest increase was measured in all the ponds sampled along the rock bluffs. Calcium concentrations varied between rock bluff ponds from 13.73 to 47.17 mg.L$^{-1}$ in 1980 and from 47.44 to 61.94 mg.L$^{-1}$ in 1981. The alkalinity varied among ponds little between years, again with the largest difference occurring in the rock bluff ponds. The rock bluff ponds had alkalinity concentrations varying from 105.83 to 164.66 mg.L$^{-1}$ in 1980 and from 198.66 to 276.50
Table 1.4: Average summer chemical composition of twenty ponds from Churchill, Manitoba during 1980 (top value) and 1981 (bottom value).

<table>
<thead>
<tr>
<th>PONDS</th>
<th>CHEMICAL COMPOSITION (mg.L⁻¹)</th>
<th>Sal. Cond.</th>
</tr>
</thead>
<tbody>
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<td>Ca  Mg  CaCO₃  SiO₃  NO₃-N TDP SRP  pH</td>
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<td>GOOSE CREEK</td>
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<td>77.12 59.13 236.83 0.059 0.67 0.008 0.006</td>
<td>5.0 5200</td>
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<tr>
<td></td>
<td>105.65 N/A 213.65 0 0.47 0.080 0.010 NA</td>
<td>1.8 1120</td>
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<tr>
<td>103</td>
<td>81.49 42.68 237.50 0.036 0.48 0.010 0.002</td>
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<td>33.97 13.25 237.50 0 0.28 0.076 0.036 NA</td>
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<td>0.0 240</td>
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<td>49.41 12.12 302.15 0 0.23 0.071 0.017 NA</td>
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<tr>
<td>106</td>
<td>188.26 2.74 346.67 0.036 0.80 0.009 0.003</td>
<td>8.6 6900</td>
</tr>
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<td>41.54 13.24 320.65 0 0.32 0.081 0.014 NA</td>
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<tr>
<td>130</td>
<td>40.75 17.15 213.25 0.098 0.82 0.009 0.004</td>
<td>0 350</td>
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<tr>
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<td>62.94 16.78 254.50 0 0.50 0.081 0.010 NA</td>
<td>NA NA</td>
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<td>ROCK BLUFFS</td>
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<td>200</td>
<td>18.98 28.25 148.33 0.054 0.65 0.089 0.011 8.55</td>
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<td></td>
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</tr>
<tr>
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<td>0.011 0.16 0.010 0.057 8.85 0.3 800</td>
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<tr>
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<td>21.03 38.06 153.50</td>
<td>0.024 0.53 0.055 0.014 8.20 0.9 1060</td>
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<tr>
<td>208</td>
<td>38.42 51.90 164.66</td>
<td>0.046 0.38 0.074 0.017 8.65 3.3 3850</td>
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</tbody>
</table>

**EXPERIMENTAL POND AREA**

| 150  | 29.06 18.64 142.17 | 0.023 0.33 0.120 0.098 7.50 0 268 |
| 155  | 19.72 24.11 114.80 | 0.014 0.28 0.063 0.013 8.05 0 192 |
| 157  | 20.76 22.38 142.33 | 0.016 0.29 0.056 0.008 8.25 0 250 |
| 159  | 20.45 20.41 134.33 | 0.020 0.33 0.040 0.009 8.45 0 239 |

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<td>15.07</td>
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<td>0.056</td>
<td>0.033</td>
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**TUNDRA**

<table>
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<tr>
<th></th>
<th>38.92</th>
<th>21.66</th>
<th>137.17</th>
<th>0.033</th>
<th>0.25</th>
<th>0.002</th>
<th>0.001</th>
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<td>34.59</td>
<td>39.39</td>
<td>130.15</td>
<td>0.007</td>
<td>0.34</td>
<td>0.038</td>
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mg.L\(^{-1}\) in 1981. The rest of the ponds had concentrations ranging from 107.83 to 346.67 mg.L\(^{-1}\) in 1980 and from 86.0 to 320.00 mg.L\(^{-1}\) in 1981. The higher values were found in the ponds along Goose Creek.

Magnesium, silicate silica and nitrate nitrogen showed no significant differences between either ponds, groups or years (Table 1.5). The magnesium concentrations ranged from 2.74 to 59.13 mg.L\(^{-1}\). The ponds along the rock bluffs decreased in average summer magnesium concentrations between 1980 and 1981 (Table 1.4). Silicate silica ranged from no detectable concentration in the Goose Creek ponds during 1981 to 0.077 measured in the rock bluff ponds. Nitrate nitrogen concentration ranged from 0.18 to 1.55 mg.L\(^{-1}\). The highest values were measured during 1981 for the rock bluff ponds.

The pH was greater than 7.0 and often more than 8.0 for all the ponds. Concentrations of free carbon dioxide approached zero in all the ponds. The percent saturation of dissolved oxygen approached 100% at all times for all the ponds. Salinity was measurable in only the Goose Creek and rock bluff area ponds. Salinity increased in 1981 in those ponds. Salinity ranged from less than 0.3 to 8.6 o/oo. Specific conductivity was also high in the ponds with some measurable amount of salinity ranging from 700 to 8300 umhos cm\(^{-1}\). Specific conductance in the ponds of the tundra and experimental pond area ranged from 132 to 580 umhos cm\(^{-1}\).
Table 1.5: Analysis of variance of the chemical composition for the twenty ponds. Listed are the F-values for the various chemical parameters between 1980 and 1981, between the four groups and between the five ponds per group. Values underlined are significant at p< 0.001 (n=80, July and August values).

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<th>YEAR</th>
<th>GROUP</th>
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<th>Y-P</th>
<th>G-P</th>
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<td>0.811</td>
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<td>1.276</td>
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<td>0.635</td>
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Table 1.6: Water Evaporation (cm. month$^{-1}$) for summer months in Churchill, Manitoba.

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<tr>
<td>1970-1979 Average</td>
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<tr>
<td>Std. Dev.</td>
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<td>1980 Average</td>
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<td>1981 Average</td>
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D. Phytoplankton Composition

A list of the species observed, author of species and mean volume of species during 1980 and 1981 is available in Appendix III. A total of 86 genera were recorded encompassing 120 taxa. Dominant and rare phytoplankton species with respect to phytoplankton biomass are listed in Appendix III. Seasonal composition of dominant phytoplankton are listed in Appendix IV. The dominant algae are defined as those contributing 5 percent or more to the biomass of any one sample over the two summer seasons. While there were more species collected in 1980 than in 1981 most of the species present in any one pond were also found in any other pond (Fig. 1.5).

The seasonal patterns of abundance for the Goose Creek ponds are observed in Figures 1.6, 1.7 and 1.8, where plots of total biomass are illustrated as percent total biomass for each algal class. Pond 102 ranged in biomass from 56.6 to 20,262.3 um$^3$.10$^3$.mL$^{-1}$ in 1980 and from 178.2 to 991.6 um$^3$.10$^3$.mL$^{-1}$ in 1981. Pond 103 ranged in biomass from 54.7 to 1222.0 um$^3$.10$^3$.mL$^{-1}$ in 1980 and from 289.4 to 3892.6 um$^3$.10$^3$.mL$^{-1}$ in 1981. Pond 105 ranged in biomass from 23.2 to 242.2 um$^3$.10$^3$.mL$^{-1}$ in 1980 and from 1378.6 to 3071.2 um$^3$.10$^3$.mL$^{-1}$ in 1981. Pond 106 ranged from 83.1 to 2004.9 um$^3$.10$^3$.mL$^{-1}$ in 1980 and from 29.2 to 1839.7 um$^3$.10$^3$.mL$^{-1}$ in 1981. Pond 130 ranged in biomass from 66.0 to 1059.6 um$^3$.10$^3$.mL$^{-1}$ in 1980. No phytoplankton samples were taken from pond 130 in 1981.
Figure 1.5: Species richness in 1980 (top) and 1981 (bottom). 120 species identified.
Figure 1.6: Seasonal variation of phytoplankton biomass (Log \( \text{um}^3.\text{mL}^{-1} \)) and class composition (\% total biomass) at ponds (a) 102 and (b) 103 during 1980 and 1981.
Figure 1.7: Seasonal variation of phytoplankton biomass (Log \(\text{um}^3 \cdot \text{mL}^{-1}\)) and class composition (% total biomass) at ponds (a) 105 and (b) 106 during 1980 and 1981.
Figure 1.8: Seasonal variation of phytoplankton biomass (log $\text{um}^3\text{mL}^{-1}$) and class composition (% total biomass) at ponds (a) 130 and (b) 208 during 1980 and 1981.
In 1980 biomass within all the Goose Creek ponds peaked in the early part of June as the ice was melting, water temperatures were increasing and solar radiation was increasing (Table 1.2). Bacillariophyceae were the most important group in the spring contributing from 45 to 82 percent of the total biomass. Through the summer, Bacillariophyceae, Chlorophyceae and Cryptophyceae were dominant classes. The Bacillariophyceae ranged from less than 1 to 91.8 percent algal biomass. The Chlorophyceae contributed from 3.8 to 90.1 percent algal biomass and the Cryptophyceae contributed from less than 1 to 87.4 percent algal biomass. In 1981, a peak in biomass was observed during August for ponds 102, 105 and 106. Bacillariophyceae was the major contributor in August with 51 to 89 percent of the total biomass. In August, the phytoplankton sample for pond 103 was lost. During both years Cyanophyceae peaked in biomass during late June to early July and again in August at pond 106. Maximum percent Cyanophyceae biomass was 19 and 21 percent for 1980 and 1981, respectively.

In 1980 phytoplankton found in May was dominated by Bacillariophyceae consisting of Diatoma elongatum, Pinnularia spp., Mastalogia smithii var. amphicephala, Pinnularia spp., Amphipora alata, Cyclotella bodanica, Tabellaria flocculosa, T. fenestrata and Eunotia praerupta. Amphipora alata significantly contributed to peaks of Bacillariophyceae biomass (>25% of the total biomass) for ponds 102, 103 and 106. During the summer Navicula spp.
Pinnularia spp., Tabellaria fenestrata, Cocconeis spp., Surirella spp., Gomphonema spp., Mastalocia smithii var. amphicephala, Diatoma elongatum, Synedra ulna and Gomphonema spp. were common at the ponds.

Common species of Chlorophyceae present during the summer included Chlamydomonas spp., Oocystis crassa, Scenedesmus bijuga, S. quadricauda, Raphidiopsis spp., Ankistrodesmus falcatus, Eudorina elegans, Pediastrum spp., Euastrum spp. and Spirogyra spp. The Chlorophyceae biomass peaked during the early part of the summer at all ponds. Eudorina elegans, Scenedesmus quadricauda and S. bijuga were significant contributors to ponds 102, 103 and 105, respectively. Pediastrum spp. and Eudorina elegans were common at pond 106 while Euastrum spp. and Tribonema spp. were common at pond 130.

The Cryptophyceae biomass peaked either in July or August for all the ponds except pond 102. Significant contributions were made by Rhodomonas minuta with Cryptomonas erosa, C. curvata, C. ovata and C. pusilla common species.

Dinobryon spp. was common at pond 105 and 130 during the 30 June sample. Gymnodinium helveticum was common at pond 105 during the July sample.

In 1981 Amphiprora alata again significantly contributed to peaks in Bacillariophyceae biomass for ponds 102, 105 and 106 in early July. The species was not observed in pond 103 for 1981. During the rest of the summer
Mastalonia smithii var. amphicephala, Stephanodiscus astrea and Pinnularia spp. were significant contributors with Navicula spp., Caloneis spp., Amphipora alata, Stephanodiscus astreae as common species.

Cyanophyceae were more prevalent in 1981 than 1980 with peaks in biomass during early July and then in August for ponds 105 and 106. Aphanocapsa spp. was common in July for pond 106. Merismopedia punctata was common at pond 106 during July and August during both 1980 and 1981.

Chlorophyceae were present throughout the sampling season at pond 106 but was only present briefly during July at ponds 102 and 103. Oocystis solitaria significantly contributed to the total biomass in July at pond 106. Eudorina elegans was common only at pond 106 during August.

In 1981 Cryptophyceae were present only at pond 103 during the beginning of July with Cryptomonas erosa significantly contributing.

Seasonal trends in algal biomass and class composition of the rock bluff ponds are given in Figures 4.8, 1.9 and 1.10. Pond 200 had biomass ranging from 36.6 to 536.5 um³.10⁻³.mL⁻¹ in 1980 and from 4.8 to 604.412.4 um³.10⁻³.mL⁻¹ in 1981. Pond 203 ranged in biomass from 44.0 to 13,040.8 um³.10⁻³.mL⁻¹ in 1980 and from 24.9 to 7872.7 um³.10⁻³.mL⁻¹ in 1981. Pond 205 had biomass ranging from 4.6 to 1218.5 um³.10⁻³.mL⁻¹ in 1980 and 8.4 to 1278.3 um³.10⁻³.mL⁻¹ in 1981. Pond 206 had a biomass range of 87.6 to 2456.2 um³.10⁻³.mL⁻¹ in 1980 and a range of 26.7 to 2142.5 um³.10⁻³. in 1981. Pond
Figure 1.9: Seasonal variation of phytoplankton biomass (log um$^3$.mL$^{-1}$) and class composition (% total biomass) at ponds (a) 200 and (b) 203 during 1980 and 1981.
Figure 1.10: Seasonal variation of phytoplankton biomass (log um³.mL⁻¹) and class composition (% total biomass) at ponds (a) 205 and (b) 206 during 1980 and 1981.
208 had a biomass range of 6.6 to 15,786.2 um$^3$.10$^3$.mL$^{-1}$ and a range of 31.4 to 44,465.0 um$^3$.10$^3$.mL$^{-1}$ in 1981. With the exception of pond 200, the ponds had a range in biomass similar for both years. Pond 200 had dried up by the end of June in 1980.

No consistent time of maximum biomass was evident for all the ponds in either year. The maximum biomass sampled for all the ponds occurred at a later date in 1981. Ponds 200, 206 and 20 had peak biomasses during late June-July in 1980 and then during August in 1981. Ponds 203 and 205 had peak biomasses in early June in 1980 and in July in 1981.

In the spring of 1980 Chlorophyceae were the most important group contributing up to 96 percent of the total biomass and with an average of 58 percent among the ponds in the spring. During the summer Chlorophyceae, Cryptophyceae and Bacillariophyceae were the most important contributors to the total algal biomass (>25% of the total biomass), with Cyanophyceae also contributing significantly at times to the biomass.

In 1981 Chlorophyceae and Bacillariophyceae were the most important contributors to the total algal biomass. The Chlorophyceae species Brachiononas Westiana contributed up to 98 percent of the total biomass during the early part of July. Cyanophyceae and Cryptophyceae also significantly contributed to the total biomass at times for ponds 208 and 200, respectively. In August Chlorophyceae was the dominant class at all the ponds contributing from 81 to 99 percent of
the total biomass.

Phytoplankton species common to the rock bluff ponds are listed in Table 1.6. Phytoplankton found in the spring of 1980 were dominated by Chlorophyceae consisting of Characiopsis spp. and Chlamydomonas spp., Navicula spp. and Mastalagia smithii var. amphiophala were common diatoms. Gymnodinium helveticum was a significant contributor to the total biomass at pond 203. Rhodomonas minuta was a common Cryptophyceae. During the summer Pediastrum spp., and Spirogyra spp. were significant contributors of Chlorophyceae. The Cryptophyceae was represented solely by Rhodomonas minuta. In Bacillariophyceae Mastalagia smithii var. amphiophala, Navicula sp. and Tabellaria fenestrata were common at ponds 200, 203, 205 and 208, with Diatoma elongatum common at pond 206. Contributors to the total biomass by Cyanophyceae consisted of Aphanocapsa spp. and Oscillatoria. spp.

In 1981 the Chlorophyceae were represented by Brachiononas Westiana in the ponds observed, with the exception of pond 206. During the summer Chlamydomonas spp. was found in large volumes in ponds 200, 203, 205 and 206. Scenedesmus quadricauda was found at pond 206. In Cryptophyceae Rhodomonas minuta and Cryptomonas eosa var. reflexa were common. The diatom Navicula spp. was common in ponds 200, 203, 205 and 206. The blue-green Aphanocapsa spp. significantly contributed to a biomass peak in pond 208. In August the Chlorophyceae were dominated by Spirogyra spp. in
ponds 200, 205 and 208 while Zygnema spp. was the dominant species at ponds 203 and 206.

Seasonal trends in total algal biomass and class composition for the ponds in the experimental area are represented in Figures 1.11, 1.12 and 1.13. Pond 150 had a biomass range from 991.3 to 2007.8 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1980 and from 190.6 to 731.6 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1981. Pond 155 had a biomass range from 186.5 to 433.9 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1980 and from 17.7 to 1368.3 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1981. Pond 157 had a biomass range from 181.8 to 860.5 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1980 and from 217.8 to 1535.3 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1981. Pond 159 had biomass ranging from 287.5 to 860.4 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1980 and from 202.2 to 1170.7 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1981. Pond 160 had a biomass range of 208.7 to 529.9 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1980 and from 147.0 to 1449.5 \( \mu \text{m}^3 \cdot 10^3 \text{mL}^{-1} \) in 1981. In 1980 all ponds except pond 159 had peak biomass in May. Ponds 155, 157 and 160 declined to a lower biomass by August. Pond 159 increased in biomass from May to a peak in August while pond 150 increased to a greater second peak in August. In 1981 all ponds sampled were found to have low biomasses in late June- mid July increasing to peak biomass in August.

In 1980 peak biomasses consisted of Chlorophyceae and/or Bacillariophyceae. During the summer Chlorophyceae, Cryptophyceae and Bacillariophyceae were the most important contributors to the total biomass, with Cyanophyceae also contributing at times to the total biomass for ponds 159, 155, 159 and 160. Chlorophyceae contributed from 0 to 56.
Figure 1.11: Seasonal variation of phytoplankton biomass (log um^3 mL^-1) and class composition (% total biomass) at ponds (a) 150 and (b) 155 during 1980 and 1981.
Figure 1.12: Seasonal variation of phytoplankton biomass (log $\mu m^3.mL^{-1}$) and class composition (% total biomass) at ponds (a) 157 and (b) 159 during 1980 and 1981.
Figure 1.13: Seasonal variation of phytoplankton biomass (log $\text{um}^3 \cdot \text{mL}^{-1}$) and class composition (% total biomass) at ponds (a) 99 and (b) 160 during 1980 and 1981.
percent of the total biomass and Bacillariophyceae from 18 to 89 percent of the total biomass during peak in biomass. In 1981 the peak biomasses in August were a result of significant contributions by Chlorophyceae with some contribution by Bacillariophyceae. Chlorophyceae contributed from 45 to 76 percent of the total biomass while Bacillariophyceae contributed from 15 to 40 percent during August. During June and July Chlorophyceae ranged from 34 to 78 percent of the total biomass.

The peaks of biomass occurring early in the season for ponds 155, 157 and 160 were dominated by Bacillariophyceae of which Pinnularia spp. was the most important species contributing from 23.7 to 55.6 percent of the total volume. Chlorophyceae was the major contributor of the late season biomass peaks of ponds 150 and 159 withSpirogyra spp. and Eudorina elegans common at pond 150 and Oocystis crassa and Oocystis borgei, Euastrum sp. and Pediastrum spp. common to pond 159. In Cryptophyceae Cryptomonas erosa was the significant contributor to the total biomass at all the ponds, with Rhodomonas minuta and Cryptomonas erosa var. reflexa also common. At ponds 159 and 160 the Cyanophyceae were also common consisting mainly of Merismopedia major at pond 159 and Aphanocapsa spp. at pond 160.

Phytoplankton found in the ponds in 1981 were dominated by Chlorophyceae consisting mainly of Oocystis crassa during the summer and Oocystis crassa and Spirogyra spp. during August. In Bacillariophyceae common species included
Mastogloia smithii var. amphicephala, Navicula spp., Pinnularia spp., Synedra ulna, Tabellaria fenestrata, T. flocculosa and Diatoma elongatum. The Cyanophyta consisted of mainly of Merismopedia major at all the ponds.

The seasonal trends in total phytoplankton biomass and class composition for the tundra ponds are represented in Figures 1.13, 1.14 and 1.15. Pond 10 had a biomass range of 16.5 to 748.8 um^3^3.10^3^ mL^-1 in 1980 and a range of 446.2 to 1649.5 um^3^3.10^3^ mL^-1 in 1981. Pond 37 had a biomass range of 250.5 to 11699.7 um^3^3.10^3^ mL^-1 in 1980 and from 184.2 to 799.5 um^3^3.10^3^ mL^-1 in 1981. Pond 73 had a biomass range of 166.2 to 839.8 um^3^3.10^3^ mL^-1 in 1980 and from 182.6 to 856.1 um^3^3.10^3^ mL^-1 in 1981. Pond 84 had a biomass range of 50.1 to 172.6 um^3^3.10^3^ mL^-1 in 1980 and from 200.5 to 321.9 um^3^3.10^3^ mL^-1 in 1981. Pond 99 had a biomass range of 160.5 to 260.4 um^3^3.10^3^ mL^-1 in 1980 and from 169.0 to 209.4 um^3^3.10^3^ mL^-1 in 1981. In 1981 pond 84 had dried up by the end of July and remained dry for the rest of the sampling period.

In 1980 the biomass peaked for the ponds in late June or August in 1980 and then later in the season during 1981. Bacillariophyceae with either Chlorophyceae or Cryptophyceae were the major contributors to the ponds in 1980. Bacillariophyceae contributed from less than 1 to 74 percent of the total biomass. Cyanophyceae contributed at times significantly to the biomass of the ponds. At ponds 10, 73 and 99 Bacillariophyceae, Cyanophyceae and Chlorophyceae
Figure 1.14: Seasonal variation of phytoplankton biomass (log um$^3$.mL$^{-1}$) and class composition (% total biomass) at ponds (a) 10 and (b) 37 during 1980 and 1981.
Figure 1.15: Seasonal variation of phytoplankton biomass (log um$^3$. mL$^{-1}$) and class composition (% total biomass) at ponds (a) 73 and (b) 84 during 1980 and 1981.
were the most important contributors to the biomass in 1981. Bacillariophyceae contributed from 14 to 74 percent of the total biomass. At pond 37 Cyanophyceae was dominant throughout the sampling period contributing from 58 to 88 percent of the total biomass while at pond 84 Chlorophyceae was a significant contributor during the sampling period ranging from 70 to 83 percent of the total biomass.

There were more species which contributed >5% of the total biomass in the tundra group of ponds than all the other groups for both years (Appendix IV). In 1980 Navicula spp., Eunotia praerupta, Caloneis spp., Tabellaria fenestrata, Mastalioa smithii var. amphicephala, Diatoma elongatum, Cymbella sp., Mastalioa smithii and Synedra acus were common diatoms. In Chlorophyta Oocystis crassa, Oocystis borgei, Cosmarium spp., Chlamydomonas spp., Characopsis spp. and Tetraedron minimum were present. In Chrysophyceae, Rhodomonas minuta was common with some occurrence of Cryptomonas erosa. When Cyanophyceae contributed significantly to the total biomass at ponds 73, 10 and 37 Merismopedia major was the main contributor for pond 73 while Aphanocapsa spp. was the main contributor for ponds 10 and 37.

For ponds 10, 73 and 99 Pinnularia spp. was a common if not significant diatom. Diatoms Mastalioa smithii, M. var. amphicephala, Tabellaria fenestrata, Navicula spp., and Caloneis spp. were also present. In Cyanophyta Aphanocapsa spp., and Merismopedia major were common. The Chlorophyceae
consisted mainly of *Eudorina elegans*, *Spirogyra* spp., *Pediastrum* spp., *Oocystis borgei*, and *Oocystis solitaria*. At pond 37 the Cyanophyceae dominated the biomass the *Aphanocapsa* spp., *Merismopedia major* and *Merismopedia punctata*. At pond 84 the Chlorophyceae dominated consisting of *Ankistrodesmus falcatus*, *Pediastrum* spp. and *Chlamydomonas* spp.

Average seasonal biomass was similar for all pond groups in 1980 (Fig. 1.16). In 1981 the average seasonal biomass was slightly greater for the rock bluff pond group although the variation was the greatest. Least biomass variations in phytoplankton community biomass occurred in the tundra ponds during both years.
Figure 1.16: Average seasonal biomass in 1980 and 1981 for twenty ponds in four geographical groups of Churchill, Manitoba. Bar denotes minimum and maximum range of seasonal biomass values.
E. Size Distribution

Seasonal fluctuations in the size classes >64, 30-64, 10-30 and <10 um for the twenty ponds are listed in Appendix V. The species were placed into the various size fractions depending on their mean comparative spherical size. Using July phytoplankton data for the twenty ponds size distributions were plotted against mean phytoplankton frequency (ln # cells mL\(^{-1}\)) (Fig. 1.17 and 1.18). In 1980 there were 20% more species in the <10 um fractions compared with 1981. In 1981 there was an increase in the larger sized species (>30 um). The size distribution of all ponds deviated significantly (p< 0.001) from normality based on a modified Kolmogorov-Smirnov test (Sokal and Rohlf 1969). A brief description of seasonal phytoplankton composition in the various size classes for each pond area follows.

In 1980 in the Goose Creek ponds the dominant size was the size range up to 30 um. *Amphiprora alata*, a euryhaline species, was common to the 10-30 um size fraction in June. In July and August the common species were *Rhodomonas minuta*, *Cryptomonas erosa* and *Oocystis crassa* which generally occurred in the <10 um size fraction.

In 1981 in the Goose Creek ponds a similar size distribution pattern to 1980 occurred with the major size classes falling in the 0-30 um size range. *Amphiprora alata* was common in the 10-30 um size fraction in the beginning of July while *Diatoma elongatum* was common for all the ponds in
Figure 1.17: Phytoplankton size distribution for ponds in Churchill, Manitoba 1980.
Figure 1.18: Phytoplankton size distribution for ponds in Churchill, Manitoba 1981.
the <10 um size fraction in July. **Stephanodiscus astrea**, **Pinnularia** spp., and **Eudorina elegans** were common in the 10-30 um size range in August.

For the rock bluff ponds the majority of the phytoplankton fell within the <30 um size fraction with the less than 10 um size fraction occurring most frequently. **Rhodomonas minuta** was the most common species under 10 um. **Pediastrum** spp. was the major contributor in the 10-30 um size fractions with **Tabellaria fenestrata**, **Pediastrum** spp., **Aphanocapsa** spp., also common. Occurrences of netplankton (>64 um) were usually filamentous algae. **Spirogyra** spp. occurred at station 203 in July and **Geminella interrupta**, **Spirogyra** spp. and **Tribonema** spp. were responsible for increases in the >30 um size fraction at station 205. Both ponds 203 and 205 were nutrient rich which would support larger species.

In 1981 the rock bluff ponds had size ranges represented than in 1980. The month of July consisted mainly of the <10 um size fraction, while the month of August consisted of the >64 um fraction. The beginning of the month of July consisted mainly of **Chlamydomonas** spp., **Brachiononas Westiana**, **Navicula** spp. and **Scenedesmus quadricauda**. **Chlamydomonas** spp., **Diatoma elongatum**, **Brachiononas Westiana**, and **Navicula** spp. contributed to the mid-July samples while **Rhodomonas minuta**, **Cryptomonas eros** var. **refexa**, **Stephanodiscus astrea**, **Navicula** spp., and **Chlamydomonas** sp. were present during the end of July. Both
ponds 206 and 208 had a large percentage of biomass in the 10-30 um size fraction during both years. In 1980 *Pediastrum* spp. was the dominant species while in 1981 *Aphanocapsa* spp. and *Surirella* sp₂ were dominant species for ponds 206 and 208, respectively. During the month of August *Spirogyra* spp. were the major contributors to the >64 um size fraction in 1981.

In the experimental pond area the ponds had phytoplankton samples consisting mainly of the <10 um size fraction (Appendix VI). A greater than 64 um size fraction became dominant for pond 150 during July as a result of the dominance of *Spirogyra* spp.. In May *Rhodomonas minuta*, *Pinnularia* spp. and *Eudorina elegans* were present, and in June the cryptomonads *Rhodomonas minuta* and *Cryptomonas erosa* var. *reflexa* were common. In July *Cryptomonas erosa* was common at all the ponds sampled. In August the green algae *Oocystis crassa* and *Euastrium* spp. were common.

In 1981 the average size fraction increased so that a large percentage of the size distribution occurred in the 10-30 um size fraction for the ponds in the experimental pond area. The end of June was dominated by *Oocystis crassa* which contributed to the 10-30 size fraction. In July the size distribution generally increased to either the 30-64 um or the >64 um size fraction and was dominated by either *Merisomopedia major* or filamentous algae, such as *Geminella interrupta* or *Spirogyra* spp.. In August *Spirogyra* spp. contributed most to the populations.
Very few dominant species (>25% of the total biomass) were common within the size fractions of the tundra ponds in 1980 (Appendix VI). A peak in the >64 um size fraction occurred in ponds 84 and 73 as a result of Spirogyra spp. and Aphanocapsa spp., respectively. Generally the dominant size fraction lay in the <10 and 10-30 um size classes. Rhodomonas minuta, Oocystis crassa, O. borgei, Chlamydomonas spp., Aphanocapsa spp., Pediastrum spp., Dinobryon spp. and Diatoma elongatum all contributed to the major size classes.

During 1981 the 10-30 size fractions contributed most to the total biomass in the tundra ponds. Pediastrum spp., Pinnularia spp. and Aphanocapsa spp. were common species contributing to the 10-30 um size fraction.

In conclusion, the majority of phytoplankton for all the groups of ponds were the nanoplankton (<64 um). For the ponds in the rock bluff area, along Goose Creek road and within the experimental pond area maximum biomass occurred in either May or June 1980, and then not until August 1981. Chlorophyceae was responsible for peak biomass in the ponds located along the rock bluff or in the experimental pond area. Bacillariophyceae was responsible for maximum biomass in the Goose Creek and tundra ponds. Increases in netplankton were represented by mainly Chlorophyceae, in particular Spirogyra spp. in the rock bluff ponds.

F. Similarities in Phytoplankton Composition

Similarities of the structure of the pond communities
are represented in Figures 1.19 and 1.20. The Jaccard index was applied to the presence-absence data of the species for the twenty pond communities during all summer data collected during 1980 and 1981. Similarity ranged from 87.4 to 11.14% with most of the ponds clustering above 50%. There were no distinct clusters between groups although ponds found in the tundra and experimental pond area were most similar. The ponds influenced by salinity were more dissimilar, being the last to cluster in 1980 and 1981. Those ponds had very weak similarity indices between each other.

The percent similarity index was applied to the ponds to compare relative abundance of the species. In 1980 fifteen of the twenty ponds were greater than 50% similar with initial clustering occurring between some of the Goose Creek and rock bluff ponds. Ponds from the experimental area were all above 50% similar but were similar individually rather than in groups. In 1981 most of the ponds along Goose Creek clustered separately from a cluster of tundra ponds. The last ponds to be added were the ponds from the experimental pond area. Similarity between most of the ponds and/or clusters were below 50% during 1981.

All ponds had more species of Cryptophyceae present during 1980 with Rhodomonas minuta and Cryptomonas erosa common. The ponds in the rock bluff area had Brachiononas Westiana, a euryhaline species, common only during 1981. The ponds located along Goose Creek road had a euryhaline species, Amphiprora alata, common during both years and
Figure 1.19: Skyline plot for Jaccard's similarity index between twenty phytoplankton communities from Churchill, Manitoba during (a) 1980 and (b) 1981. This summarizes the results of clustering by showing the clusters, and the value of similarity at which they were formed. The ponds below the horizontal lines correspond to the members of the clusters.
Figure 1.20: Skyline plot for percent similarity index between twenty phytoplankton communities from Churchill, Manitoba during (a) 1980 and (b) 1981. This summarizes the results of clustering by showing the clusters, and the value of similarity at which they were formed. The ponds below the horizontal lines correspond to the members of the clusters.
contributing to the peaks in biomass. Of all four groups the ponds located on the tundra had the most number of common species.
DISCUSSION

Meteorological differences between 1980 and 1981 affected the development of phytoplankton biomass within the ponds. The temperature during the spring is an often cited factor in the timing of phytoplankton peaks in biomass (Reynolds 1984). The temperature in the spring of 1980 was warmer and the maximum occurred earlier than in 1981. Correspondingly, the ponds in the experimental pond area, rock bluffs and along Goose Creek Road experienced peak biomass earlier in 1980 than in 1981.

Meteorological differences between the two years also contributed to differences in chemical composition. In 1981 evaporation rates exceeded precipitation rates for the months of May, June and August. Evaporation of the pond waters would result in an increase in some of the measured chemical concentrations. As it was, total dissolved phosphorus, soluble reactive phosphorus and calcium concentrations were higher in 1981. The salinity and specific conductance values of the ponds along Goose Creek road and the rock bluffs were also higher in 1981.

Resource gradients determined the sequence of size dominance throughout the summer. Although the ponds had a high proportion of small sized phytoplankton over both years, large sized phytoplankton, especially large filamentous greens and colonial blue-greens, occurred only during the late summer. In ponds 203 and 205 large sized
plankton were abundant infrequently throughout the summer. Regulating factors of phytoplankton size could be available nutrients, light, temperature, or turbulence. These density independent factors would promote r-selected species, the fast growing smaller-sized species. Density dependent factors, on the other hand, would support the K-selected species which are able to withstand periods of deficient nutrients, during which they could physiologically adapt by lowering their half saturation constant. In ponds 203 and 205, water chemistry data indicate high nutrient concentrations which would explain the presence of larger-sized plankton. It would seem then that generally most of the algal composition of the ponds is regulated by non-density dependent factors. In the case of nutrient rich ponds, density dependent factors become more important in the regulation of the abundance of phytoplankton populations.

Salinity possibly produced some differences in species composition. The most obvious were those of *Brachionomas Westiana*, found only in the rock bluff ponds, and *Amphiprora alata*, found only in the Goose Creek ponds. These two pond types were also the most dissimilar from the other ponds in the types of species present. Good (1981) also found zooplankton composition differences as a result of high conductivities which are associated with increased salinity. *Daphnia magna* was found to occur in rock bluff ponds and in some Goose Creek ponds (ponds 103 and 105) with high
conductivities.

Low nitrogen to phosphorus ratios have often been cited to determine the presence of bluegreens. In 1981 filaments of greens and non-nitrogen fixing colonies of bluegreens occurred late in August of 1981. At this time the nitrate-nitrogen to total dissolved phosphorus ratio increased to greater than 60:1 over the season as the soluble reactive phosphorus and total dissolved phosphorus concentrations declined. An increasing total nitrate to total phosphorus ratio is characterized first by diatoms and bluegreens and then at high N:P ratios (>25) by green algae (Reynolds 1978; Rhee and Gotham 1980). Therefore the high N:P ratios of the ponds supported the presence of the green algae but also prevented the growth of blue-green algal blooms.

Calcium precipitation may have reduced the phosphorus levels within the tundra ponds. With an increase in water temperature early in the mornings came an increase in visible calcium precipitation and a difficulty in filtering water samples for chemical analysis. This occurred only in the tundra and experimental pond area ponds. Precipitation of calcium carbonate may be induced by increasing temperatures, bacterial metabolism or photosynthetic utilization of carbon dioxide (Wetzel 1975). The formation of calcium carbonate in waters of high phosphorus concentrations leads to coprecipitation of phosphate with the carbonate (Otsuki and Wetzel 1972). Coprecipitation
would then tend to occur diurnally varying directly with water temperatures. When daily water temperatures were high, phosphorus may not be available for phytoplankton uptake and growth. As calcium concentration increased over the season because of evaporation, less and less phosphorus would then be available to the phytoplankton.

The groups of ponds had different proportions of the major classes of phytoplankton. The rock bluff ponds generally had Chlorophyceae and Bacillariophyceae as major contributors to the total biomass, while the ponds along Goose Creek road were generally dominated by Bacillariophyceae. The ponds found on the tundra and within the experimental pond area had major contributions by Bacillariophyceae, Chlorophyceae and Cyanophyceae with no general seasonal trend observed for any of the ponds. This lack of a seasonal trend would also suggest that allogetic processes were regulating phytoplankton abundance and composition.

Lund (1962) found the more oligotrophic lakes were dominated by diatoms and more eutrophic lakes by a mixture of diatoms and Cyanophyceae. According to the findings of a survey by Prescott (1963) there were more Chrysophyta in the more northern lakes. Hilliard (1959) found Bacillariophyceae to be a major contributor in subarctic lakes while Sheath and Munawar (1974) and Sheath et al. (1975) found Bacillariophyceae, Chlorophyceae and Cyanophyceae to be the major species groups. Unicellular flagellates comprised of
species from Chlorophyceae, Chrysophyceae and Cryptophyceae were most numerous in arctic and subarctic lakes studied by Kalff (1965), Rigler (1970), and Stanley (1976). Alexander and Barsdate (1971) found flagellates dominated the winter, while species of Chlorophyceae and Cyanophyceae were the major species groups during the summer. Therefore within the arctic there is great seasonal variation of major algal taxonomic groups.

The Cryptophyceae were major contributors to the algal communities of all the ponds during 1980 but only present in low volumes in 1981. Maeda and Ichimura (1973) found that flagellates such as cryptomonads have a lower temperature optimum and Rhodomonas spp. have been considered characteristic of oligotrophic conditions (Findenegg 1965). Again the lower temperatures and nutrient concentrations of the summer of 1980 were responsible for differences in phytoplankton between 1980 and 1981.

All the ponds had greater proportions of nanoplankton than netplankton. Nanoplankton (<64 um) have dominated arctic and subarctic ponds during the ice-free conditions in Alaska (Kalff 1967ab, 1972), Russia (Winberg et al. 1973) and Canada (Rigler 1970; Sheath and Munawar 1974; Sheath et al. 1975). Netplankton increased in percent total volume for the ponds in Churchill during peaks in biomass. The increases in biomass were generally composed of the filamentous Chlorophyceae species Spirogyra spp.. Netplankton was also more prevalent late in the summer of
1981. Sheath et al. (1975) found netplankton important contributors to the peaks in biomass during mid-June and the end of August for shallow arctic lakes. The higher phosphorus concentrations of 1981 could also have enhanced the dominance of netplankton during peaks in algal biomass (Kalff 1972; Sheath et al. 1975).

In an attempt to classify the ponds into trophic levels, the compound index of classification of Thunmark (1945) and Nygaard (1949) was applied to the ponds. All the ponds in both 1980 and 1981 resulted in a value of >3.0 which would indicate that the ponds were eutrophic. While the chemical composition of the ponds did not indicate any nutrient limitation to the phytoplankton the ponds lacked dominance by eutrophic indicator species such as Anabaena, Aphanizomenon, Melosira, Fragilaria and Asterionella (Rawson 1956). A major problem in applying the compound index to the Churchill ponds was the emphasis made on the presence of desmids in oligotrophic waters. In the ponds in the Churchill area very few species of desmids were present probably because of the high calcium and alkalinity concentrations in the ponds. Desmids prefer low pH habitats. (Flensburg and Sparling 1973; Reynolds 1984). Waters high in calcium concentration do support high diatom population (Talling and Talling 1965). The diatom index does not use desmid species but rather the ratio of the number of centric diatoms to the number of pennate diatoms. A value less than 0.2 was calculated for all the ponds. Based on this value
the ponds would then be classified as oligotrophic. The sampling of the ponds was not extensive enough to determine a mean annual phytoplankton biomass value although for the ponds the average summer biomass appeared to be less than 1 g.m\(^{-3}\). This biomass would place the ponds in the oligotrophic classification based on biomass (Munawar 1981).

The potential development of eutrophic conditions in Churchill, Manitoba is possible but may not occur because phosphorus availability might be dominated by calcite formation. During a dry summer season the ponds had fairly high levels of total phosphorus and nitrate nitrogen. These levels were within the range quoted by Lund (1969) for eutrophic lakes. But calcium concentrations were also high. The range quoted by Lund (1969) would therefore overestimate the potential for increased phytoplankton growth. Thus by increasing the nutrient levels in the ponds to levels whereby the calcite would be saturated with phosphorus phytoplankton composition could stimulate a change. Although biomass between years was not comparable because of insufficient data, netplankton was seemingly more prominent in 1981, especially in the Goose Creek and rock bluff ponds. Nutrients were also higher in concentration in 1981. An increase in the proportion of netplankton has also shown to reflect increasing trophic status (Watson and Kalff 1980). The morphology of the ponds also provides favorable conditions for maintenance of high levels of nutrients. The shallow ponds (maximum depths <2 m) permits constant mixing
of the water column by wind providing a continuous replenishment of nutrients by disturbing the loose flocculated sediments whereby phosphorus may be released into the water column.

There is a high degree of variation in species composition and cell numbers between arctic lakes and ponds (Prescott 1953; Kalff 1965; Dickman 1971; Stanley 1976). Sheath and Munawar (1974) found large numbers of species very ephemeral with many species present for only short periods of time during the ice-free growing season. While the collection of samples from the ponds of this study were not frequent enough to provide a detailed seasonal succession of community structure, the data obtained suggested there was no spatial pattern with respect to pond type or no seasonal trends indicative of resource competition.

In conclusion, the Churchill area experiences a variable environment in temperature, net radiation, and precipitation. All these resources are non-density dependent factors. The phytoplankton populations of all the ponds are very similar in composition and have little dominance by any one species or class for any extended period of time. Any differences in chemical composition between ponds did not seem to affect the phytoplankton population but rather by the presence of only two euryhaline species in ponds with salinities. The rock bluff and Goose Creek ponds had higher levels of salinity, conductivity and nitrogen and
phosphorus. Seasonal biomass of the rock bluff and goose creek ponds were not higher than the other ponds possibly because of the effect of zooplankton grazing. A slight increase in seasonal average biomass for rock bluff ponds in 1981 may be a result of increased nutrients. Higher proportions of netplankton may be a result of available phosphorus which may vary diurnally. Therefore it seems that non-density dependent factors regulate the phytoplankton composition and abundance in the ponds of the Churchill area.
CHAPTER TWO

MICROSCALE SPATIAL AND TEMPORAL HETEROGENEITY IN
PHYTOPLANKTON OF TUNDRA PONDS
INTRODUCTION

Phytoplankton populations were similar in composition and structure among arctic ponds in Churchill, Manitoba. While phytoplankton composition and biomass occur on macroscales, maintenance and productivity of the phytoplankton populations occur on smaller scales (Harris 1980). It is hypothesized that on these microscales there are spatial and temporal heterogeneities of phytoplankton distribution within a pond.

Accurate determinations of phytoplankton biomass are critical but difficult when sampling bodies of freshwater regardless of their size. Sampling phytoplankton involves a collection of water from a known location horizontally and vertically. Phytoplankton do not inhabit homogeneous environments. Changes in light, temperature and nutrients are but a few temporal variances that affect phytoplankton distribution. Differences in phytoplankton physiology among species, together with a system's physical and chemical characteristics, produce spatial and temporal variances. Together the temporal and spatial differences produce variability in phytoplankton distribution ranging from minutes and centimeters (short-term) to months and kilometers (long-term) (Reynolds 1984).

To explain the nature of phytoplankton patchiness Richerson et al. (1970) developed the concept of "contemporaneous disequilibrium". The concept shows a mosaic
of phytoplankton microhabitats within each of which the species composition and growth rate are unique. The patches are maintained until a physical or biological perturbation of the system occurs (Reynolds 1984). Any perturbation which fluctuates in time could lead to spatial variability within phytoplankton populations. Temporal variations on the environment include day-length (Eppley et al. 1968), total irradiance and attenuation (Talling 1966, 1971), temperature, thermal structure (Lund et al. 1963; Reynolds 1973; Reynolds and Wiseman 1982), and nutrient availability (Eppley et al. 1971; Harrison et al. 1977). George and Edwards (1976) and Therriault et al. (1978) found wind speed inversely related to horizontal patchiness of phytoplankton. Wind had a profound effect on phytoplankton distributions especially when the winds were greater than 5 m.sec\(^{-1}\). Grazing on phytoplankton by zooplankton has only been implied as a cause of horizontal variability of phytoplankton abundance (Mackas 1977; Therriault and Platt 1978).

The ponds in Churchill are characterized by shallow waters, relatively flat bottoms and are usually void of a distinct littoral zone. Chemical and physical parameters support the belief that the ponds are well mixed systems. Good (1981) and Hebert et al. (1980) found *Heterocope septentrionalis* and *Daphnia middendorffiana* to aggregate in patches in the Churchill ponds. Would phytoplankton also tend to be patchy? And what controls phytoplankton
patchiness? In Chapter One phytoplankton abundance changed in biomass and composition monthly and yearly. If these ponds are not then well-mixed does the sampling method used overcome patchiness to provide us with a good estimate of phytoplankton biomass and composition in a pond. The microscale variability must be first understood in order to be confident in extrapolating results to the macroscale (month, year).

Whereas Chapter One dealt with long-term or macroscale changes in phytoplankton in Churchill, this chapter will concentrate on shorter term changes in space and time. It is hypothesized that there are microscale (centimeters) and mesoscale (meters) differences in the spatial distribution of phytoplankton within the ponds.
MATERIALS AND METHODS

A. Spatial Scales

Two tests of spatial differences in phytoplankton within a pond were undertaken. The first dealt with microscale spatial differences across the pond and the effect of zooplankton on phytoplankton abundance.

Two ponds situated along the rock bluffs were selected for their small size and for the fact that one pond had zooplankton present and the other pond had reduced zooplankton grazing pressures. The pond with zooplankton present had *Daphnia pulex*, and *Diaptomus* spp. with numbers of 48.6 and 11.0 animals per 10L, respectively. The pond with reduced zooplankton pressures had *Daphnia pulex* and *Diaptomus* spp. with numbers of 24.6 and 11.2 animals per 10L, respectively.

Petri dishes (10 cm) were taped side by side, without spaces between the dishes, along a 2" by 4" board in such a manner that the lined up dishes ran from one end of the pond to the other. The board rested on the banks of opposite sides of the pond. To sample the phytoplankton population the board was rotated dipping the petri dishes into the top (0-3 cm) of the pond. The board was righted and the water samples were individually removed from the petri dishes. Preservation and enumeration were carried out as in Chapter One.

The second test dealt with analysis of the mesoscale
spatial heterogeneity of phytoplankton populations and an
evaluation of the sampling method used throughout the study
to calculate for phytoplankton biomass within subarctic
ponds. To test for spatial differences in phytoplankton
within a single pond, phytoplankton samples were collected
separately from four stations evenly spaced around the
perimeter of the pond and from one station in the centre of
the pond. At the same time a bulk sample was collected
consisting of equal quantities of samples from each of the
five locations. From the bulk sample a mixed subsample was
then removed.

B. Temporal Scales

To test for temporal differences in phytoplankton a
phytoplankton sample was removed from one location with a
vertical hose sampler at time intervals of one minute for a
maximum period of thirty minutes. Preservation and
enumeration of the phytoplankton samples were carried out as
previously described in Chapter One.

Species diversity was calculated using the Simpson
diversity index D. The Simpson diversity index is considered
to be suitable for aquatic ecosystems as it is independent
of the frequency distribution of abundances and may be only
mildly independent of sample size (Washington 1984). Simpso's D is an unbiased estimation of the probability
that two individuals chosen at random and independently from
a population will be found to belong to the same group.
Simpson's $D = \sum_{i=1}^{S} \frac{n_i (n_i - 1)}{n(n-1)}$

where $S$ is the number of species in a sample, $n_i$ is the number of individuals in a species $i$ of a sample from a population and $n$ is the number of individuals in a sample from a population.

The percentage similarity index was used as an index of similarity of the structure of two communities. The percentage similarity index is presented in Appendix I.

Comparison between species, total phytoplankton volume and numbers and community structure were correlated using the Pearson Product Moment correlation coefficient. The coefficient indicates the degree of relationship between paired data sets as described by Sokal and Rohlf (1969) where:

$$r_{1,2} = \frac{\sum y_1 y_2}{\sqrt{\sum y_1^2 \sum y_2^2}}$$

$y_1$ and $y_2$ are the variables whose correlation is to be estimated.
RESULTS

A. Spatial Scales

Phytoplankton abundance in the rock bluff ponds was patchy with zooplankton or with reduced grazing pressures (Fig. 2.1). The microscale distribution of phytoplankton was different between the two ponds (Fig. 2.2) (t-test = 2.2462, n=20, p<0.05). Patches of no algal species were evident in both ponds suggesting that the species distributions between the ponds were also different on the mesoscale as well.

The presence of zooplankton reduced the frequency of high abundances of phytoplankton. The distributions of phytoplankton abundances for each pond were both normally distributed based upon a modified Kolmogorov-Smirnov test (Sokal and Rohlf 1969).

On the mesoscale, the combined subsample for the five stations had a total phytoplankton volume and phytoplankton abundance between the largest sample (D) and the smallest phytoplankton sample (B) from the five stations (Fig. 2.3). Counting precision was within 10% error.

Total phytoplankton volumes of the five samples ranged from 267.5 to 572.1 $\text{um}^3 \cdot 10^3 \text{. mL}^{-1}$. The mixed subsample had a total phytoplankton volume of 454.4 $\text{um}^3 \cdot 10^3 \text{. mL}^{-1}$ (Table 2.1). The mean volume of the five samples was $402.8 + 128.0 \text{um}^3 \cdot 10^3 \text{. mL}^{-1}$. The total counts ranged from 328 to 1084 cells $\text{mL}^{-1}$ for the five samples with a mean value of 650.6 + 284.6 cells $\text{mL}^{-1}$. The mixed sample had total counts of 632 cells.
Figure 2.1: Phytoplankton abundance across the width of rock bluff ponds: one with zooplankton (top) and one with reduced zooplankton grazing pressures (bottom). Samples were taken from continuous 10 cm intervals across the ponds.
Figure 2.2: Histogram of phytoplankton abundance for ponds with zooplankton (top) and with reduced zooplankton grazing pressures (bottom).
Figure 2.3: Total phytoplankton volume (top) and counts (bottom) for samples from five locations within the pond (A-E) and for a sample combining subsamples from all five locations (MIXED).
Table 2.1: Total phytoplankton volume for samples from five stations within a tundra pond (A-E) and for a mixed sample combining samples from all five stations (MIXED).

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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>x</th>
<th>std.</th>
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**Simpson Diversity Index**

| Total Count | 624 | 728 | 492 | 1084 | 328 | 650.6 | 254.53 | 632 |

**Total Volume**

| 493.7 | 267.5 | 376.5 | 0.572.4 | 304.9 | 402.8 | 414.2 | 454.4 | 454.4 |

**Cell Volume**

| 1.0 | 10.3 | 1 |
mL⁻¹.

The major contributors to the phytoplankton composition of the various locations and the mixed subsample were Chlorophyceae and either Bacillariophyceae or Cryptophyceae. Although the total phytoplankton volume of the mixed subsample agreed well with the mean volume of the five samples only the volumes of Chlorophyceae and Cryptophyceae were close to the respective mean volumes from the five samples. Total volumes of Bacillariophyceae and Cyanophyceae from the mixed subsample were greater than any of the five separate samples, while the volume of Chrysophyceae was lower in the mixed sample than the mean volume of the separate samples (Table 2.1).

The total number of species increased by compositing of the samples from the five locations although the diversity of the community decreased (Table 2.1). Random distribution of the more rare species produced the appearance of some species only in the mixed sample such as, Merismopedia major, Spirogyra spp. and Synedra acus. Species present in significant numbers in two or more of the samples resulted in presence of the species in the mixed sample (Table 2.2). Species present in all samples were represented in the mixed sample, such as Cryptomonas erae var. reflexa and Oocystis crassa. Gymnodinium helveticum was present in significant volume because of its size but not in sufficient numbers to become present in the mixed sample.
Table 2.2: Comparison of phytoplankton volume, counts among samples from five locations within the pond (A-E) and a combined sample from the five locations (MIXED).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>MIXED</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rhodomonas minuta</em></td>
<td>+</td>
<td>**</td>
<td>#</td>
<td>**</td>
<td>-</td>
<td>#</td>
</tr>
<tr>
<td>Cryptomonas erosa var. reflexa</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Oscillatoria sp.</td>
<td>+</td>
<td>#</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anabaena sp.</td>
<td>#</td>
<td>+</td>
<td>+</td>
<td>#</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Merismopedia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>major</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
<tr>
<td>Fragilaria virescens</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Achanthes affinis</td>
<td></td>
<td>+</td>
<td>#</td>
<td>-</td>
<td>#</td>
<td>#</td>
</tr>
<tr>
<td>Synedra acus</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
<tr>
<td>Synedra ulna</td>
<td>-</td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
<tr>
<td>Nitzschia sp.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
<td>-</td>
</tr>
<tr>
<td>Ankistrodesmus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>falcatus</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Oocystis borgei</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Oocystis crassa</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Characiopsis sp.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Spirogyra sp.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
<tr>
<td>Taxon</td>
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<td>-</td>
<td>-</td>
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<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Tribonema sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnodinium</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>helveticum</td>
<td>+</td>
<td>*</td>
<td>-</td>
<td>+</td>
<td>*</td>
<td>-</td>
</tr>
</tbody>
</table>

* = >5% total volume  
# = >5% total counts  
+ = rare  
- = absent
B. Temporal Scales

When one location was sampled repeatedly at one minute intervals for thirty minutes changes in volume were correlated to changes in species belonging to primarily Cyanophyceae and Chlorophyceae (Fig. 2.4, Table 2.3). Total algal volume ranged from 155.99 to 1363.4 $10^3$ um$^3$.mL$^{-1}$ over the thirty minutes.

The major algal group contributing to the samples was the Chlorophyceae which contributed from 34 to 98% of the total volume (Fig. 2.4). The Cyanophyceae were the next important class contributing from 0.1 to 36.8% of the total phytoplankton volume. Species contributing more than 5% of the total volume included species such as Merismopedia major, Ankistrodesmus falcatus, A. spiralis, Oocystis crassa, O. borgei and Eudorina elegans.

Two peaks in Bacillariophyceae resulting in percent total volumes of 51 and 37 percent total volume were caused by collecting a colony of Fragilaria intermedia and the large Pinnularia sp. (Fig. 2.4).

Similar to changes in total volume, a plot of number of cells over time produced a peak after nineteen samples had been removed (Fig. 2.5). While volume fluctuated repeatedly after thirteen samples the cell count had only one major peak thus the influence of large rare species. The counts ranged from 131 to 1148 cells mL$^{-1}$. Both total volume and total counts had major peaks at the nineteen minute sample. Some representative species which contributed significantly
Figure 2.4: Total phytoplankton volume and composition for each sampling minute (1-30).
Table 2.3: Pearson product-moment correlation coefficient between total volume, total counts, and various species total volumes for the time series. Level of significance: underscore = significant at 5%, double underscore = significant at 1%.

<table>
<thead>
<tr>
<th>#</th>
<th>VOL</th>
<th>RHO</th>
<th>ANA</th>
<th>MER</th>
<th>AN1</th>
<th>AN2</th>
<th>OOB</th>
<th>OCC</th>
<th>EUD</th>
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</thead>
<tbody>
<tr>
<td>VOL</td>
<td><strong>770</strong></td>
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<td></td>
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<tr>
<td>RHO</td>
<td><strong>644</strong></td>
<td><strong>593</strong></td>
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<td>ANA</td>
<td><strong>873</strong></td>
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<tr>
<td>MER</td>
<td><strong>646</strong></td>
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<td><strong>191</strong></td>
<td><strong>408</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>AN1</td>
<td><strong>459</strong></td>
<td><strong>551</strong></td>
<td><strong>143</strong></td>
<td><strong>131</strong></td>
<td><strong>732</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>AN2</td>
<td><strong>756</strong></td>
<td><strong>475</strong></td>
<td><strong>415</strong></td>
<td><strong>477</strong></td>
<td><strong>595</strong></td>
<td><strong>346</strong></td>
<td><strong>260</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OOB</td>
<td><strong>770</strong></td>
<td><strong>554</strong></td>
<td><strong>366</strong></td>
<td><strong>546</strong></td>
<td><strong>750</strong></td>
<td><strong>709</strong></td>
<td><strong>564</strong></td>
<td></td>
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<tr>
<td>OCC</td>
<td><strong>323</strong></td>
<td><strong>539</strong></td>
<td><strong>268</strong></td>
<td><strong>214</strong></td>
<td><strong>042</strong></td>
<td><strong>333</strong></td>
<td><strong>099</strong></td>
<td><strong>085</strong></td>
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</tr>
<tr>
<td>EUD</td>
<td><strong>136</strong></td>
<td><strong>389</strong></td>
<td><strong>541</strong></td>
<td><strong>049</strong></td>
<td><strong>002</strong></td>
<td><strong>093</strong></td>
<td><strong>017</strong></td>
<td><strong>011</strong></td>
<td><strong>156</strong></td>
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<tr>
<td>FRG</td>
<td><strong>111</strong></td>
<td><strong>427</strong></td>
<td><strong>118</strong></td>
<td><strong>074</strong></td>
<td><strong>138</strong></td>
<td><strong>049</strong></td>
<td><strong>131</strong></td>
<td><strong>109</strong></td>
<td><strong>064</strong></td>
</tr>
</tbody>
</table>

96
(♯= cells mL⁻¹; VOL= phytoplankton volume; RHO= Rhodomonas minuta; ANA= Anabaena flos-aquae var. intermedia Wor. fa. spiroides; MER= Merismopedia major; AN₁= Ankistrodesmus falcatus; AN₂= Ankistrodesmus spiralis; OOB= Oocystis borgei; OOC= Oocystis crassa; EUD= Eudorina elegans; FRG= Fragilaria intermedia)
Table 2.4: Percentage similarity coefficients comparing phytoplankton abundance and volume from samples from five stations (A-E) and a combined sample of the five stations (MIXED).

### PHYTOPLANKTON COUNTS

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>MIXED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100</td>
<td>37.30</td>
<td>43.72</td>
<td>60.05</td>
<td>16.80</td>
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<tr>
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<td>100</td>
<td>43.70</td>
<td>65.70</td>
<td>3.60</td>
<td>36.20</td>
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<td>3</td>
<td>100</td>
<td>44.39</td>
<td>16.90</td>
<td>61.70</td>
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<tr>
<td>4</td>
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<td>100</td>
<td>10.70</td>
<td>37.60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
<td>100</td>
<td>66.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MIXED</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

### PHYTOPLANKTON VOLUME

<table>
<thead>
<tr>
<th></th>
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<th>3</th>
<th>4</th>
<th>5</th>
<th>MIXED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100</td>
<td>38.5</td>
<td>48.67</td>
<td>72.59</td>
<td>59.97</td>
<td>46.29</td>
</tr>
<tr>
<td>2</td>
<td>100</td>
<td>36.79</td>
<td>46.14</td>
<td>43.17</td>
<td>39.45</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>100</td>
<td>56.04</td>
<td>51.32</td>
<td>57.50</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>100</td>
<td>57.46</td>
<td>49.92</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>100</td>
<td></td>
<td>52.25</td>
<td></td>
<td></td>
<td></td>
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<td>MIXED</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>100</td>
</tr>
</tbody>
</table>
Figure 2.5: Total phytoplankton counts and total counts of *Oocystis crassa* (OOC), *Merismopedia major* (MER), *Rhodomonas minuta* (RE0), and *Ankistrodesmus falcatus* (ANK) over the sampling period of 1-30 minutes.
to the total numbers of cells are plotted against time in Fig. 2.5. A peak in *Merismopedia major* and *Ankistrodesmus falcatus* corresponds to a minor peak in total number at the fourteen minute sample while a peak in *Rhodomonas minuta* and *Merismopedia major* contributed to the nineteen minute sampling.

Similarity between one sample and the next consecutive sample was tested using the percent similarity index. Applying percent counts of each species to the similarity index resulted in an eventual decline in similarity coefficient over the thirty minutes (Fig. 2.6). Using percent volume of each species the similarity coefficient dropped below 50% approximately every five minutes (Fig. 2.6). After twenty minutes most samples fell below a similarity coefficient of 50%. At the fourteen minute sample both total volume and cell counts were at a peak and very dissimilar to samples removed one minute later. From the 13 to 15 minute samples there was an obvious break in pattern of species. There was a reduction of species number with an increase in abundance of those species present which were significant in either volume or number throughout the sampling period. During the major peak in total volume and total counts the similarity coefficients remained above 50%.

Variations in the number of species and/or species abundance were tested against volume, and counts between all pairs (Table 2.3). All species represented in Table 2.3, except *Eudorina elegans*, contributed >5% to the total
Figure 2.6: Percentage similarity coefficients of the total phytoplankton population between each sampling minute (1-30) based on (a) total counts and (b) total volume.
phytoplankton counts. *Eudorina elegans* significantly contributed to the total biomass of at least one sample out of the thirty samples. The species were all significantly correlated to the changes in volume at the 5% significance level (Table 2.3). The species, excluding *Eudorina elegans* and *Fragilaria intermedia*, were also significantly correlated to variations in total phytoplankton counts. Most species varied in number with more than one other species.
DISCUSSION

The temporal variability was larger than the spatial variability of phytoplankton abundance for the Churchill pond. The ratio between variance and mean is often used as a patchiness index (Sandusky and Horne 1978). The patchiness index was then applied to the phytoplankton volume of the five locations and then compared with the patchiness index value of the samples removed every minute for thirty minutes. One of the stations used in the mixed sample was also used in the time sequence. Immediately following the collection of the five stations the collection of samples over thirty minutes was performed. The patchiness index for the mixed sample was 33.3 while the index values for samples taken after 4, 14, and 30 minutes were 11.5, 131.9 and 161.0, respectively. The time taken to collect the samples, which was under 5 minutes, was not as critical as was the collection of more than one sample. The assumption that the spatial distributions remain relatively fixed during the time taken to sample them all, providing the sampling is completed in 5 minutes or less, (Platt and Denman 1980) is a valid assumption in the case of sampling phytoplankton biomass in Churchill ponds. But it is obvious that the phytoplankton populations are constantly changing with time. Rapid changes in distribution according to Harris (1980) is a reflection of rapid environmental fluctuations.

The patchiness index for the ponds with zooplankton and
with reduced grazing pressures was 33.2 and 36.2, respectively. These index values agree well with the value from the mixed sample. Sampling a number of stations in one pond, in this case five, was sufficient to represent the variable phytoplankton number or biomass within the pond. Little difference between the ponds in patchiness index also supports the suggestion of the influence of non-density dependent variables on the phytoplankton population in the arctic ponds.

Patchiness of phytoplankton is intermittent with no preferred or dominant length scale (Platt and Dénman 1980). To obtain a mixed sample stations separated by approximately 100 m were sampled with no previous inclination as to the spatial variability in phytoplankton. In density dependent situations patches of phytoplankton are maintained so long as the dynamics of the population change sustaining it exceed the rate at which the patch is diffusively eroded at its edges (Reynolds 1984). For patches on the order of meters (< 1 km), behavioral response to flow patterns (advective, convective) outweigh the effect of biological processes (Harris 1980, Reynolds 1984). Any patch of algae less than 100 meters will be destroyed rapidly by horizontal diffusion (Okubo 1978). The separate stations were not similar in total abundance or total volume (Table 2.4). McAlice (1970) found significant differences in population density between samples if spacing between collections were greater than 10 cm. He found plankton to be non-random over
a range of $10^{-2}$ to $10^5$ meters.

Wind stress plays an important role in the spatial variability of the phytoplankton. Wind speeds greater than 4 meters per second are able to break down density gradients at one meter. At those wind speeds, small scale (mm, sec) patchiness collapses (Reynolds 1984). Wind stress exerts a measurable mixing effect on the surface layer water (Therriault and Platt 1981). The domination of the physical processes over the biological and chemical processes results in the small scale clustering being frequently modified or suppressed (Therriault and Platt 1978; Therriault et al. 1978; Reynolds 1984). The wind speed in Churchill averaged more than 15 km hr$^{-1}$ during the summer months (Table 1.2), winds sufficient to reduce small scale horizontal clustering, and yet this was not observed. The relationships between wind speed and phytoplankton distribution were developed for large bodies of water. The ponds in Churchill on the other hand are small, with low-lying vegetation surrounding the pond. This would result in varying wind speeds and direction over the surface of the ponds with generally insufficient fetch for mixing. The species that significantly varied with the total volume of the samples collected over time included unicellular, colonial, flagellated and non-flagellated species (Table 2.3), indicating that processes other than growth rates of the species were responsible for the spatial heterogeneity in phytoplankton biomass and abundance. Clustering of cells
occurred between the various stations for the flagellated species, such as *Rhodomonas minuta* and *Gymnodinium helvetica*, the positively buoyant species, such as *Anabaena* sp. and *Oscillatoria* sp. and the negatively buoyant species, such as *Synedra ulna* and *Fragilaria intermedia* (Table 2.5). While the movement of motile species is too slow (0.1-1.0 mm/sec\textsuperscript{-1}) to overcome wind driven currents with greater velocities (Reynolds 1984), wind induced currents may affect the horizontal variability of the buoyancy control of species (Sandusky and Horne 1978; Reynolds 1984). For this pond in Churchill the stations were stable long enough to sample but because of potential and varying wind stress, multiple stations were required to sample to eliminate potential fluctuations in horizontal biomass variability (Table 2.1).

Variability in grazing pressure by zooplankton is often cited as an explanation to phytoplankton patchiness. Only circumstantial evidence exists though. Therriault and Platt (1978) found ammonia levels correlated with phaeopigments and with the variance in chlorophyll \textsubscript{a}. Zooplankton return ammonia to the water by excretion and defaecation (Wetzel 1975) and thus were assumed to be present when ammonia levels were high. No other nutrients correlated with chlorophyll \textsubscript{a}. Also, negative correlations between zooplankton and phytoplankton abundances have been found in the ocean (Mackas 1977). In the present study, the presence of zooplankton did not control phytoplankton patchiness.
Further research is obviously required to determine the effect of zooplankton on phytoplankton distributions and possibly more importantly vice-versa. In density dependent situations, zooplankton may control the phytoplankton distribution and abundance (Reynolds 1984), but when non-density dependent factors are regulating the phytoplankton distribution and abundance the phytoplankton populations may then regulate the zooplankton populations. One suggestion may be to study phytoplankton distributions and composition within and outside visible patches of phytoplankton.

Zooplankton were found to reduce the abundance of phytoplankton. In the Churchill rock bluff ponds Good (1981) found calanoid copepods; Diaptomus victoriaensis, D. tyrrelli and D. arcticus, and cladocerans; Daphnia middendorffiana, D. pulex and D. magna. The calanoid copepods and many cladocerans including Daphnia are filter feeders. Food is selected by the width of the opening between the carapace valves (upper limit) and the areal density of the setae (lower limit) (Gliwicz 1980). The critical factor in food size has been found to be particle width (Nadin-Hurley and Duncan 1976). This suggests that the filter feeders feed on a wide range of phytoplankton sizes. While zooplankton grazing may be selective on algal species, the phytoplankton abundance was not reduced to very low levels since the phytoplankton abundance is critical to zooplankton maintenance and growth in population (Reynolds
1984).

The general relationship between patch size and diffusion rate is such that one kilometer is equivalent to a time scale ranging from one day (Harris 1980) to a maximum of approximately ten days (Platt and Denman 1980). For patches less than 100 m the time scale becomes equivalent to the time scale on the order of minutes to less than one day maximum. Small scales on the order of meters and hours are affected primarily by advective and convective flow patterns since biological processes only begin to outweigh the horizontal diffusion rates at larger scales of kilometers and days (Harris 1980). Over time and space the variation in proportion of classes was greatest with the smallest classes (Table 2.2, Fig. 2.4) while the proportion of classes that were significant to the total volume (>25% total volume) were not affected. Sandusky and Horne (1978) found that the patchiness of a particular species is less during the period when its biomass is greatest. Temporal and spatial variability resulted though in fluctuations in the presence or absence of particular species (Table 2.2). As any individual species is unlikely to adopt a permanent position in a particular parcel of water discontinuities are inevitable on small scales (Reynolds 1984). While no general conclusions about the size of patches within the pond could be reached the five stations located within the pond were sufficiently unique to warrant mixing of the samples and then removing a subsample to provide a mean volume and
composition of the phytoplankton community of the pond for that particular sampling day.

The sampling procedure should be able to smooth out the variability caused by the physical and chemical environment, in order to confidently represent the biological processes. Knowledge of physical and chemical perturbations to a system will then determine the length and time scales of the sampling procedures.
Chapter Three

PHOSPHORUS DYNAMICS AND PRODUCTIVITY IN TUNDRA PONDS
INTRODUCTION

If arctic phytoplankton communities are regulated by non-density dependent factors as suggested in Chapter One then the response of a phytoplankton population to an addition of a nutrient would depend upon which scales were regulated or uncoupled by the non-density dependent factors. These time scales include the availability of the nutrient to the phytoplankton species, the uptake rates of the nutrient and the growth of the phytoplankton population. In hypothesizing that phosphorus regulates phytoplankton productivity in arctic ponds, one must determine where the added phosphorus is going and whether it is reaching the biotic compartment. Although phosphorus may be present, determined by chemical analyses, phosphorus may not be available for utilization by the phytoplankton. The molybdenum-blue method used here often fails to distinguish between dissolved and colloidal forms (Rigler 1968). Also, some phytoplankton species can utilize dissolved organic phosphorus through the production of alkaline phosphatases (Nalewajko and Lean 1980). Using radio-labelled phosphorus to follow the incorporation of phosphorus into algal cells attempts to estimate the availability of orthophosphorus to phytoplankton populations. Orthophosphate is rapidly taken up by phosphorus deficient phytoplankton and bacteria (Lean and White 1983). To test whether the phytoplankton in arctic ponds were phosphorus deficient, chemical phosphorus
additions were made in the field. The phytoplankton community was subsequently examined for changes in phytoplankton composition and abundance. Radiotracer phosphorus kinetics were used to estimate orthophosphate competition between biological and non-biological fractions in the field and laboratory.

Whole-lake fertilizations with phosphorus were studied initially for the enhancement of fish production (Nelson and Edmondson 1955; Parsons et al. 1972). Whole lake fertilizations in temperate lakes have been studied by Schindler et al. (1973), in subarctic regions by Kalff (1965, 1967ab), Schindler et al. (1974), Kalff et al. (1975), Stanley and Daley (1976) and Prentki et al. (1980), and in European subarctic regions by Jansson (1978) and Lundgren (1978). Phytoplankton responded to the fertilization by increasing their productivity and/or standing crops. Nutrient enrichments of the lakes and ponds concluded that the phytoplankton were often phosphorus limited and that phosphorus availability was the key to controlling eutrophication in these regions.

Phosphorus available to tundra ponds is controlled by extrinsic and intrinsic factors. Extrinsically phosphorus enters the ponds through rainfall and overland flow mainly occurring during spring melt. Intrinsically, phosphorus is controlled and cycled by vascular plants, bacteria, zooplankton and sediments (Prentki et al. 1980). Excessively long cold winters act in slowing mineralization of organic
phosphorus within the system.

In hypothesizing that the phytoplankton are phosphorus limited, an increase in phosphorus loading should increase the ponds capacity to support greater phytoplankton production and maintain larger standing crops of phytoplankton. A shift in species dominance towards more persistent froms, such as cyanophyta, may even occur.

To distinguish between whether availability or utilization was limiting the use of the nutrient resource, a test was made between adding a single dose of phosphate phosphorus and multiple additions of phosphate phosphorus. Should multiple additions maintain a high phytoplankton productivity level which would then result in higher phytoplankton biomass in comparison to a single equivalent dose, then it would suggest that resident communities were having problems in tracking and utilizing the resource as opposed to inadequate inputs of phosphorus.

Phosphorus present in freshwaters consists of phosphorus in suspension in particulate matter and phosphorus in dissolved form. Usually more than 90 percent of the phosphorus in lake water is in the form of particulate phosphorus (Wetzel 1975). Particulate phosphorus includes phosphorus in organisms, phosphorus adsorbed onto inorganic complexes and phosphorus adsorbed onto dead organic matter. The dissolved forms of phosphorus consist of orthophosphate, the most important form of phosphorus for phytoplankton nutrition, polyphosphates and phosphorus
adsorbed onto organic colloids (Wetzel 1975). Colloids are included in the dissolved fraction as they typically pass through 0.45 μm membrane filters although they are a high molecular weight phosphorus compound (Burnison and Leppard 1983).

Added phosphorus is incorporated very rapidly by phytoplankton and bacteria. The uptake of phosphorus varies with nutrient availability (Rigler 1964; Lean and White 1983) and species (Lean and Nalewajko 1976). Cycling between particulate phosphorus, low molecular weight phosphorus compounds, colloidal phosphorus and phosphate phosphorus is often very rapid (Lean 1973) in oligotrophic conditions. In this process, part of the colloidal phosphorus fraction becomes unavailable to further uptake by sedimentation. Sedimentation of the particulate phosphorus also represents another loss of phosphorus from the system. Phosphorus is added though to the system through inputs by influents, rain and air borne particles and from the littoral zone. Phosphorus is released as mainly organic phosphorus during lysis and decomposition. Bacteria further degrade dissolved organic phosphorus to dissolved inorganic phosphorus which is rapidly utilized by phytoplankton and bacteria.

To study the phosphorus phytoplankton interactions six tundra ponds were chosen for phosphate phosphorus additions. To three of the ponds a single addition of phosphorus was made. A response by the phytoplankton either by increased productivity or increased biomass would indicate that there
was a simple lack of resource, eg. phosphorus. To the other three ponds multiple additions of phosphorus were made. If there was only a response by the phytoplankton communities to the multiple additions and not to the single addition of phosphorus then some other resources or non-density dependent factors might be controlling the phytoplankton populations.
MATERIALS AND METHODS

A. Barriers

Six ponds were divided by a polyethylene plastic barrier in 1980. The plastic was suspended above the water surface by a wooden frame and formed a curtain down below the sediment-water interface. This provided a double thickness of plastic between the two sides of the ponds.

In the beginning of the summer season of 1981 the barriers were rechecked for damage to the structures and replacements of either the supports or the plastic barriers were made where necessary.

B. Phosphorus Additions

Phosphorus, in the form of \( \text{KH}_2\text{PO}_4 \), was added in solution to one side of the divided ponds. The second half of each of the ponds was used as a control. To the three ponds (56, 57, 58) which were to receive one pulse of phosphorus per season, a phosphorus addition of 2.0 gm. m\(^{-2}\) (weight/area) (Table 3.1) was added at the beginning of the summer seasons of 1980 and 1981. The phosphorus was initially dissolved in pond water and then discharged into the surface waters by means of draining the mixture off the side of a moving raft.

To another three ponds (162, 166, 167) phosphorus was added as ten weekly additions of 0.2 gm. m\(^{-2}\) each (Table 3.1) in 1980 and 1981. Phosphorus was initially dissolved
Table 3.1: Physical characteristics of ponds: fertilized side (P) and control side (C).

<table>
<thead>
<tr>
<th>POND</th>
<th>AVERAGE SURFACE AREA (m⁻²)</th>
<th>MAXIMUM POND DEPTH (m)</th>
<th>MAXIMUM KARST DEPTH (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>56-P</td>
<td>1004.71</td>
<td>0.744</td>
<td>0.192</td>
</tr>
<tr>
<td>-C</td>
<td>1356.63</td>
<td>0.735</td>
<td>0.192</td>
</tr>
<tr>
<td>57-P</td>
<td>4034.46</td>
<td>0.750</td>
<td>0.226</td>
</tr>
<tr>
<td>-C</td>
<td>3090.23</td>
<td>0.838</td>
<td>0.226</td>
</tr>
<tr>
<td>58-P</td>
<td>423.07</td>
<td>0.439</td>
<td>0.287</td>
</tr>
<tr>
<td>-C</td>
<td>2383.84</td>
<td>0.436</td>
<td>0.287</td>
</tr>
<tr>
<td>162-P</td>
<td>544.20</td>
<td>0.671</td>
<td>0.189</td>
</tr>
<tr>
<td>-C</td>
<td>598.09</td>
<td>0.719</td>
<td>0.189</td>
</tr>
<tr>
<td>166-P</td>
<td>1755.81</td>
<td>0.671</td>
<td>0.311</td>
</tr>
<tr>
<td>-C</td>
<td>2959.79</td>
<td>0.792</td>
<td>0.311</td>
</tr>
<tr>
<td>170-P</td>
<td>2524.97</td>
<td>0.640</td>
<td>0.192</td>
</tr>
<tr>
<td>-C</td>
<td>1214.27</td>
<td>0.509</td>
<td>0.192</td>
</tr>
</tbody>
</table>
in pond water and then added to the ponds. Surface additions from the sides of the ponds proved to save time and minimized sediment disturbances in comparison with additions through the use of a raft.

C. Chemical Analyses

Water samples for chemical analyses were obtained from five locations including the four corners and the center of each side of the barriers of each pond. Samples were collected in both 1.0 L glass bottles and 125 mL glass BOD bottles at approximately 10 cm below the surface of the pond water. All samples were placed in a covered box and transported to the laboratory for analyses. Water samples were obtained once a week for all six pond in 1980. In 1981, samples were collected once a month. In 1980 water samples for measurements of total dissolved phosphorus and soluble reactive phosphorus were collected one hour and two hours after the initial phosphorus additions and once a week thereafter. In 1981 samples for total dissolved phosphorus and soluble reactive phosphorus were obtained one to two days after the initial phosphorus additions and once a month thereafter.

Samples were analysed for total dissolved phosphorus, soluble reactive phosphorus, nitrate nitrogen, silicate silica (molybdate reactive silica), total alkalinity, calcium, magnesium and dissolved oxygen as described in Chapter One.
D. Phosphorus Dynamics

i. Total Uptake Kinetics: Field Studies

To determine how phosphorus was partitioned in the particulate phosphorus compartment and in the dissolved phosphorus compartment, phosphate phosphorus was added to a tundra pond located in the experimental pond area which was not included in the fertilization experiments.

In the field 3 plexiglass tubes (20.32 cm internal diameter, 1.5m length) were placed in a pond located in the experimental pond area which had no chemical phosphorus added. Two of the tubes were open to the sediments while the third tube had plastic covering the bottom so as to prevent the sediment-water interaction. The tubes were left untouched overnight to allow the sediments to settle and to allow physical and chemical conditions to stabilize. Original concentrations were: 0.05 mg.L\(^{-1}\) total dissolved phosphorus and 0.04 mg.L\(^{-1}\) soluble reactive phosphorus. Phosphorus, \(K_2(PO)_4\), was added to bring each tube to a concentration of 0.2 mg.L\(^{-1}\). Integrated water samples were removed using a hose pipe sampler for total dissolved phosphorus and soluble reactive phosphorus at 1, 3, 5, 10, 15 and 30 minutes and at subsequent one hour intervals for up to 5 hours after the phosphorus addition.

ii. a) Biological Uptake Kinetics: Field Studies

Radiophosphorus uptake by particulate material was
studied in situ. A plexiglass tube was placed into the sediments of the control sides and the fertilized sides of ponds 162 and 56 (2 tubes per pond) on July 23, 1981. Phosphorus had been added to the fertilized side of pond 162 two days prior to setting up the tubes. Phosphorus had been added to the fertilized side of pond 56 one month prior to setting up the tubes. The tubes in pond 56 held 45 cm of water and 3.5 cm of sediment. The tubes in pond 162 held 27 cm of water and 17.5 cm of sediment. The experiment started at 5.15 am when 0.5 Ci of carrier-free $^{33}$P-orthophosphoric acid was added to each of the tubes in pond 162. At 6.30 am 0.5 Ci of carrier-free $^{33}$P-orthophosphoric acid was added to each of the tubes in pond 56.

Water samples within the tubes were removed from the top 2 cm, middle and bottom-2 cm depths by slowly lowering a syringe attached to a meter stick into the respective tube. Total radiophosphorus was measured by removing 0.1 mL aliquots from each depth for every 15 minutes for the first hour and then every third hour up to 57 hours. The aliquots were immediately added to 20 mL Aquasol. Radiophosphorus uptake by particulate material was measured by removing 5 mL aliquots from each depth at 3 hour intervals up to 57 hours. The aliquots were immediately filtered through millipore filters (25 mm, 0.45 um), rinsed with dilute HCl to minimize calcium carbonate adsorption of phosphorus, and rinsed with distilled water and then placed in 20 mL Aquasol.
iii. b) Biological Uptake Kinetics: Laboratory Studies

To determine the effect of phosphorus additions on phosphorus uptake by biological particulate material, pond water was collected at 8 am from pond 162 from both the fertilized and control sides of the day before and the day after phosphate phosphorus was added to the fertilized side of pond 162. 150 mL subsamples were added to 250 mL Erlenmeyer flasks. The samples were constantly mixed by a magnetic stirring bar. The samples were maintained in a water bath at 10-12 C with natural sunlight providing illumination.

At time zero, 10 uCi of carrier-free \(^{33}\)P-orthophosphoric acid, HCl free, was added. Aliquots of 5.0 mL were removed within 5 seconds of the radiotracer addition and at intervals of 3, 6, 9, 12, 15 and 20 minutes and at subsequent ten minute intervals up to two hours. The aliquots were filtered at a vacuum of 25 mm Hg through 0.45 um HA Millipore filters (25 mm diameter). 5.0 mL of filtered distilled water was used to rinse the filters. The filters were then rinsed with dilute HCl to minimize calcium carbonate adsorption of phosphorus. Total \(^{33}\)P activity was measured by removing 1.0 mL unfiltered aliquots and adding the aliquot to Aquasol. The total and filtered aliquots were assayed in Aquasol (NEN) in a Beckman model LS 3150 P, liquid scintillation counter.

The rate constant, \(k\), for net phosphorus uptake was computed by plotting the \(^{33}\)P remaining in the filtrate over
time on a natural logarithm scale. The slope approximates the uptake rate constant (Lean and Nalewajko 1976).

E. Productivity and Heterotrophy

The primary production rates of the phytoplankton community were estimated using the carbon-14 technique (Steeman-Nielson 1952) modified by Vollenweider et al. (1969b).

Ponds 162 and 56 were arbitrarily chosen as representative ponds receiving single and multiple additions of phosphorus at which phytoplankton productivity measurements would be performed. During the summer of 1980 the fertilized and control sides of both ponds were measured at five day intervals for ten weeks. During the summer of 1981 productivity and heterotrophy on both the fertilized and control sides of the two ponds were measured once a week for ten weeks.

Bulk water samples were obtained from both sides of each pond. For each side three light and one dark 300 mL Pyrex BOD bottles were filled from the corresponding bulk sample. The bulk water sample was obtained by collecting water samples from five locations of that particular side (four locations around the perimeter and one location in the center) using a hose sampler. The contents of one ampoule (1.0 mL = 1.0 uCi = 37 GBq) of sodium $^{14}$C-bicarbonate was inoculated into each bottle. Into one light bottle 1.0 mL formalin was added. This bottle was termed the killed
control bottle. One killed control bottle and one dark bottle were similarly treated with \(^{14}\text{C}\)-glucose (1.0 mL = 1.0 \( \mu \text{Ci} \approx 37 \text{ GBq} \)) for each sides of the ponds. Once the bottles were filled and injected, the bottles were suspended from the wooden frame of the barrier on corresponding sides. The bottles were allowed to lie horizontally above the sediments such that the bottles were not in shade either from the barrier or from another bottle.

Duration of exposure varied from 3-4 hours beginning at 10:00-11:00 EST. Following incubation the bottles were transported to the laboratory in a light-tight container. The bottles, with one exception because of delayed transportation, were not injected with formalin for the approximate half-hour trip to the laboratory. With the addition of formalin there is the danger of rupturing some of the more delicate plankton, as well as cell leakage of \(^{14}\text{C}\) (Kalff 1965).

Upon arrival in the laboratory a 100 mL subsample from each bottle was separately filtered onto Membrane filters (Millipore HA, 47 mm, 0.45 um). Vacuum applied to the filtering apparatus did not exceed 25 mm of Hg in order to reduce the possibility of rupturing fragile cells (Arthur and Rigler 1967).

Before removal of the filters the walls of the funnel and the filter were rinsed with filtered pond water. The filter was then folded, sample inwards, and placed in a 20 mL glass scintillation vial. Aquasol was added to the
filters in the vials. Aquasol was chosen as it is a ready mixed xylene-based fluor which provides slightly higher counting efficiencies for wet filters.

Radioactivity was measured using a Beckman liquid scintillation spectrophotometer, Model LS 3150P. Efficiency of counting was determined by use of an external standard. Standardization of the working solution was obtained by dispensing one ampoule into a 300 mL BOD bottle filled with filtered pond water and removing 1.0 mL to a scintillation vial containing fluor for subsequent counting.

The total inorganic carbon available for photosynthesis was calculated from the total alkalinity (Rainwater and Thatcher 1960) and a conversion factor (Saunders et al. 1962) using the pH and temperature of the ponds. Organic and inorganic carbon assimilation per cubic metre per hour was determined using the equations (Appendix I) determined by Lind (1979) and simplified by Vollenweider (1969).

Phytoplankton samples were collected from both sides of all six ponds at the same time as when production rates of ponds 56 and 162 were being measured in situ. Samples were similarly collected, preserved and enumerated as previously described in Chapter One.
RESULTS

A. Physical

The ponds were ice-free by June 1980. Pond water temperatures increased following closely to air temperature. Within the tubes placed into the fertilized and control sides of ponds 162 and 56, temperature and pH varied over time (Fig. 3.1). No differences were detected with depth. During daylight hours the temperature and pH increased and then both temperature and pH decreased to a minimum during the short night of approximately four hours. The increases in temperature were not correlated with the increases in pH for both ponds ($r=0.2211$, $n=31$, $p>0.10$). Six hours separated the peaks in temperature and pH. Plots of the two ponds suggest that both ponds were similar. Conductivities ranged from 210 to 492 useimens in 1980 and 250 to 550 useimens in 1981.

In the beginning of the summer water levels were high because of snow and ice run-off. Overflow between ponds was common. As the summer progressed and before phosphorus additions were made the pond water levels had declined. No overflow between ponds was observed for the rest of the summer. In July and August precipitation was high resulting in water levels to rise in 1980 (Table 3.2). In 1982 water levels continued to decline throughout the summer season.

The ponds averaged 0.66 m in maximum depth. Of the maximum water depth up to 35.2% was composed of a loosely
Figure 3.1: Temperature and pH of water column in tubes set into pond 162.
Table 3.2: Change in water depth of ponds between July and August in 1980 and 1981.

<table>
<thead>
<tr>
<th>Pond</th>
<th>1980</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td>56</td>
<td>+12.45</td>
<td>-4.00</td>
</tr>
<tr>
<td>57</td>
<td>+11.43</td>
<td>-3.71</td>
</tr>
<tr>
<td>58</td>
<td>+5.08</td>
<td>-12.76</td>
</tr>
<tr>
<td>162</td>
<td>+13.72</td>
<td>-2.00</td>
</tr>
<tr>
<td>166</td>
<td>+4.83</td>
<td>-15.00</td>
</tr>
<tr>
<td>170</td>
<td>+18.80</td>
<td>-6.50</td>
</tr>
</tbody>
</table>
arranged thick sediment layer. The sediment layer was easily disturbed by human intervention or wave action. Littoral vegetation was scarce.

B. Chemistry

The single addition of phosphorus resulted in an increase in total dissolved phosphorus and soluble reactive phosphorus only on the day of the addition (Fig. 3.2). Within one week after the addition and during the remaining weeks of sample collections there was no significant difference between the fertilized side and the control sides in total dissolved and soluble reactive phosphorus for ponds 56 and 58. For pond 57 the total dissolved phosphorus values were significantly higher on the fertilized side of the pond (t-test=2.884, n=33, p<0.001) (Table 3.3).

For the ponds which received multiple additions, measurements of total dissolved phosphorus and soluble reactive phosphorus were taken on both sides one hour and two hours after the addition of phosphorus. In two hours 17-76% of the added total dissolved phosphorus and 30-100% of the soluble reactive phosphorus disappeared from the water column (Fig. 3.3). Measurements of total dissolved phosphorus and soluble reactive phosphorus were significantly higher on the fertilized sides of the ponds (Table 3.4). Assuming a mean depth of 0.5 to 1.0 m the additions of 2 g.m⁻² and 0.2 g.m⁻² should have resulted in concentrations of 1-2 mg.mL⁻¹ and 0.1-0.2 mg.mL⁻¹. Such
Figure 3.2: Soluble reactive phosphorus (ug.L$^{-1}$; top) and total dissolved phosphorus (ug.L$^{-1}$; bottom) concentrations on the fertilized (■) and control (□) sides of pond 56 during the summer of 1980.
Figure 3.3: Soluble reactive phosphorus (ug.L⁻¹; top) and total dissolved phosphorus (ug.L⁻¹; bottom) concentrations of the fertilized (■) and control (□) sides of pond 162 during the summer of 1980. The bar indicates the decline in soluble phosphorus from immediately after fertilization (maximum value) to two hours after fertilization (minimum value).
Table 3.3: Correlation (R) and common t-statistic (T) of the chemical composition between the fertilized and control sides of ponds 56, 57 and 58 for the summer months of 1980. T-test values underlined are significant at \( p < 0.05 \).

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>56</th>
<th>57</th>
<th>58</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>T</td>
<td>R</td>
</tr>
<tr>
<td>Nitrate</td>
<td>0.846</td>
<td>0.231</td>
<td>0.803</td>
</tr>
<tr>
<td>Silicate</td>
<td>0.919</td>
<td>0.359</td>
<td>0.899</td>
</tr>
<tr>
<td>TDP**</td>
<td>0.927</td>
<td>1.186</td>
<td>0.380</td>
</tr>
<tr>
<td>SRP**</td>
<td>0.988</td>
<td>1.312</td>
<td>0.101</td>
</tr>
<tr>
<td>Alk*</td>
<td>0.942</td>
<td>1.151</td>
<td>0.848</td>
</tr>
<tr>
<td>Ca*</td>
<td>0.774</td>
<td>0.493</td>
<td>0.651</td>
</tr>
<tr>
<td>DO*</td>
<td>0.827</td>
<td>0.397</td>
<td>0.888</td>
</tr>
<tr>
<td>Mg*</td>
<td>0.664</td>
<td>0.059</td>
<td>0.926</td>
</tr>
</tbody>
</table>

* 1980 and 1981 data combined
** includes 1 and 2 hour data
levels were never observed in the ponds. The added phosphate phosphorus either was rapidly taken up by phytoplankton and bacteria or became adsorbed onto inorganic material. Total dissolved phosphorus and soluble reactive phosphorus concentrations ranged from 0.028 to 0.127 mg.L\(^{-1}\) and 0.000 to 0.088 mg.L\(^{-1}\) for the ponds receiving one phosphorus addition. Total dissolved phosphorus and soluble reactive phosphorus concentrations ranged from 0.000 to 0.022 mg.L\(^{-1}\) and 0.000 to 0.013 mg.L\(^{-1}\) on the control sides and from 0.00 to 0.40 mg.L\(^{-1}\) and 0.000 to 0.091 mg.L\(^{-1}\) on the multiple phosphorus addition sides of ponds 162, 166, and 170.

In 1981 total dissolved phosphorus and soluble reactive phosphorus concentrations were always higher on the single fertilized sides than their respective control sides. For the ponds receiving multiple additions, total dissolved phosphorus and soluble reactive phosphorus were similar between sides (Table 3.4). 1981 chemical composition is listed in Appendix VII.

Nutrients were initially high as a result of spring melt-off then quickly declined. During July and August concentrations gradually increased possibly as a result of evaporation. No differences in concentrations of nutrients, other than phosphorus, were measured between the control and fertilized sides of the ponds (Table 3.3 and 3.4). For ponds fertilized once, nitrate nitrogen ranged from 0.07 to 0.48 mg.L\(^{-1}\) in 1980 and 1981. Silicate silica concentrations ranged from 2.0 to 55.0 mg.L\(^{-1}\) in 1980 and increased up to
Table 3.4: Correlation (R) and the common t-statistic (T) of the chemical composition between the fertilized and control sides of pond 162, 166 and 170 for the summer months of 1980. T-test values underlined are significant at p<0.05.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>162</th>
<th>166</th>
<th>170</th>
<th>162</th>
<th>166</th>
<th>170</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nitrate</td>
<td>0.914</td>
<td>0.169</td>
<td>0.793</td>
<td>1.084</td>
<td>0.860</td>
<td>0.183</td>
</tr>
<tr>
<td>Silicate</td>
<td>0.749</td>
<td>0.600</td>
<td>0.911</td>
<td>0.691</td>
<td>0.779</td>
<td>0.186</td>
</tr>
<tr>
<td>TDP**</td>
<td>0.226</td>
<td>4.796</td>
<td>0.369</td>
<td>1.865</td>
<td>0.045</td>
<td>1.975</td>
</tr>
<tr>
<td>SRP**</td>
<td>0.118</td>
<td>4.606</td>
<td>0.284</td>
<td>3.237</td>
<td>0.293</td>
<td>3.430</td>
</tr>
<tr>
<td>Alk*</td>
<td>0.924</td>
<td>0.201</td>
<td>0.891</td>
<td>0.849</td>
<td>0.846</td>
<td>2.017</td>
</tr>
<tr>
<td>Ca*</td>
<td>0.961</td>
<td>1.379</td>
<td>0.919</td>
<td>0.570</td>
<td>0.818</td>
<td>1.992</td>
</tr>
<tr>
<td>DO*</td>
<td>0.883</td>
<td>1.145</td>
<td>0.663</td>
<td>0.202</td>
<td>0.833</td>
<td>1.009</td>
</tr>
<tr>
<td>Mg*</td>
<td>0.760</td>
<td>0.239</td>
<td>0.746</td>
<td>0.007</td>
<td>0.777</td>
<td>0.078</td>
</tr>
</tbody>
</table>

* 1980 and 1981 data

** includes 1 and 2 hour data
Figure 3.4: Nitrate-nitrogen (mg.L⁻¹; top) and silicate-silica (mg.L⁻¹; bottom) concentrations on the fertilized (■) and control (□) sides of pond 56 during the summer of 1980.
Figure 3.5: Dissolved oxygen (mg.L\(^{-1}\)), total alkalinity (mg CaCO\(_3\).L\(^{-1}\)), calcium (mg.L\(^{-1}\)) and magnesium (mg.L\(^{-1}\)) concentrations on the fertilized (■) and control (□) sides of pond 56 during the summer of 1980.
114% in 1981. Increased concentrations of silicate silica, nitrate nitrogen, total dissolved phosphorus and soluble reactive phosphorus occurred during times of increased winds and precipitation. Calcium concentrations ranged from 9.94 to 77.07 mg.L\(^{-1}\) in 1980 and from 7.25 to 57.58 mg.L\(^{-1}\) in 1981. Calcium showed a surprising decrease during late July but continued to increase during August. Magnesium ranged from 0 to 37.08 mg.L\(^{-1}\) in 1980 and 15.91 to 84.54 mg.L\(^{-1}\) in 1981. Alkalinity also declined during July 1980: Total alkalinity ranged from 60 to 229 mg.L\(^{-1}\) in 1980 and from 70.3 to 196.0 mg.L\(^{-1}\) in 1981. Dissolved oxygen concentrations decreased slightly over the summer in both years. Concentrations ranged from 8.35 to 14.29 mg.L\(^{-1}\) in 1980 and 8.8 to 13.5 mg.L\(^{-1}\) in 1981 with saturation approaching 100% at all times.

For ponds fertilized ten times during the summer season in both 1980 and 1981, nitrate nitrogen ranged from 0.076 to 0.482 mg.L\(^{-1}\) in 1980 and from 0.07 to 1.30 mg.L\(^{-1}\) in 1981. Silicate silica ranged from 0 to 46.8 mg.L\(^{-1}\) in 1980 and from 6.0 to 50.0 mg.L\(^{-1}\) in 1981. Calcium and magnesium fluctuated in concentration during the summer. Magnesium concentrations ranged from 0.00 to 30.96 mg.L\(^{-1}\) in 1980 and from 5.81 to 76.47 mg.L\(^{-1}\) in 1981. Calcium concentrations ranged from 14.45 to 68.45 mg.L\(^{-1}\) in 1980 and from 17.61 to 57.18 mg.L\(^{-1}\) in 1981. Alkalinity concentrations ranged from 107.0 to 217.8 mg.L\(^{-1}\) in 1980 and from 60.0 to 229.0 mg.L\(^{-1}\) in 1981. Dissolved oxygen declined over the summer although
per cent saturation always approached or exceeded 100%. Dissolved oxygen concentrations ranged from 8.15 to 13.27 mg.L\(^{-1}\) in 1980 and from 10.9 to 13.1 mg.L\(^{-1}\) in 1981. Nutrient measurements did not vary more than 20 percent between triplicate samples for any of the tundra ponds.

C. Phosphorus Dynamics

The addition of phosphate phosphorus to the plexiglass tubes in the tundra pond resulted in no significant difference in the total dissolved phosphorus and the soluble reactive phosphorus concentrations between the tubes with or without sediments (t-test, p< 0.05). Although there was some increase in total dissolved phosphorus (Table 3.5), it appears as if most of the phosphorus is trapped in the particulate fraction on the filters. This particulate fraction would include phytoplankton, bacteria, stable inorganic complexes or particles, including calcite, and phosphorus adsorbed onto dead particulate organic matter. Over 95% of the phosphate phosphorus added moved into this particulate phase within one minute. Phytoplankton samples removed prior to the addition of phosphorus to tubes A, B, and C contained algal volumes of 876, 114, and 41 \(\mu m^3.mL^{-1}\). This suggests that the size of the phytoplankton populations did not greatly affect the removal of phosphate phosphorus, suggesting that phosphorus was not being trapped into the biological particulate compartments.

In the study of diurnal fluxes of radiophosphorus the
Table 3.5: Effect of added phosphate-phosphorus (0.2 mg.L\(^{-1}\)) on total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) within a water column with (Tube A and B) and without (Tube C) sediment.

<table>
<thead>
<tr>
<th>TIME (hour)</th>
<th>TUBE A TDP SRP (mg.L(^{-1}))</th>
<th>TUBE B TDP SRP (mg.L(^{-1}))</th>
<th>TUBE C TDP SRP (mg.L(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>.02</td>
<td>.09 .04</td>
<td>.04 .04</td>
<td>.06 .04</td>
</tr>
<tr>
<td>.05</td>
<td>.09 .04</td>
<td>.04 .04</td>
<td>.06 .04</td>
</tr>
<tr>
<td>.08</td>
<td>.08 .03</td>
<td>.04 .04</td>
<td>.05 .03</td>
</tr>
<tr>
<td>.17</td>
<td>.08 .03</td>
<td>.04 .04</td>
<td>.05 .03</td>
</tr>
<tr>
<td>.25</td>
<td>.08 .04</td>
<td>.03 .03</td>
<td>.05 .03</td>
</tr>
<tr>
<td>.50</td>
<td>.07 .03</td>
<td>.06 .04</td>
<td>.06 .04</td>
</tr>
<tr>
<td>1</td>
<td>.07 .04</td>
<td>.07 .03</td>
<td>.05 .04</td>
</tr>
<tr>
<td>2</td>
<td>.07 .04</td>
<td>.07 .04</td>
<td>.05 .04</td>
</tr>
<tr>
<td>3</td>
<td>.07 .04</td>
<td>.06 .04</td>
<td>.05 .04</td>
</tr>
<tr>
<td>4</td>
<td>.07 .04</td>
<td>.07 .04</td>
<td>.05 .04</td>
</tr>
<tr>
<td>5</td>
<td>.07 .04</td>
<td>.07 .04</td>
<td>.05 .04</td>
</tr>
</tbody>
</table>
seston from control sides of ponds 56 and 162 rapidly took up the radiophosphorus within 3 hours (Fig. 3.6) suggesting phosphorus limitation by the seston. After 12 hours there was less radiophosphorus in the particulate fraction. On the fertilized sides particulate material took up less radiophosphorus. The addition of phosphorus to these sides may have saturated the binding sites of the particulate fractions.

The addition of phosphate phosphorus to pond 162 lowered the uptake of phosphorus by the particulate fraction (Fig. 3.7). Phosphorus uptake before the phosphate phosphorus addition was more than 20% compared with approximately 5% after the phosphorus addition. It was obvious that the fertilization of the pond had reduced the uptake of phosphorus even during the time between additions. The control side of the pond had a turnover time, measured as the inverse of the uptake rate constant, of 20 minutes while the fertilized side had a turnover time of 2500 minutes after the phosphorus addition. Particulate material from the control side of the pond had an initially steep uptake of phosphorus and a short turnover time. This type of plot represents phosphorus depletion in the pond water with phosphorus exchange occurring mainly with biological and non-biological particulate phosphorus and with insignificant formation of organic phosphorus (Leân and Nalewajko 1979). When particulate material is not limited by phosphorus and where the particulate phosphorus to soluble reactive
Figure 3.6: Average percent radiophosphorus uptake by particulate material in tubes set into fertilized (■) and control (□) sides of ponds 56 (top) and 162 (bottom).
Figure 3.7: Radiophosphorus uptake by particulate material in fertilized (P) and control (C) sides of pond 162 which had been receiving continual weekly phosphorus inputs of 0.2 mg.m$^{-2}$. 
phosphorus ratio is low turnover times become much longer (Nalewajko and Lean 1980), as was observed for the fertilized side of pond 162.

D. Phytoplankton Composition
Seasonal phytoplankton biomass and composition of ponds 56 and 162 are represented in Figures 3.8 to 3.11. There were no significant differences between the fertilized sides and the control sides of either pond (Table 3.6 and 3.7). Seasonal fluctuations in some of the common species contributing more than 5% to the total biomass are illustrated in Figures 3.12 to 3.15. Species composition was similar between the fertilized and control sides of all ponds. Major phytoplankton classes were Bacillariophyceae, Chlorophyceae and Cryptophyceae. In respect to the ponds receiving single additions of phosphorus per year, total biomass peaked during August in 1980. Bacillariophyceae was abundant during periods of low total biomass during early to mid-season. *Tabellaria fenestrata*, *Diatoma elongatum* and *Pinnularia* spp. were common species. Chlorophyceae and Cyanophyceae contributed up to 91% of the algal biomass during periods of high biomass. *Aphanocapsa* spp., *Merismopedia* major, *Chlamydomonas* spp., *Oocystis borgei*, *Eudorina elegans* and *Crucigenia* spp. were common species. The Cryptophyceae, mainly consisting of *Rhodomonas minuta*, contributed up to 59% following spring thaw. The Euglenophyceae, Chrysophyceae and Dinophyceae did not
Figure 3.8: Seasonal variations in phytoplankton biomass (µm$^3$·mL$^{-1}$) and class composition from the control (a) and fertilized (b) sides of pond 56 during 1980.
Figure 3.9: Seasonal variations in phytoplankton biomass (µm$^3$·mL$^{-1}$) and class composition from the control (a) and fertilized (b) sides of pond 56 during 1981.
Figure 3.19: Seasonal variations in phytoplankton biomass (µm³.mL⁻¹) and class composition from the control (a) and fertilized (b) sides of pond 162 during 1980.
Figure 3.11: Seasonal variations in phytoplankton biomass (μm$^3$·mL$^{-1}$) and class composition from the control (a) and fertilized (b) sides of pond 162 during 1981.
Table 3.6: Common t-statistic of phytoplankton classes between the fertilized and control sides of ponds 56, 57 and 58 for the summer months of 1980 and 1981. T-test values underlined are significant at p<0.05, n=8.

<table>
<thead>
<tr>
<th>ALGAL CLASS</th>
<th>1980</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td>56</td>
<td>0.195</td>
<td>0.051</td>
</tr>
<tr>
<td>57</td>
<td>0.764</td>
<td>3.457</td>
</tr>
<tr>
<td>58</td>
<td>0.842</td>
<td>0.452</td>
</tr>
<tr>
<td>CYANO</td>
<td>1.975</td>
<td>1.014</td>
</tr>
<tr>
<td>1.804</td>
<td>0.687</td>
<td>1.366</td>
</tr>
<tr>
<td>1.014</td>
<td>0.284</td>
<td></td>
</tr>
<tr>
<td>BACILL</td>
<td>0.357</td>
<td>0.223</td>
</tr>
<tr>
<td>0.995</td>
<td>0.807</td>
<td>1.156</td>
</tr>
<tr>
<td>0.369</td>
<td>0.284</td>
<td></td>
</tr>
<tr>
<td>CHLORO</td>
<td>0.395</td>
<td>0.638</td>
</tr>
<tr>
<td>0.585</td>
<td>1.443</td>
<td>2.153</td>
</tr>
<tr>
<td>1.420</td>
<td>0.918</td>
<td></td>
</tr>
<tr>
<td>CHRYSO</td>
<td>0.440</td>
<td>0.595</td>
</tr>
<tr>
<td>0.539</td>
<td>0.232</td>
<td>1.918</td>
</tr>
<tr>
<td>0.501</td>
<td>0.918</td>
<td></td>
</tr>
<tr>
<td>OTHER</td>
<td>1.000</td>
<td>0.000</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOMASS</td>
<td>1.189</td>
<td>0.414</td>
</tr>
<tr>
<td>0.255</td>
<td>1.333</td>
<td>1.853</td>
</tr>
<tr>
<td>1.037</td>
<td>0.918</td>
<td></td>
</tr>
</tbody>
</table>
Table 3.7: Common t-statistic of phytoplankton classes between the fertilized and control sides of ponds 162, 166 and 170 for the summer months of 1980 and 1981. Values underlines are significant at p<0.05, n= 8.

<table>
<thead>
<tr>
<th>ALGAL CLASS</th>
<th>1980</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>162</td>
<td>166</td>
</tr>
<tr>
<td>CRYPT</td>
<td>1.070</td>
<td>1.807</td>
</tr>
<tr>
<td>CYANO</td>
<td>0.467</td>
<td>1.349</td>
</tr>
<tr>
<td>BACILL</td>
<td>1.159</td>
<td>0.438</td>
</tr>
<tr>
<td>CHLORO</td>
<td>1.784</td>
<td>0.159</td>
</tr>
<tr>
<td>CHRYSO</td>
<td>1.113</td>
<td>0.493</td>
</tr>
<tr>
<td>OTHER</td>
<td>1.000</td>
<td>0.437</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOMASS</td>
<td>1.211</td>
<td>0.048</td>
</tr>
</tbody>
</table>
Figure 3.12: Seasonal succession of select species which contributed > 5% to the total phytoplankton biomass at pond 56 on the fertilized side over the summer months of 1980 and 1981.

(Aph= Aphanocapsa spp., Eua= Euastrum spp., Cro= Cryptomonas ovata, Pin= Pinnularia spp., Rho= Rhodomonas minuta, Dia= Diatom elongatum, Cre= Cryptomonas erosa, Tab= Tabellaria fenestrata, Eud= Eudorina elegans, Oos= Oocystis crassa, Mer= Merismopedia punctata, Chl= Chlamydomonas spp., Oob= Oocystis borgei, Spi= Spirogyra spp., Cru= Merismopedia major, Nav= Navicula sp., Eun= Eunotia praerupta, Zyg= Zygogyna pectinatum)
Figure 3.13: Seasonal succession of select species which contributed > 5% to the total phytoplankton biomass at pond 56 on the control side over the summer months of 1980 and 1981. (see Figure 3.12 for descriptions of abbreviations)
Figure 3.14: Seasonal succession of select species which contributed > 5% to the total phytoplankton biomass at pond 162 on the fertilized side over the summer months of 1980 and 1981. (see Figure 3.12 for descriptions of abbreviations)
Figure 3.15: Seasonal succession of select species which contributed > 5% to the total phytoplankton biomass at pond 162 on the control side over the summer months of 1980 and 1981. (see Figure 3.12 for descriptions of abbreviations).
individually contribute at any time more than 25% to the total biomass. In 1981 peaks in biomass occurred either during mid-season or later in the summer. During the summer season the ponds were dominated by Chlorophyceae which contributed up to 81% total biomass. *Eudorina elegans*, *Oocystis crassa*, and *O. borgei* were common species. The Bacillariophyceae, mainly consisting of *Pinnularia* spp., again increased in biomass (< 39%) generally during low periods of biomass in the first half of the season. A second peak of Bacillariophyceae, again consisting mainly of *Pinnularia* spp., occurred during August (< 51%). The Cyanophyceae contributed only up to 32% total biomass. *Aphanocapsa* spp., *Merismopedia major* were common species. Cryptophyceae increased in biomass only during early July (10%). *Cryptomonas ovata* was present while *Rhodomonas minuta* was absent.

For the ponds which received multiple additions of phosphorus total biomass increased over the season with peaks occurring later in the season for the fertilized sides in 1980. Early in the season fluctuations in total biomass were reflected in all the classes. Towards the second half of the season Bacillariophyceae dominated the total biomass (<87%). *Navicula* spp., *Tabellaria fenestrata* and *Pinnularia* spp. were common species. The Cryptophyceae, consisting mainly of *Rhodomonas minuta*, peaked early in the season (<62%) and then fell off very rapidly. In 1981 Bacillariophyceae and Chlorophyceae dominated the
Table 3.8: Analysis of variance of the phytoplankton classes for ponds 56, 57, and 58. Listed are the F-values for the various phytoplankton classes between 1980 and 1981, among the three ponds and between the fertilized and control sides of each pond. Values underlined are significant at $p<0.05$, values double-underlined are significant at $p<0.001$, $n = 8$.

<table>
<thead>
<tr>
<th>ALGAL CLASS</th>
<th>YEAR</th>
<th>POND</th>
<th>TREAT. Y-P</th>
<th>Y-T</th>
<th>P-T</th>
<th>YPT</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRYPT</td>
<td>28.310</td>
<td>0.584</td>
<td>0.018</td>
<td>1.122</td>
<td>0.065</td>
<td>0.677</td>
</tr>
<tr>
<td>CYANO</td>
<td>9.485</td>
<td>7.762</td>
<td>3.949</td>
<td>5.957</td>
<td>5.009</td>
<td>2.316</td>
</tr>
<tr>
<td>BACILL</td>
<td>1.009</td>
<td>0.712</td>
<td>2.374</td>
<td>0.293</td>
<td>0.079</td>
<td>1.602</td>
</tr>
<tr>
<td>CHLORO</td>
<td>0.022</td>
<td>2.115</td>
<td>1.651</td>
<td>0.769</td>
<td>0.521</td>
<td>0.799</td>
</tr>
<tr>
<td>CHRYSO</td>
<td>0.418</td>
<td>0.177</td>
<td>0.013</td>
<td>1.362</td>
<td>0.189</td>
<td>0.151</td>
</tr>
<tr>
<td>OTHER</td>
<td>2.165</td>
<td>1.815</td>
<td>2.479</td>
<td>2.059</td>
<td>1.719</td>
<td>2.355</td>
</tr>
<tr>
<td>TOTAL BIOMASS</td>
<td>3.013</td>
<td>4.505</td>
<td>0.123</td>
<td>2.657</td>
<td>1.871</td>
<td>0.189</td>
</tr>
</tbody>
</table>
Table 3.9: Analysis of variance of phytoplankton classes for ponds 162, 166 and 170. Listed are the F-values for the various phytoplankton classes between 1980 and 1981, among the three ponds and between the fertilized and control sides of each pond. Values underlined are significant at p<0.05, values double-underlined are significant at p<0.001, n=8.

<table>
<thead>
<tr>
<th>ALGAL CLASS</th>
<th>YEAR</th>
<th>POND</th>
<th>TREAT.</th>
<th>Y-P</th>
<th>Y-T</th>
<th>P-T</th>
<th>YPT</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRYPT</td>
<td>7.981</td>
<td>1.685</td>
<td>0.642</td>
<td>1.168</td>
<td>0.105</td>
<td>0.786</td>
<td>1.800</td>
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<tr>
<td>CYANO</td>
<td>1.448</td>
<td>3.739</td>
<td>2.404</td>
<td>0.665</td>
<td>1.799</td>
<td>0.389</td>
<td>1.212</td>
</tr>
<tr>
<td>BACILL</td>
<td>0.143</td>
<td>1.115</td>
<td>1.989</td>
<td>1.044</td>
<td>0.013</td>
<td>0.587</td>
<td>0.763</td>
</tr>
<tr>
<td>CHLORO</td>
<td>0.004</td>
<td>2.173</td>
<td>2.125</td>
<td>2.549</td>
<td>0.016</td>
<td>0.900</td>
<td>2.323</td>
</tr>
<tr>
<td>CHRYSO</td>
<td>6.581</td>
<td>1.494</td>
<td>4.083</td>
<td>1.731</td>
<td>2.512</td>
<td>0.848</td>
<td>1.556</td>
</tr>
<tr>
<td>OTHER</td>
<td>4.935</td>
<td>5.649</td>
<td>0.001</td>
<td>1.578</td>
<td>0.744</td>
<td>0.141</td>
<td>0.994</td>
</tr>
<tr>
<td>TOTAL BIOMASS</td>
<td>0.018</td>
<td>1.589</td>
<td>0.028</td>
<td>0.356</td>
<td>0.013</td>
<td>0.681</td>
<td>1.987</td>
</tr>
</tbody>
</table>
phytoplankton population. Chlorophyceae peaked during mid-season (<72%) whereas Bacillariophyceae dominated biomass in August (<91%). Oocystis crassa, Chlamydomonas spp., and Eudorina elegans contributed to the Chlorophyceae. Navicula spp., Pinnularia spp., and Tabellaria fenestrata contributed to the Bacillariophyceae. Cryptophyceae were not as prominent as in the preceding year. Rhodomonas minuta had declined whereas Cryptomonas ovata increased in abundance. Euglenophyceae contributions were higher in 1981; 1.1% compared to 0.3%.

In summary, species composition was similar between the fertilized and control sides of the ponds (Tables 3.6 and 3.7). Cryptophyceae was more abundant during 1980 (Tables 3.8 and 3.9) possibly as a result of meteorological differences (see Chapter One). Rhodomonas minuta had increased biomass on the fertilized sides of the ponds receiving multiple additions. Cyanophyceae was also more abundant in 1980 in the ponds receiving single additions of phosphorus. Overall there seemed to be no significant change in phytoplankton composition as a result of increased phosphorus loadings.

E. Productivity

The seasonal variation of phytoplankton biomass, productivity, heterotrophy and chlorophyll a are presented in Figures 3.13 to 3.16. All parameters were collected on the same day between 10:00 and 14:00. Seasonal averages are
Figure 3.16: Seasonal variations in total phytoplankton biomass (mg.10^{-6}.mL^{-1}), chlorophyll a (mg.m^{-3}), productivity (mgC.m^{-3}.hr^{-1}), and heterotrophy (10^{-3}.mgC.m^{-3}.hr^{-1}) from the fertilized (■) and control (□) sides of pond 56 during the summer of 1980.
Figure 3.17: Seasonal variations in total phytoplankton biomass (mg.10^{-6}.mL^{-1}), productivity (mgC.m^{-3}.hr^{-1}) and heterotrophy (10^{-3}mgC.m^{-3}.hr^{-1}) from the fertilized (●) and control (□) sides of pond 56 during the summer of 1981.
Figure 3.18: Seasonal variations in total phytoplankton biomass (mg.10^-6.mL^-1), chlorophyll a (mg.m^-3), productivity (mgC.m^-1.hr^-1) and heterotrophy (10^-3 mgC.m^-3.hr^-1) from the fertilized (■) and control (□) sides of pond 162 during the summer of 1980.
Figure 3.19: Seasonal variations in total phytoplankton biomass (mg $10^{-6}$ mL$^{-1}$), productivity (mgC $m^{-3}$ hr$^{-1}$) and heterotrophy ($10^{-3}$ mgC $m^{-3}$ hr$^{-1}$) from the fertilized (■) and control (□) sides of pond 162 during the summer of 1981.
Table 3.10: Seasonal range of phytoplankton biomass, chlorophyll $a$, productivity and heterotrophy for the fertilized (P) and control (C) sides of ponds 56 and 162.

<table>
<thead>
<tr>
<th></th>
<th>56</th>
<th></th>
<th>162</th>
<th></th>
</tr>
</thead>
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<tr>
<td></td>
<td>BIOMASS (mg.$10^{-6}$mL$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>Mean</td>
<td>498.060</td>
<td>810.071</td>
<td>273.106</td>
</tr>
<tr>
<td></td>
<td>Min</td>
<td>164.300</td>
<td>150.910</td>
<td>45.320</td>
</tr>
<tr>
<td></td>
<td>Max</td>
<td>1346.500</td>
<td>2500.000</td>
<td>406.910</td>
</tr>
<tr>
<td>1981</td>
<td>Mean</td>
<td>473.192</td>
<td>394.682</td>
<td>486.131</td>
</tr>
<tr>
<td></td>
<td>Min</td>
<td>57.000</td>
<td>67.810</td>
<td>62.110</td>
</tr>
<tr>
<td></td>
<td>Max</td>
<td>958.420</td>
<td>807.241</td>
<td>1112.710</td>
</tr>
<tr>
<td></td>
<td>CHLOROPHYLL $a$ (mg.m$^{-3}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>Mean</td>
<td>0.845</td>
<td>0.974</td>
<td>1.732</td>
</tr>
<tr>
<td></td>
<td>Min</td>
<td>0.000</td>
<td>0.454</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Max</td>
<td>2.346</td>
<td>2.104</td>
<td>4.280</td>
</tr>
<tr>
<td>1981</td>
<td>Mean</td>
<td>0.861</td>
<td>0.483</td>
<td>1.209</td>
</tr>
<tr>
<td></td>
<td>Min</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>PRODUCTIVITY (mgC.m$^{-3}$hr$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>Mean</td>
<td>1.488*</td>
<td>2.049*</td>
<td>1.246*</td>
</tr>
<tr>
<td></td>
<td>Min</td>
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<td>0.209</td>
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</tr>
<tr>
<td>HETEROTRPHY (mgC.10^-3 m^-3 hr^-1)</td>
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* t-test significant at p<0.05
recorded in Table 3.10. No differences between control and fertilized sides of the ponds were observed for phytoplankton biomass, heterotrophy, or chlorophyll a. Productivity was significantly higher for the multiple fertilized side (t-test = 2.056, p<0.05) and lower for the single phosphorus addition side (t-test = 2.203, p<0.05) than their respective control sides. No diurnal variations during daylight hours were observed. Total phytoplankton biomass, chlorophyll a and heterotrophy decreased over June and July 1980 whereas productivity increased. As biomass increased in August 1980, productivity, heterotrophy and chlorophyll a decreased. In 1981 productivity, biomass and heterotrophy fluctuated over the season with the phosphorus addition sides generally higher than the control sides. Continual loading of phosphorus on a weekly basis did result in an increase in productivity, suggesting that a more steady-state source of nutrients (as opposed to actual loading) has more affect on phytoplankton production in arctic ecosystems than single pulse events.

F. Phytoplankton Size Composition

The seasonal variation of net and nanoplanckton are given in Figures 3.20 and 3.21. The phytoplankton were grouped into various size classes depending on their mean spherical diameter. Netplankton were considered phytoplankton with mean spherical diameters greater than 64 um. Species smaller than 64 um were considered nanoplankton
Figure 3.20: Seasonal variations of phytoplankton size fractions from the fertilized (top) and control (bottom) sides of pond 56 during the summers of 1980 and 1981.
Figure 3.21: Seasonal variations of phytoplankton size fractions from the fertilized (top) and control (bottom) sides of pond 162 during the summers of 1980 and 1981.
Table 3.11: Common t-statistic of phytoplankton size fractions between the fertilized and control sides of ponds 56, 57, 58, 162, 166 and 170 for the summer of 1980 and 1981. Values underlined are significant at $p<0.05$, values double-underlined are significant at $p<0.001$, n=16.

**ALGAL SIZES**

<table>
<thead>
<tr>
<th>YEAR</th>
<th>POND</th>
<th>&lt;10um</th>
<th>10-30um</th>
<th>30-64um</th>
<th>&gt;64um</th>
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<td>0.775</td>
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<td>1.363</td>
<td>1.921</td>
</tr>
<tr>
<td></td>
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<td>1.313</td>
<td>0.862</td>
<td>0.284</td>
<td>0.405</td>
</tr>
<tr>
<td></td>
<td>170</td>
<td>0.997</td>
<td>0.566</td>
<td>1.415</td>
<td>0.160</td>
</tr>
</tbody>
</table>
and further subdivided into <10, 10-30, 30-64 um size classes.

At times netplankton significantly contributed to the total biomass of all ponds during both years. In the ponds with only one phosphorus addition, netplankton contributed more to the total biomass in 1980. Netplankton contributions ranged up to 95.5% in 1980 and up to only 34.1% in 1981. Cyanophyceae, consisting of Aphanocapsa spp., and Merismopedia major, and Chlorophyceae, consisting of Spirogyra spp., contributed to the peaks in netplankton in both years.

In the ponds with multiple additions of phosphorus, netplankton contributions to the total biomass were higher on the phosphorus addition sides only in 1980 (Table 3.11 and 3.12). The proportions of netplankton were lower than in the preceding year. Netplankton contributions to total phytoplankton biomass ranged up to 55.9% in 1980 and up to 95.6% in 1981. Netplankton peaked in August for all ponds with Zygnema pectinata, Spirogyra sp. and Aphanocapsa spp. common during the month.

Nanoplankton contributed the most to the total phytoplankton biomass over the summers of 1980 and 1981. For the ponds with single additions of phosphorus, the <30 um size class contributed most to the nanoplankton during 1980 and 1981. Oocystis crassa, Chlamydomonas spp., and Eudorina elegans were common species. The 30-64 um size fraction fluctuated throughout the season with Merismopedia major the
most frequently occurring species at all the ponds. For the ponds with multiple additions of phosphorus most of the nanoplanckton fell within the 0-30 um range with very few in the 30-64 um size range. In 1980 in pond 162 the 30-64 um size class was significantly higher on the control side with a seasonal average of 23.2% total biomass compared with 3.9% on the fertilized side (t-test=2.485, n=8, p<0.05). In 1981 there was no significant differences between the fertilized and control sides of the ponds for the various nanoplanckton size classes (t-test, n=8, p>0.01; Table 3.11). Tabellaria fenestrata and Spirogyra spp. were common in the 30-64 um size class. Pinnularia spp., Chlamydomonas spp., and Oocystis crassa were common in the <30 um size class.

Between 1980 and 1981, for the single addition ponds the most obvious difference was the reduction in the >64 um size fraction composed primarily of Cyanophyceae. In 1981 the 30-64 um size class increased although not to the same extent as the >64 um size fraction in 1980. Cyanophyceae was the major contributor in both years in the netplankton.

For the ponds with multiple additions of phosphorus the proportion of netplankton significantly decreased for both sides of the ponds between 1980 and 1981 (ANOVA, F=18.161, n=16, p<0.001). In 1980 the phosphorus addition sides had significantly more netplankton (t-test=2.307, n=8, p<0.05). In 1981 there was no significant difference in the proportions of netplankton between the phosphorus addition and control sides. The 30-64 um size class fluctuated the
most between the years, ponds and sides as a result of being composed of blue-green filaments and diatom colonies which generally contributed most to the netplankton fraction.

G. Similarity

All the ponds in the phosphorus loading experiments were very similar (Fig. 3.22) in species composition. Using Jaccard's percent similarity index all the pond populations grouped at levels greater than 50%. For both 1980 and 1981 the sides of the ponds which had phosphorus added clustered at a higher similarity percent than the control sides. The control sides of ponds 57 and 58 were always the last ponds to cluster.
Figure 3.22: Skyline plot of (a) Jaccard's similarity index and (b) percent similarity index between the fertilized and control sides of ponds 56, 57, 58, 162, 166 and 170. This summarizes the results of clustering by showing the clusters, and the value of similarity at which they were formed. The ponds below the horizontal lines correspond to the members of the clusters.
Discussion

It might be initially puzzling that the ponds which received a total of 2.0 mg m$^{-2}$ (based on surface area) did not respond with increased phytoplankton biomass. Phytoplankton biomass, productivity and chlorophyll a values for all the ponds, both fertilized and control sides, were considered indicative of oligotrophic conditions (Vollenweider 1968). Phosphorus alone did not evoke a phytoplankton response for lakes in northwestern Ontario (Schindler et al. 1973) nor for ponds in Alaska (Kalff 1965). The phosphorus added to the ponds in Churchill was quickly removed from solution, probably by calcite adsorption as opposed to biological uptake. Additions of phosphorus to arctic ponds in Sweden and Canada resulted in the phosphorus being rapidly removed from solution (Nelson and Edmondson 1955; O'Brien and deNoyelles 1974) where 80-90% of the phosphorus was recovered in the organic phosphorus fractions (Jansson 1978).

In short term experiments Stanley and Daley (1976) found no increases in phytoplankton photosynthesis. However in whole pond experiments they reported a large increase in biomass and productivity. Additions of phosphorus to ponds in Barrow also resulted in increased photosynthesis and phytoplankton biomass (Prentki et al. 1980). Within bags set in a lake, Schindler et al. (1974) were able to increase phytoplankton biomass but not chlorophyll a levels with the addition of only 5 ug P L$^{-1}$. Where phytoplankton did respond
to phosphorus additions, the effect was enhanced if nitrogen additions were included (Nelson and Edmondson 1955; O'Brien and deNoyelles 1974; Schindler and Fee 1974; Jansson 1978). Phosphorus alone was sufficient in some cases to initiate a response in the phytoplankton as a result of nitrogen fixation (Jansson 1978). But although the phytoplankton were phosphorus limited, additions of phosphorus shifted the N:P ratios whereby the phytoplankton quickly became nitrogen limited.

In the spring, accumulated winter snow melted and the resultant runoff which overflowed the ponds. Anaerobic conditions during the winter ice cover together with high turnover times of water could have caused a loss of phosphorus retained in the lake from the preceding summer. In the Churchill ponds, nutrients were high from spring runoff in the first year before phosphorus additions. In the following year the ponds had thawed before sampling took place. This prevented us from determining whether the normally high levels of phosphorus were further elevated from the previous year's phosphorus additions. Jansson (1978) found that a high turnover rate of the system did not contribute to a flux of phosphorus out of the lake. Instead phosphorus was retained within the sediments.

There is conflicting evidence suggesting that the phytoplankton may not have been able to take up the inputs of phosphorus. Jansson (1978) found that the additions of phosphorus went directly to the sediments where algae
covering the bottom took up a large portion of the phosphorus. This is in agreement with Kalff (1965) where ponds with highly organic sediments showed no response, in terms of phytoplankton productivity, to additions of phosphorus. Instead, there was abundant growth of moss over the sediments. In Barrow, Alaska phytoplankton in tundra ponds appeared to take up phosphorus (i.e., increased photosynthesis) when phosphorus was added. Alexander et al. (1980) explained that the phytoplankton rapidly took up the phosphate of which most was rapidly released back into the environment in an organic form. This seems to be in contradiction with the hypothesis that the phytoplankton were phosphorus limited. It was observed though, that epipelagic algae were more abundant than phytoplankton and rapidly increased photosynthetically following phosphorus additions. This would suggest that the phosphorus was migrating toward the sediments.

The sediments of the ponds may control the availability of phosphorus to phytoplankton. The pond waters were saturated with dissolved oxygen all summer long. Generally under aerobic conditions phosphate and other ions are retained in the sediments (Mortimer 1971). Meretta Lake in the Northwest Territories had high influxes of phosphorus to the sediments. There the sediments retained the phosphorus even though oxygen tensions were low (Schindler et al. 1973, 1974). In Barrow Alaska, phosphorus that entered the tundra ponds quickly moved to the sediments. There it was mostly
sorbed onto a hydrous iron complex. Phosphate phosphorus concentrations remained low in the overlying waters as a result of slow turnover ratios in the sediments (Prentki et al. 1980). Phosphorus concentrations would be expected to increase following disturbances to the sediment-water interface. Severe weather phenomena (Nalewajko and Lean 1974) and active benthic organisms (Prentki et al. 1980) would contribute to erratic phosphorus inputs.

Phosphorus may be rapidly removed from solution by adsorption onto inorganic complexes. Calcium concentration and pH levels were sufficiently high in the Churchill ponds to lead to calcite formation. Utilization of free carbon dioxide by photosynthesis encourages the formation of calcium carbonate. Calcium carbonate precipitation was observed in the tundra pond waters during warm sunny days. Calcium carbonate coprecipitates with phosphorus resulting in a flux of phosphorus to the sediments (Reynolds 1984). In Barrow, Alaska phosphorus was found to adsorb onto ferric hydroxides. Although iron concentrations were not measured for this study, future studies involving the Churchill ponds should include further investigation into the effect of inorganic complexes on phosphorus concentrations.

Abiotic phosphorus uptake may be very important in waters with high concentrations of calcium (Otuski and Wetzel 1971). The ponds in the experimental area of Churchill had calcium concentrations >25 mg.L⁻¹. Calcite can remove phosphorus from the water but the association is weak.
(Green et al. 1978). Phosphorus is adsorbed on the calcite surface and the reaction consumes hydrogen ions driving the pH even higher (Avnimelech 1980). This increase in pH has been associated with only low to moderate productivity (Murphy et al. 1983).

Within the ponds a calcium complexing of the added phosphorus may be taking place. In low phosphate concentrations (= control side of ponds) the small amount of radiophosphorus added went directly into the particulate fraction, not including the acid soluble fraction. After approximately one day the radiophosphorus began to recycle. In the sides of the ponds which received phosphate phosphorus additions of which most was in the particulate fraction or in the sediments, the added radiophosphorus was not immediately taken up. The bottom layer of particulate material along the sediment-water interface was—the first level in the water column to take up the radiophosphorus. Kalff (1965) found that added phosphorus only increased biomass along the sediment-water interface, where the algae were the first to utilize phosphorus which was settling to the bottom. pH was also at its peak when the particulate fraction took up the radiophosphorus. If photosynthetic consumption was high at this time and precipitation of calcium complexes were also occurring, phosphorus would then be required by the phytoplankton and bacteria community. Murphy et al (1983) found a reduction in dissolved phosphorus was correlated with an increase in pH and a

175
reduction in calcium but not necessarily with primary production or algal biomass. The resulting phosphorus limitation produced a rapid uptake of radiophosphorus by particulate material.

The main extrinsic source of phosphorus to the ponds is from atmospheric input, weathering of rocks and enrichment by wildlife. The sediments of the shallow ponds could be an important sink of phosphorus. With the mixing depth of the ponds extending to the sediments all summer and the system being aerobic, it would be plausible to assume little return of phosphorus from the sediments although physical processes, such as diffusion and wind currents, may result in some phosphorus return to the water.

The presence of permafrost within the sediments of the tundra ponds keeps the sediments cool even during the summer which slows down mineralization of organic compounds and organic complexes (Hobbie 1980). After the scavenging affect of calcite on phosphorus, the complex sediments out. In organic rich waters further complexing of the phosphorus and calcium may occur. Differences in organic content between the rock bluff and tundra ponds may help to explain differences in their phytoplankton composition. It would be interesting to continue experiments on phosphorus-calcium-phytoplankton interactions within the rock bluff ponds.

Phosphorus uptake is an energy dependent reaction and algae by either photosynthesis or respiration can supply the
necessary energy (Nalewajko and Lean 1980). Phosphorus adsorption by calcite is dependent on pH. So further research is also required to study diurnal and seasonal variations in phosphorus uptake, calcium concentration and photosynthesis and respiration and their effects on the growth and periodicity of phytoplankton in tundra ponds.

Zooplankton may also exert a strong control on the phytoplankton-phosphorus interaction. When zooplankton were removed from subponds in Barrow, Alaska phytoplankton productivity and biomass immediately increased. Alexander et al. (1980) concluded that high densities of zooplankton exhibited strong grazing pressures on the phytoplankton community. The high filtering rates of Daphnia were used to explain the high algal productivity and yet low algal biomass in the ponds. High grazing pressures and high rates of nutrient regeneration would then favor the smaller, faster growing phytoplankton (Reynolds 1984) which dominated all the Churchill ponds, and all arctic ponds (Rigler 1973; Hobbie 1980).

In the Churchill area the tundra ponds are phosphorus limited because of the competition between the biological and non-biological compartments. Potassium phosphate added to the surface of the ponds immediately increases the total dissolved and soluble reactive phosphorus concentrations. Within minutes only a fraction of the added orthophosphorus remains in the dissolved fraction probably as a result of the scavaging effect of the calcium carbonate.
When only one addition of phosphorus was made to the ponds within a few days no soluble reactive phosphorus was detected. Neither productivity nor biomass responded to the loading. Basically the overall biomass must be related to total nutrient stocks and if over the season one pulse shows no difference in orthophosphorus then the stocks are not available. A small infrequent perturbation such as a single addition of phosphorus would not result in a biomass change since it could easily become buffered by non-density dependent factors such as calcium concentrations and environmental factors which occur on daily frequencies.

When phosphorus was added routinely, productivity increased although biomass did not. The increased levels of soluble phosphorus over the season made more phosphorus available to the phytoplankton possibly by saturation of the calcium. Increased productivity indicates that the phytoplankton were able to recognise the phosphorus but because it was not in continuous supply the increased productivity was not channelled into increased biomass. Harris (1980) states, "An external perturbation sets into motion a whole series of responses. If the perturbation is sufficiently small or rapid, then purely physiological responses will take care of the stimulus. If however, the stimulus is longer lasting or of greater magnitude, then the responses will go deeper and deeper until ultimately growth rate and community structures will be affected". Therefore to observe changes in composition and biomass, phosphorus
loading would have to become more frequent probably approaching a continuous flow. Therefore, the ponds were regulated by non-density dependent factors which could only be uncoupled if density dependent factors altered the availability and probably the utilization of phosphorus. Single nutrient loading-biomass models do not apply to the arctic ponds studied at Churchill, Manitoba.
CHAPTER FOUR

NUTRIENT ADDITIONS TO BAG ENCLOSURES
INTRODUCTION

Nitrogen, phosphorus and silica—the latter in the case of diatoms and some chrysophytes—are macronutrients which are most often limiting to phytoplankton growth. The most frequently cited ratio of N:P for phytoplankton nutrient requirements is 15:1 (Fuhs et al. 1972). In typical phytoplankton diatoms, the element silica constitutes 10 to 30 per cent of the dry weight (Lund 1965). A reduction in concentration or alteration of nutrient ratios could possibly limit phytoplankton growth. To test whether the phytoplankton biomass in the tundra is limited by the availability of macronutrients: phosphorus, nitrogen, silica and carbon were added to phytoplankton samples and enclosed in plastic bags containing filtered pond water.

Phosphorus occurs in natural waters mainly as inorganic soluble reactive phosphorus or in organic compounds. Dissolved phosphates are derived from weathering of phosphatic minerals present in catchment soils. Orthophosphorus, measured as soluble reactive phosphorus, is the form of phosphorus preferred by phytoplankton.

Phosphorus is a main component of nucleic acids and of adenosine triphosphate. Phosphate uptake can occur rapidly via a specific transport system and phosphorus may be stored in vacuoles and in the cytoplasm for utilization during periods of low external phosphorus concentration (Rigler 1964). Under phosphorus starvation, cells initially utilize
stored orthophosphorus and when depleted no further growth occurs.

Uptake of nutrients are explained by the Monod equation, describing Michaelis-Menten enzyme kinetics, when steady state conditions are similar. Therefore when limiting nutrients are added an increase in phytoplankton biomass occurs. But under non-steady state conditions the half-saturation constants for growth are generally lower than for uptake (Tilman and Kilham 1976). The uncoupling of growth from uptake often occurs because of variations in the environment. Physiological or community responses, density dependent factors, serve to buffer the growth rate of the population against these fluctuations (Harris 1980).

Nitrogen may limit phytoplankton growth seasonally or may limit specific plankton. The principal requirement for nitrogen by algae is in the synthesis of amino acids and proteins. Several forms of nitrogen are available to algae in freshwaters. These forms of nitrogen include nitrate, nitrite and ammonia ions as well as dissolved organic nitrogenous compounds. Plankton can utilize nitrate, nitrite and ammonia (Anita et al. 1975), through the mediation of enzymes in the plasmalemma. Certain cyanobacteria can fix atmospheric nitrogen dissolved in the water under a normally impoverished nitrogenous state. Nitrogen may limit phytoplankton growth especially when phosphorus concentrations are relatively high such as in temperate eutrophic lakes or when nitrate is depleted in the
epilimnion during summer (Reynolds 1978).

Internal concentrations of carbon, nitrogen and phosphorus must be maintained for maximum phytoplankton growth and maintenance. The ratio of C:N:P for phytoplankton is about 100:15:1 (Fuhs et al. 1972). A carbon source was therefore included in the experiment as carbon dioxide flux can be relatively high and can result in periods of imbalance due to carbon dioxide utilization or production (Round 1981).

Silica content in freshwater is limited by the rate of rock and soil weathering, water flow and solubilization of sediments. Diatom populations (Reynolds 1984). Silica is present in solution in the form of orthosilicic acid. Although methods to determine silica concentration often measure only soluble reactive silica, Golterman (1967) showed that diatoms could also utilize colloidal silica. Orthosilicic acid, required for the formation of diatom valves during cell division, is transferred from the water into an intracellular pool by a carrier enzyme located at the cell surface. Soluble reactive silica is used up rapidly during fast diatom growth and may become limiting (Pearsall 1932; Kilham and Titman 1976; Reynolds 1973).

The Churchill tundra ponds may become phosphorus limited by the calcite formations discussed in Chapter Three. To test whether the tundra ponds were generally nutrient limited nitrogen, phosphorus, silica, and carbon were added to bag enclosures containing natural phytoplankton populations. The potential growth rate of
phytoplankton within each bag was calculated as a measure of response by the phytoplankton to nutrient additions assuming a nutrient is not limiting if an increase in the nutrient produces no significant stimulation in algal growth (Gibson 1971). Growth rate of phytoplankton was measured from calculated biomass data as the change in biomass over the incubation period. A change in nutrient ratios by the addition of one or two nutrients could also influence the composition and dominance of phytoplankton assemblages (Kilham and Kilham 1980). Changes in phytoplankton assemblages were also observed.

The use of clear plastic bags were both a disadvantage and an advantage to the study of nutrient limitation. Sakshaug (1980) summed up the more important sources of error as follows:

i) Water samples have to be collected and transferred into flasks or impermeable bags. The bags are then returned to their point of collection in order to keep the experimental environment the same as the natural one. This invokes considerable handling and the possibility of exposing the phytoplankton to sudden changes in the environment.

ii) If zooplankton are removed by sieving the enclosed phytoplankton will exhibit growth characteristics approaching those of a batch culture. In warm oligotrophic waters phytoplankton growth may result in nutrient deficiency whereas in eutrophic waters phytoplankton may
exhibit a considerable increase in biomass.

iii) For long incubation times, growth of phytoplankton and/or bacteria on the walls of the bags may interfere with measurements.

These errors were reduced by initially diluting the samples and then exposing the phytoplankton to short incubation times (6 days). The bags provided a quick and inexpensive method of estimating nutrient limitation by phytoplankton in Churchill tundra ponds.
MATERIALS AND METHODS

Water and bulk phytoplankton samples for the limiting nutrient assay were obtained from a non-fertilized tundra pond in August of 1980. Clear polyethylene bags were filled with 900-mL of pond water which had previously been filtered through Whatman GF/C glass fiber filters. A 100 mL bulk phytoplankton sample was then added to each bag after filtration through a zooplankton net.

Phosphate phosphorus, \( \text{KH}_2\text{PO}_4 \), silicate silica, \( \text{SiO}_3 \), nitrate nitrogen, \( \text{KNO}_3 \), and sodium bicarbonate were added in various combinations to the bags. The chemicals were initially dissolved in distilled water and then added to the bags in final concentrations of 5, 25, 125 and 625 \( \text{ug.L}^{-1} \). Four control bags were set up in which the addition of chemicals was omitted. For additions of only phosphate phosphorus 1 L Pyrex culture flasks were used. Duplicates were set up for all chemical combinations.

The top of the bags were drawn together by a plastic tie to allow gaseous exchange with the atmosphere and to prevent spilling of the contents. Bags were suspended in the pond by attachment to overhanging bushes. This allowed for in situ temperature and light changes. Phytoplankton samples were obtained by removing the bags from the water, mixing the contents and pipetting a 10 mL subsample. Samples were obtained on day one and day six. Samples were preserved and enumerated as previously described in Chapter One.
Results

Percent change in phytoplankton composition after 5 days incubation following all nutrient additions are listed in Appendix XI.

When single nutrients were added in low concentrations (< 25 ug.L⁻¹) to individual bags, the phytoplankton populations within the bags increased in biomass compared with the control (Fig. 4.1). An increase in Bacillariophyceae, in particular *Praegilaira construens* and *F. crotonensis*, was observed for additions of 5 ug.L⁻¹ phosphate phosphorus and nitrate nitrogen. An increase in Chlorophyceae, especially *Chlamydomonas* spp., *Oocystis borgei*, and *Tetraedron minimum*, was observed in the bag into which sodium bicarbonate was added. Silicate silica produced an increase in Chrysophyceae, primarily *Chrysochromulina parva*. The increases in biomasses were mainly in the <5 um size range (Fig. 4.2, 4.3, 4.4, 4.5). Only the addition of 5 ug.L⁻¹ phosphate phosphorus produced an increase of species in the >30 um size range. Overall, however, growth rates did not vary significantly from the control (t-tests, p>0.10, n=2).

Combined additions of nitrate nitrogen, and phosphate phosphorus produced the maximum increase in phytoplankton biomass of all the nutrient combinations when concentrations of 125 and 625 ug.L⁻¹ were used in 1:1 ratios (Fig. 4.6) (t-tests; 125N:125P, t=6.422, n=2, p<0.10; 625N:625P,
Figure 4.1: Effect of added nutrients (ug. L\(^{-1}\)) on phytoplankton growth rate. Growth rate = \( \ln \) (Biomass after 5 days - Biomass at time zero). Bar indicates minimum and maximum values.
Figure 4.2: Size distribution of phytoplankton population after 5 days incubation following a 5 ug.L\(^{-1}\) phosphate-phosphorus addition.
Figure 4.3: Size distribution of phytoplankton population after 5 days incubation following a 5 ug.L⁻¹ nitrate-nitrogen addition.
5N

LOG # CELLS

0 1 2 3 4 5

MEAN SPHERICAL DIAMETER (µm)

CONTROL
Figure 4.4: Size distribution of phytoplankton population after 5 days incubation following a 5 ug.L$^{-1}$ silicate-silica addition.
Figure 4.5: Size distribution of phytoplankton population after 5 days incubation following a 5 ug.L$^{-1}$ sodium bicarbonate addition.
t=38.167, n=2, p<0.05). For those combinations there was a decrease in Chlorophyceae with either an increase in Bacillariophyceae (Pinnularia spp., Synedra ulna, Mastaloria smithii) or Chlorophyceae (Oocystis solitaria, Zygnema pectinatum). There was an increase in abundance of species in all sizes (Fig. 4.7).

Combined additions of nitrate nitrogen and sodium bicarbonate produced an increase in phytoplankton biomass for most combinations where nitrate nitrogen concentrations were > 25 ug.L\(^{-1}\) (Fig. 4.8). Changes in percent total biomass for the algal classes over the 5 days were not consistent between bags. Generally though, Bacillariophyceae increased whereas Chrysophyceae and Chlorophyceae decreased. Some representative diatom species include Pinnularia spp., Fragilaria construens, Synedra ulna and Nitzschia spp.. With the addition of nitrate nitrogen and sodium bicarbonate the species abundance increased and the cell size distribution of the phytoplankton population widened (Fig. 4.9).

Low concentrations of sodium bicarbonate (5-25 ug.L\(^{-1}\)) combined with various concentrations of phosphate phosphorus produces increases in phytoplankton biomass (Fig. 4.8) (t-tests; 5C:125P, t=13.459, n=2, p<0.05; 25C:5P, t=168.662, n=2, p<0.01; 25C:625P, t=25.191, n=2, p<0.05). The increases were characterized by increases in Bacillariophyceae, mainly, Mastaloria smithii, Synedra ulna, Fragilaria crotonensis and Cyclotella spp.. Biomass increases were reflected in an increase in abundance of species over a size range similar
Figure 4.6: Effect of added nutrients (ug. L\(^{-1}\)) on phytoplankton growth rate. Growth rate = Ln (Biomass after 5 days - Biomass at time zero). Bar indicates minimum and maximum values.
NUTRIENTS ADDED (µg L⁻¹)

GROWTH RATE
LN(Numl⁻¹)}
Figure 4.7: Size distribution of phytoplankton population after 5 days incubation following a 125 ug.L\(^{-1}\) nitrate nitrogen and 125 ug. L\(^{-1}\) phosphate phosphorus addition.
Figure 4.8: Effect of added nutrients (ug. L\(^{-1}\)) on phytoplankton growth rate. Growth rate = Ln (Biomass after 5 days - Biomass at time zero). Bar indicates minimum and maximum values.
Figure 4.9: Size distribution of phytoplankton population after 5 days incubation following a 25 ug.L\(^{-1}\) nitrate nitrogen and 5 ug. L\(^{-1}\) sodium bicarbonate addition.
to the control bags (Fig. 4.10).

Combinations of silicate silica with either sodium bicarbonate, nitrate nitrogen or phosphate phosphorus did not produce significant increases in biomass (Fig. 4.11) (t-tests, n=2, p>0.10), although there was generally either an increase in Bacillariophyceae or Chlorophyceae. Representative species included Stephanodiscus astea, Mastalonia smithii, Synedra ulna, Oocystis borgei, O. crassa, Eudorina elegans and Spirogyra spp. Combinations of silica with phosphorus and nitrogen showed a decrease in species abundance over the algal size range whereas silicate silica and sodium carbonate produced a wider size spectra than controls (Fig. 4.12, 4.13, 4.14).
Figure 4.10: Size distribution of phytoplankton population after 5 days incubation following a 5 ug.L\(^{-1}\) sodium bicarbonate and 125 ug.L\(^{-1}\) phosphate phosphorus addition.
Figure 4.11: Effect of added nutrients (ug. L⁻¹) on phytoplankton growth rate. Growth rate = \ln \left( \text{Biomass after 5 days} - \text{Biomass at time zero} \right) \cdot \text{Bar indicates maximum and minimum values.}
Figure 4.12: Size distribution of phytoplankton population after 5 days incubation following a 125 ug.L\(^{-1}\) silicate-silica and 125. ug.L\(^{-1}\) phosphate phosphorus addition.
Figure 4.13: Size distribution of phytoplankton population after 5 days incubation following a 125 ug. L\textsuperscript{-1} silicate-silica and 125 ug.L\textsuperscript{-1} nitrate nitrogen addition.
Figure 4.14: Size distribution of phytoplankton population after 5 days incubation following a 125 ug. L$^{-1}$ silicate silica and 25 ug.L$^{-1}$ sodium bicarbonate addition.
DISCUSSION

The addition of nutrients to phytoplankton populations in bag enclosures suggest that the phytoplankton in tundra ponds are potentially limited by phosphorus and nitrogen when added in equal amounts. Combined additions of nitrogen and phosphorus produced an increase in phytoplankton biomass. This is similar with eutrophication studies by Kalff (1965), Schindler et al. (1974), Schindler (1977) and Reynolds (1978). Kalff (1965) found that additions of nitrogen and phosphorus during the summer increased phytoplankton productivity whereas phosphorus alone did not. During the spring there was sufficient concentrations of nutrients in the melt-off to support the algal growth. The experiments were repeated in ponds with inorganic and organic bottoms. Ponds with bottoms covered with an organic layer showed no response to N and P additions.

In sewage polluted Meretta Lake, large inputs of nitrogen and phosphorus increased phytoplankton biomass although neither phosphorus nor nitrogen were returned from the sediments (Kalff and Welch 1974). In another experiment in the Experimental Lakes Area Schindler (1977) found nitrogen and phosphorus additions produced dense standing crops of phytoplankton although he could not predict what composition of phytoplankton would respond. In one lake Chlorophyceae became dominant whereas Bacillariophyceae, and Cyanophyceae became dominant in the other lake.

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Rhee (1978) found that differences in optimum N:P ratios for phytoplankton within a freshwater system influenced their mutual competition along N:P gradients. Reduction of the N:P ratio in the water by increasing phosphorus levels caused phytoplankton populations to become dominant in nitrogen fixing cyanobacteria (Schindler 1977; Reynolds 1978). A high N:P ratio favored chlorophytes or chrysophytes. Over the short incubation period, Bacillariophyceae and Chlorophyceae were favored. It is obviously difficult to say which algal classes would have become dominant given an extended period of incubation.

Silica additions did not increase the phytoplankton standing crop although it did favor dominance by Bacillariophyceae when in the presence of phosphorus or Chrysophyceae when added alone. Silica is used by diatoms and some Chrysophyceae for cell wall formation. Evidence suggests that diatoms take up little more silicic acid than is required to complete cell division and that luxury uptake rarely occurs (Lund 1965). Lund (1964) showed that Asterionella in Windermere was reduced after depleting silica concentration during its growth phase. The diatoms were able to survive the low silica concentrations and were potentially able to reestablish themselves when silica concentrations improved.

Carbon limitation is rarely demonstrated during fertilization experiments. The addition of carbon with either phosphorus or nitrogen increased biomass although not
to the same extent as for the addition of nitrogen and phosphorus together. Schindler (1971) found atmospheric invasion of CO₂ sufficient to support the high phytoplankton standing crop caused by inputs of nitrogen and phosphorus. He could not explain the increased production when carbon and phosphorus were added. Carbon dioxide in water may be limiting though due to relatively high pH and/or calcium carbonate precipitation (Reynolds 1984). Although the ponds did not exhibit extraordinarily high pH, the pH was sufficiently high to limit free CO₂ in the waters. There has been some mention that calcium carbonate precipitation does in fact occur in the ponds in which case the addition of sodium carbonate would be of some benefit to the phytoplankton populations.

Generally Bacillariophyceae increased the most in percent total biomass following nutrient additions. An increase in biomass is a result of growth increase minus loss of viable cells. Sedimentation and grazing pressures, both loss process, were reduced for the phytoplankton populations within the bag enclosures. The large non-motile plankton, especially diatoms, have the highest sinking rates of all plankton (Reynolds 1984). As was suggested in Chapter Two vertical mixing of tundra ponds may not be as high as initially assumed. In contrast the phytoplankton populations within the bag enclosures located at the end of the pond were susceptible to any wave or wind action on the surface of the pond. Diatoms are abundant in well mixed systems.
which suspend the cells and recruit new growth from physiologically resting propagules (Reynolds 1984). As was observed silicate-silica did not limit phytoplankton growth and therefore would have supported diatom growth.

Zooplankton were filtered from the bag enclosures at the beginning of the experiment which would have reduced grazing pressures on the phytoplankton populations. The most common zooplankton in the tundra ponds, copepods and cladocerans, readily ingest diatoms (Reynolds et al. 1982; M. Morris personal communication). Reduced grazing and sedimentation pressures on diatoms may explain their increase in growth following nutrient additions.

With an increase in diatoms there was only infrequent increases in size distribution. The size range of all the populations within the enclosures generally remain below 30 um. Filtering the zooplankton samples before inoculation through a zooplankton net could have removed the larger species and/or filamentous algae. Most species had mean spherical diameters less than 30 um. Since most of the diatoms observed were pennate diatoms, the surface area to volume ratio was large and their smallest diameter was less than 30 um. Therefore changes in volume may not be observed as changes in mean spherical diameter distributions. Based on their longest dimension, pennate diatoms are considered netplankton. Pennate diatoms such as Fragilaria spp., Mastalugia smithii and Synedra ulna were common in bags with increased phytoplankton biomass. Although small
phytoplankton and bacteria are favored initially for their rapid colonization and rapid growth where the supply of nutrients is in excess of their demands, it is the larger slow growing forms which are later selected since they are able to live closer to the environmental carrying capacity (Kilham and Kilham 1980).

Competition for nutrients will be the principal density dependent factor most often determining the species competition and population dynamics of phytoplankton populations in equilibrium conditions (Titman 1976; Tilman 1978). Coexistence of species occurs when the growth rate of different species is limited by a different resource or by uncoupling between the resource and the phytoplankton community. Differences in nutrient physiology of species, nutrient supply rates, species specific mortality rates and dependence of these factors on the elements of the physical environment, namely, temperature, light, pH and other nutrients, also encourage coexistence of phytoplankton species. Patchiness in nutrients due to point sources, run-off advection, diel zooplankton migration could also alter the relative abundance of populations based on the populations ability to exploit the limiting resource (Turpin and Harrison 1979).

One disadvantage of using enclosure bags to study nutrient-phytoplankton interactions is the tendency for the system to exhibit growth characteristics approaching those of a batch culture (Sakshaug 1980). Within the bag
enclosures the physical environment is modified and restrained. Under steady state condition, without grazing by zooplankton and chemical complexing from the sediments, the addition of limiting nutrients results in an increase in net growth of phytoplankton. Conversely, in a natural aquatic system environmental perturbations serve to uncouple nutrient uptake from growth over a short period (Harris 1980).

The tundra ponds are generally under non-steady state conditions which would suggest that additions of both phosphorus and nitrogen would have a limited effect on phytoplankton composition and biomass. Phosphorus and nitrogen concentrations in the ponds are generally high in the spring and become reduced during the summer. Nutrient limitation is then more likely to occur in the summer when algal uptake exceeds rate of external supplies. It is therefore possible that the addition of nitrogen and phosphorus to the ponds during the summer could result in increased phytoplankton standing crop. Additions however, must be sufficient to overcome a flux of nitrogen and phosphorus to the sediments and as noted in Chapter Three loadings must be continuous. Phytoplankton growth would then be limited by self-shading or by the limitation of other nutrients. Once the additions ceased one would expect the ponds to probably return quickly to natural conditions because of the scavaging of phosphorus by the calcite and sedimentation to the sediments. Further research should
include experimental fertilization of the tundra ponds with nitrogen and phosphorus together. Zooplankton-phytoplankton-nutrient interactions require further attention.
CONCLUSIONS

Non-density dependent factors tend to regulate phytoplankton composition and biomass in ponds in the Churchill area. The environment was variable diurnally, monthly and yearly in terms of temperature, irradiance, precipitation, wind and nutrient availability. Increased net radiation and reduced precipitation from 1980 to 1981 resulted in an increase in nutrient concentrations in the ponds, yet little change was observed in the phytoplankton biomass. Total dissolved phosphorus, soluble reactive phosphorus and calcium increased in all the ponds in 1981. Differences in pond morphology enhanced the concentration of the nutrients especially in the rock bluff ponds which because of their small surface area: volume ratio showed the largest increases in total dissolved phosphorus, soluble reactive phosphorus, silicate silica, nitrate nitrogen, calcium and salinity. Even with these differences the phytoplankton populations of all the ponds in the Churchill area were similar in composition and biomass with little dominance by any one species or class for any extended period of time.

Nutrients, in particular phosphorus, may not be available for phytoplankton utilization. Calcium concentrations were often greater than 25 mg L⁻¹ and increased over the summer period as the ponds evaporated. Calcium-phosphorus complexing was observed during
temperatures over 12°C. The possibility of calcium reducing phosphorus availability by adsorption and the potential cycling as related to temperature contributed to the similarity of phytoplankton composition between ponds regardless of nutrient concentration differences.

Temporal and spatial variability in phytoplankton abundance and composition operated on microscales of minutes and centimeters. Variability was not due to zooplankton grazing or species specific differences. Phytoplankton abundance was patchy regardless of zooplankton grazing pressures. Phytoplankton species that significantly varied temporally and spatially with phytoplankton abundance included unicellular, colonial, flagellated and non-flagellated species indicating that processes other than growth rates and mobility of the species were responsible for the heterogeneities in phytoplankton biomass and composition.

Rapid changes in phytoplankton distribution were influenced by non-density dependent variables, such as wind stress, since the temporal and spatial scales were too small for the physiological response of the phytoplankton to the changing environment. To provide an estimate of phytoplankton composition and biomass of the whole pond multiple samples were required to reduce horizontal spatial heterogeneities. Also it was determined that sampling procedures were sufficient over the time required to collect multiple samples.
The phytoplankton populations in the tundra ponds were phosphorus limited because of the competition between the biological and non-biological compartments. Potassium-phosphate added to the surface of the ponds immediately increased the total dissolved and soluble reactive phosphorus concentrations in the water. But within minutes the phosphorus entered the particulate fraction possibly because of the scavaging effect of calcium.

When only one addition of phosphorus per year was made to the ponds within a few days no soluble phosphorus was detected. Neither productivity nor biomass responded to the single loading. This suggests that the phytoplankton population was buffered against changes in biomass in response to the phosphorus' addition by non-density dependent factors such as calcium concentrations and meteorological fluctuations which occur on daily frequencies.

When phosphorus was added routinely, productivity increased although biomass did not. The increased levels of soluble phosphorus over the season made more phosphorus available to the phytoplankton possibly by saturation of the calcium. Increased productivity indicated that the phytoplankton were able to use the phosphorus but because it was not in continuous supply the raised levels of productivity were not channelled into a change in biomass. To observe changes in phytoplankton composition and biomass, phosphorus loading would have to become more frequent probably approaching a continuous flow. Therefore, the ponds
were regulated by non-density dependent factors which altered the availability and probably the utilization of phosphorus.

When nutrients were added to phytoplankton population samples within bag enclosures, phosphorus and nitrogen, when added in equal amounts, produced a maximum increase in phytoplankton biomass. Within the bag enclosures the physical environment was modified and restrained. With grazing by zooplankton and chemical complexing from the sediments the change in biomass may not occur as environmental perturbations serve to uncouple nutrient uptake from growth. The tundra ponds are generally under non-steady state conditions which would suggest that further additions of both phosphorus and nitrogen would have a limited effect on phytoplankton composition and biomass unless there was a continuous flow of nutrients into the system.
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APPENDIX I

EQUATIONS

SIMILARITY INDICES

Jaccard's similarity index Washington 1984

\[ = \frac{n_{ij}}{n_i + n_j - n_{ij}} \]

where: \( n_{ij} \) = number of species common to samples \( i \) and \( j \);
\( n_i \) = number of species in sample \( i \);
\( n_j \) = number of species in sample \( j \).

Percent similarity index Washington 1984

\[ = \frac{100 - 100 \sum |a-b|}{100 \sum a + 100 \sum b} \]

where: \( a \) and \( b \) are, for a given species \( i \), percentages of the total samples \( i \) and \( j \) which that species represents. The absolute value of their difference is summed over all species.

PHYTOPLANKTON PRODUCTIVITY

Chlorophyll \( a \) Lind 1979

Chlorophyll \( a \) concentration corrected for
Phaeophytin =
28.9 (abs. before acid) (abs. at 665-750 nm) -
abs. after acid (abs. at 665-750 nm)

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extract volume = \( V_l \) of sample filtered.
path length = \( l \)
= mg. ml\(^{-1}\) lake water

Productivity

\[ \text{mg} \text{C} \text{ml}^{-1} \text{hr}^{-1} = \frac{^{14}\text{C} \text{counted light bottle} - \text{dark bottle}}{^{14}\text{C} \text{added} \times 10^3 \times \text{available} \times \text{bottle volume sample volume} \times 1.06 \times 10^3 \times \text{hr}^{-1} \text{incubated.} \]

Heterotrophy

\[ \text{mg} \text{C} \text{ml}^{-1} \text{hr}^{-1} = \frac{^{14}\text{C} \text{counted dark bottle} - \text{control bottle}}{^{14}\text{C} \text{added} \times 10^3 \times \text{available} \times \text{bottle volume sample volume} \times 1.06 \times 10^3 \times \text{hr}^{-1} \text{incubated.} \]

where: \(^{14}\text{C} \text{added} = 1.22 \times 10^6 \text{ cpm per } 100 \text{ ml labelled solution strength in } \mu \text{g} \times \text{ml labelled solution added per bottle.} \]

\(^{14}\text{C} \text{counted} = \text{scintillation counts-background counts} \times \text{efficiency}^{12} \]

\(^{12}\text{C} \text{available (prod.)} = \text{total alkalinity in } \text{mg} \text{l}^{-1} \text{ determined by titration methods of Rainwater and Thatcher (1960).} \]

\(^{12}\text{C} \text{available (heter.)} = \text{assumed to be 1.0 as glucose concentration unknown.} \]
APPENDIX II
VOLUME FORMULA FOR BIOMASS ESTIMATES

FORMULA

\[ V(\text{sphere}) = \frac{4}{3}\pi r^3 \]

\[ V(\text{cone}) = \frac{1}{3}\pi r^2 h \]

\[ V(\text{double cone}) = \frac{5}{12}\pi r^2 h \]

\[ V(\text{rod}) = \pi r^2 h \]

\[ V(\text{ellipsoid}) = 4\frac{1}{3}\pi r^2 \left(\frac{h}{2}\right) \]

\[ V(\text{parallelepiped}) = Lwh \]

where;

\( r = \text{radius} \)

\( h = \text{height} \)

\( L = \text{length} \)

\( w = \text{width} \)

EXAMPLES

Anabaena, Cosmarium (2xV),
Chlamydomonas

Dinobryon, Staurastrum (6xV)

Ceratium, Synedra, Ankistrodesmus

Oscillatoria, Asterionella,
Pediastrum

Cryptomonas, Gymnodinium, Phacus

Tabellaria, Pinnularia
## APPENDIX III

### PHYTOPLANKTON SPECIES AND VOLUMES

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<th>SPECIES</th>
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### CRYPTOPHYCEAE

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### CYNOPHYTA

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### KANTHOPHYCEAE

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**Chrysothamnaceae**

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**Bacillariophyceae**

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1. sp.
2. sp.
Centronema pseudotussis VOIGT
Ceratoneis artic FUETLING
Ceratoneis sp.
Distichocystis sp.
Diatomella pseudostyles EULenstein
D. plumosa FUETLING
Dimetopus silesiacus var. spirulata H. W. PALFS
Ensignella sp.
Gemmula sp.
Gemmula elongata LINDB. AGARCH
1. G. fusca LINDB. WEEBER
Gemmula vulgaris EGHY
D. vulgaris EGHY
D. vulgaris var. linearis GRUNOW
G. intermedia FUETLING CLEVE
G. linearis EHRL. GRUNOW
Exacmea suprafuerti EMENBERG
Exacmea tricuspidata EMENBERG
Fragilaria capucina DESMAZIERES
2. Fragilariopsis FITTON
F. virescens PALFS
F. pseudonema sp.
G. pseudostyles sp.
Mastagalagia sp. THWAITES
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APPENDIX IV

Species composition of phytoplankton of twenty ponds from Churchill, Manitoba in 1980. Species which contributed .5% (*) and .5% (**) of the total biomass are included.
### APPENDIX V

Seasonal biomass of the most common species that contributed 5% or more to the total phytoplankton biomass at the Churchill ponds, 1980 and 1981.

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Navicula sp. 6.6

31.7.81 Mastalagia smithii var. amphicephala 67.6
Amphipora alata 21.4

23.8.81 Pinnularia sp. 49.5
Amphipora alata 17.2
Merismopedia punctata 9.4
Navicula sp. 9.2

106 20.5.80 Mastalagia smithii var. amphicephala 62.3
Rhodomonas minuta 12.7
Navicula sp. 7.5

7.6.80 Navicula sp. 29.0
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Pediastrum sp. 12.7
Eudorina elegans 11.6
Gonatozygon monotaenium 4.9

30.6.80 Mastalagia smithii var. amphicephala 32.5
Rhodomonas minuta 29.6
Merismopedia punctata 17.4

25.7.80 Rhodomonas minuta 46.0
Diatoma vulgare 27.8
Eudorina elegans 14.6
Navicula sp. 8.5

24.8.80 Synedra ulna 25.2
Merismopedia punctata 16.9
Mastalagia smithii var. amphicephala 12.1

9.7.81 Amphiporora alata 42.9
Pinnularia sp. 8.2
Zygnema pectinatum 8.1
Navicula sp. 7.2
Merismopedia punctata 6.3

19.7.81 Oocystis crassa 35.6
Mastalagia smithii var. amphicephala 26.4
Navicula sp. 10.6
Stephanodiscus astaea 8.2
Amphora veneta 6.8

23.8.81 Stephanodiscus astraera 15.8
Aphanocapsa sp. 15.1
Eudorina elegans 12.6
Pinnularia sp. 12.4
Navicula sp. 10.3
Amphipora alata 7.2
Merismopedia punctata 5.9

130 25.5.80 Oocystis crassa 26.1
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APPENDIX VI

Seasonal fluctuations in size classes (percent total biomass) for 20 ponds in Churchill, Manitoba.

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CHEMICAL DATA

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APPENDIX VIII

PHYTOPLANKTON BIOMASS AND CLASS COMPOSITION

FOR

PONDS 57, 58, 166 AND 170.

Ponds 57 and 58 received one addition of phosphorus, 2.0
gm.m$^{-2}$, in the beginning of the summers of both 1980 and
1981. Ponds 166 and 170 received weekly additions of
phosphorus, 10 x 0.2 gm.m$^{-2}$ during the summers of 1980 and
1981. Each pond was divided into a phosphorus addition side
(P) and a control (C) side. Phytoplankton biomass and class
composition for the phosphorus addition side and control
side of the ponds are illustrated.
APPENDIX IX

PHYTOPLANKTON SIZE FRACTIONS

FOR

PONDS 57, 58, 166 AND 170.

Ponds 57 and 58 each received one addition of phosphorus, 2.0 g.m\(^{-2}\) in the beginning of both summers of 1980 and 1981. Ponds 166 and 170 received weekly additions of phosphorus, 10 x 0.2 g.m\(^{-2}\), during the summers of both 1980 and 1981. Each pond was divided into a phosphorus addition side (P) and a control side (C). Phytoplankton size fractions, based on the mean spherical diameter, of the ponds are illustrated.
Ponds 57 and 58 each received one addition of phosphorus, 2.0 g.m.\(^{-2}\), in the beginning of both of the summers of 1980 and 1981. Ponds 166 and 170 both received weekly additions of phosphorus, 10 x 0.2 g.m.\(^{-2}\), during the summers of both 1980 and 1981. Each pond was divided into a phosphorus addition side (P) and a control side (C).

(see Figures 3.12-3.15 for description of abbreviations)
APPENDIX XI

Percent Change in Phytoplankton Composition after 5 Days Incubation Following Nutrient Additions.

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VITÆ AUCTÓRIS

Isobelle McGregor Gray

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Bachelor of Science: Biology

University of Windsor
Windsor, Ontario
May 1980

Master of Science: Biology

University of Windsor
Windsor, Ontario
April 1987