Physical and Chemical Control of Phytoplankton Nutrient Status in Lakes and Oceans

by

Stephanie Jane Guildford

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PHYSICAL AND CHEMICAL CONTROL OF PHYTOPLANKTON

NUTRIENT STATUS IN LAKES AND OCEANS

BY

STEPHANIE JANE GUILDFORD

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

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Abstract

Nutrient supply ratio and degree of water column stratification determined the type and degree of nutrient-deficiency in both freshwater and marine environments and in both Arctic and temperate water. The interrelationship of physical and chemical factors with phytoplankton nutrient status was studied in four geographically distinct natural systems. Comparison of physical and chemical gradients in relation to phytoplankton nutrient status within each of the four systems and between the geographically distinct systems showed that predictions concerning phytoplankton nutrient status could be made from environmental observations.

In Northwestern Ontario, nine lakes located on the Canadian Shield were studied for five years to determine how lake size affected phytoplankton nutrient status. The lakes ranged in size from small (0.29 km^2) to Lake Superior (82 300 km^2). All nine lakes had TN:TP molar ratios over 65 and were P-deficient. However, the lakes over 20 km^2 were less P-deficient than those under 20 km^2. Deeper mixed layers in the larger lakes resulted in slightly lower mean water column light intensity in the larger lakes, but light did not limit phytoplankton growth. Longer particle retention in the deeper mixed layers of larger lakes allowed greater nutrient regeneration and provided a greater supply of P.

Phytoplankton nutrient status measurements and physical and chemical measurements were made in St. Margaret's Bay, Nova Scotia along a 9 km transect from an inshore aquaculture site to an offshore station during August and September

of 1990. The frequency of N-deficiency was higher in the offshore stations, while the frequency of increased Si uptake was higher near the aquaculture sites.

In a cruise during April 1991 from the continental shelf off Nova Scotia to the Sargasso Sea north of Bermuda, the TN:TP molar ratio was 26 in the upper water column on the Shelf, 36 in Slope water and 50 in the Sargasso Sea. While the nutrient status measurements indicated no N or P deficiency in the well mixed Shelf or Slope water, there were indications of strong N and P deficiency in the stratified Sargasso Sea water.

In the Barrow Strait in the Eastern Arctic, nutrient status measurements were made during August of 1989 and 1991. The TN:TP molar ratio on the Arctic continental shelf was 19. Density stratification from melting pans of ice created shallow well illuminated mixed layers that quickly became strongly N-deficient. Frequent wind events, which mixed the water column, resulted in light-limited photosynthesis due to the deep mixed depths.

Whenever samples were strongly nutrient-deficient, relative carbon turnover (as indicated by photosynthesis at optimum light normalized to particulate carbon) was low. When no nutrient deficiency was indicated, relative carbon turnover at optimum light was high. TN:TP molar ratios greater than 50 resulted in P deficiency in stably stratified water columns while lower values favoured N deficiency.

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Chapter 1

General Introduction

The nutrient status of phytoplankton growing under nutrient-limited conditions is indicated by growth rate (Droop 1974; Healey and Hendzel 1980). By examining the relationship between nutrient status and the wide range of the physical and chemical conditions provided in lakes and oceans, critical factors which control phytoplankton growth can be determined. The objective of this study has been to apply a common suite of nutrient status indicators to a broad range of freshwater and marine environments to obtain a holistic understanding of the control of phytoplankton growth.

Theoretical Basis of Phytoplankton Nutrient Status Measurements

Phytoplankton need light and nutrients to grow. If light is adequate then the nutrient status of the phytoplankton will determine the relative growth rate. Droop (1968, 1970) described the growth rate of nutrient-limited phytoplankton as a function of the internal cell quota of the limiting nutrient:

$$\mu = \overline{\mu}\left(1 - \frac{kq}{Q}\right) \qquad (1.1)$$

which can be written to represent relative growth as follows:

$$\frac{\mu}{\overline{\mu}} = \left(1 - \frac{kq}{Q}\right) \qquad (1.2)$$

where μ is the specific growth rate $\overline{\mu}$ is the specific growth rate at infinite substrate concentration; Q is the cell quota of the limiting nutrient; and kq is the subsistence

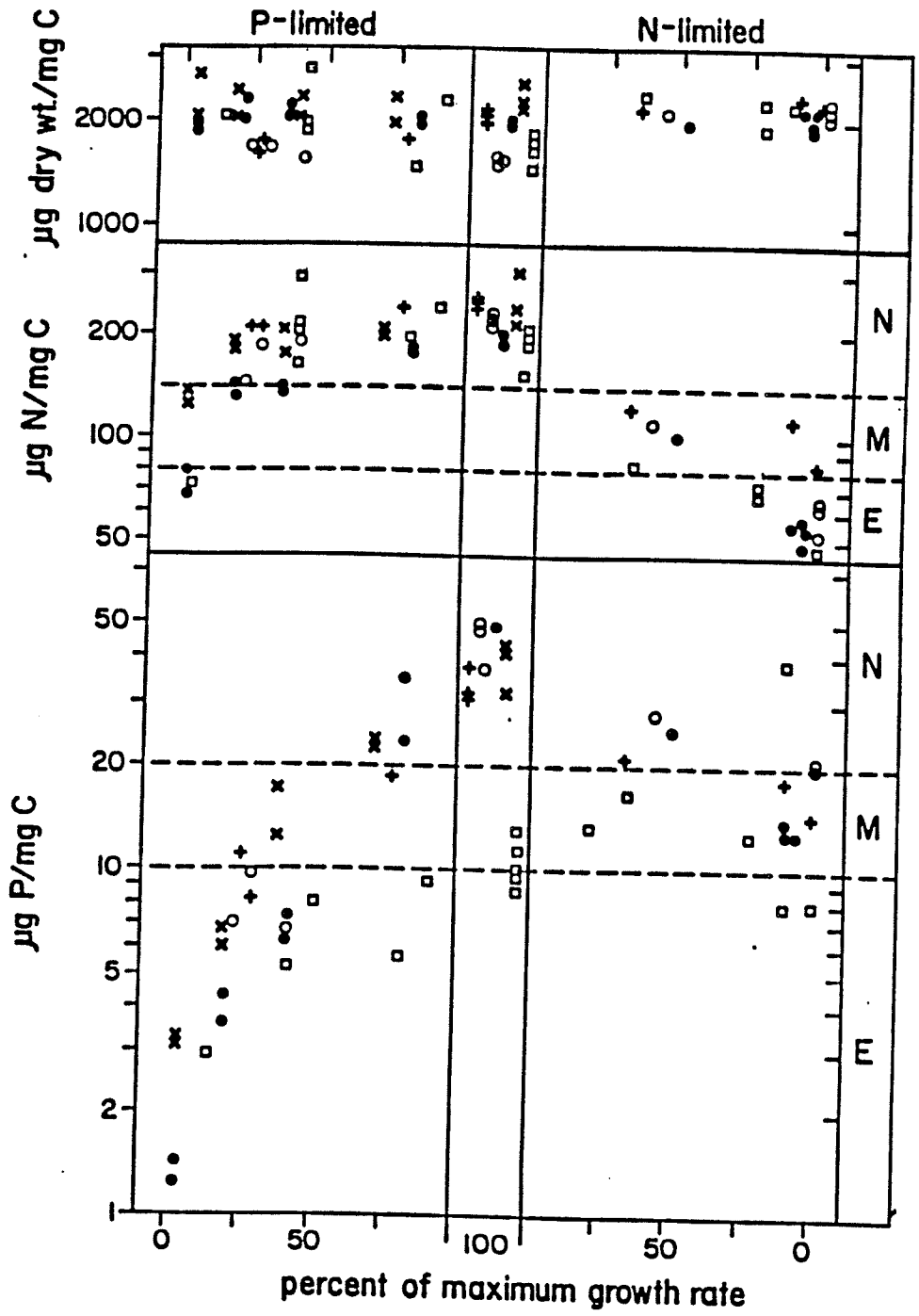
quota, Q at $\mu = 0$. The Droop relationship between growth rate and internal concentration is the basis for nutrient status measurements based on cellular composition. Figure 1.1, taken from Healey and Hendzel (1980), shows that in P- or N-limited cultures five different species of freshwater algae exhibit increasing cell P or N relative to cell C with increasing P- or N-limited growth rate. In the same way that the composition of a cell can be an indicator of nutrient-limited growth, some metabolic cellular processes have been identified that are reliable indicators of nutrient-limited growth. For example, the enzyme alkaline phosphatase is induced in algae under conditions of P-deficiency in steady state culture (Healey and Hendzel 1980). Potential or nutrient-saturated rates of uptake of N or P in N- or P-limited culture were similarly demonstrated to have an inverse relationship to growth rate in many species of freshwater algae in culture (Healey and Hendzel 1979a).

In nature, the cellular growth rate may be only one of many factors controlling the growth of the phytoplankton population. Population growth rate is the sum of growth and loss rates for each species in the community. The following equation describes the population growth rate:

$$\frac{dN}{dt} = \mu N - k_w N - k_s N - k_d N - k_g N \qquad (1.3)$$

where dN/dt is the population growth rate, N is the abundance of a phytoplankton species, μ is the cellular growth rate, k_w is loss due to dilution, k_s is loss due to

Figure 1.1. Particulate dry weight, N, and P per unit particulate C as a function of P- and N-limited growth rates. *Scenedesmus quadricauda* (●), *Chlamydomonas reinhardi* (○), *Anabaena variabilis* (X), *Pseudoanabaena catenata* (+), *Cryptomonas erosa* (□). Horizontal broken lines indicate division points between no (N), moderate (M), and extreme (E) N or P deficiency based on a literature survey (from Healey 1975).


P-limited
N-limited
µg dry wt/mg C
2000
1000
µg N/mg C
200
100
50
N
M
E
µg P/mg C
50
20
10
5
2
1
N
M
E
0
50
100
50
0
percent of maximum growth rate

sinking, k_d is loss due to death, and k_g is loss due to grazing. Although cellular growth rate is the only variable in the population growth rate equation that can be estimated from nutrient status measurements, inferences can be made concerning the other variables in the population growth rate equation once some indication of the cellular growth rate is known. For example, if nutrient status measurements indicate extreme nutrient-deficiency which in turn indicates a low cellular growth rate, then it becomes clear that in order for the population to be maintained, loss factors must be low and population growth rates will be low and approximate cellular growth rates. If cellular growth rate is high and populations are low, this indicates loss factors are important in controlling the population growth.

Factors Modifying Nutrient Status

Factors that affect phytoplankton nutrient status directly include light (light-limitation can replace nutrient-limitation (Healey 1983; Guildford et al. 1987; Pennock and Sharp 1994)), nutrient supply (the lower the concentration of the limiting nutrient, the more nutrient-deficient the algae (Healey 1975)) and nutrient supply ratio (different nutrients may be limiting at different supply ratios (Healey and Hendzel 1980; Tilman 1982; Sommer 1989; Hendzel et al. 1994). These direct effects are clearly demonstrable in culture. In steady state culture, inputs equal losses and the phytoplankton nutrient status is balanced in relation to these steady state inputs and losses (at either high or low relative growth rates). In nature, it has been suggested (Harris 1986) that nutrient status measurements will not be useful

because steady state conditions are rare and high variability of individual factors will allow multiple factors to become important in controlling phytoplankton growth. However, the measurements used can be just as easily indicative of the rapidly changing conditions of a batch culture entering or leaving nutrient deficiency. Their utility is not dependent on steady state conditions. Some clear demonstrations of individual factors affecting phytoplankton nutrient status have been demonstrated in nature. At the Experimental Lakes Areas in northwestern Ontario, manipulation of TN:TP in whole ecosystems demonstrated that nutrient ratios affect nutrient status (Healey and Hendzel 1980). At Southern Indian Lake, a reservoir in northern Manitoba, changes in nutrient supply and mean water column light intensity affected phytoplankton nutrient status (Hecky and Guildford 1984; Guildford et al. 1987). These were both natural environments and not in true steady state but the factors affecting nutrient status were strong enough that clear patterns were seen.

Temperature can control phytoplankton growth in culture when light and nutrient supply are adequate (Eppley 1972; Healey 1983) but in nature, temperature limitation of phytoplankton growth rates is difficult to demonstrate due to inability to eliminate potentially limiting and interacting factors such as light, nutrients and grazing. Temperature in freshwater and temperature and salinity in seawater are major forces determining whether the water column is stratified, the depth of stratification and how long stratification remains intact. For example, tropical lakes have deeper mixed layers than temperate lakes of comparable size. Wind, pressure changes and currents also affect stratification. Stratification affects both light and

nutrient supply. In a shallow mixed layer, mean water column light intensity will be much higher than a deep mixed layer (Hecky and Guildford 1984) for the same light extinction coefficient; thus, shallow mixed layers are more likely to contain nutrient-limited phytoplankton and deep mixed layers are more likely to contain light-limited phytoplankton. Density stratification acts as a barrier to the transfer of nutrients from nutrient-rich deep water to nutrient-poor upper mixed layers. Wind events, spring warming, fall cooling, the presence of ice at higher latitudes all affect nutrient status by affecting nutrient supply from deeper waters.

Nutrients are supplied externally in runoff and precipitation with the influence of runoff decreasing with distance from the land mass. Certain forms of the nutrients carbon and nitrogen, such as CO_2 and N_2 can be fixed directly from the atmosphere in addition to being supplied in other forms in runoff and precipitation. The geology of the land will determine the ratio of nutrients near land, while the ratio of nutrients in precipitation and vertical mixing will be important offshore. The other important source of nutrients, and by far the most difficult to quantify, is regeneration. If the only source of nutrients to phytoplankton was external, as in steady state cultures, it would be straightforward to measure the ambient nutrient concentrations and make predictions about what nutrient will limit phytoplankton growth and to what extent. In nature, regeneration by and differential loss of nutrients to bacteria, protozoa, zooplankton and fish and algae themselves make quantifying nutrient supply rates and nutrient supply ratios very complex. That is why nutrient status measurements are useful. The measurements are usually designed to address the cell or cellular

processes rather than the external concentration of nutrients. It is important to distinguish cellular and cellular process-based nutrient status measurements from enrichment bioassays. Once phytoplankton has been removed from its *in situ* environment and placed in a container (even in very large container), nutrient regeneration processes are affected (Hecky and Kilham 1988).

Uses of Phytoplankton Nutrient Status Measurements

Phytoplankton nutrient status measurements indicate the specific nutrient or nutrients controlling phytoplankton growth (Healey and Hendzel 1980; Hecky and Kilham 1988; Suttle et al. 1991). Knowledge of which nutrient is the growth limiting nutrient for algae in a lake or coastal area is critical for managing water quality and the control of nuisance and toxic algae (Schindler 1977; Sakshaug and Olsen 1986; Lean 1987; Harrison et al. 1990a; Smayda 1990; Lohman and Priscu 1992; Carmichael 1992; Joint and Pomroy 1993). Nutrient status measurements can be used to demonstrate a lack of nutrient-deficiency and indirectly support evidence for limitation by other factors such as light (Hecky and Guildford 1984; Guildford et al. 1987; Agusti et al. 1990; Pennock and Sharp 1994). Nutrient status measurements can be used to understand and make predictions about the outcome of competition between different phytoplankton species (van Donk and Kilham 1990; Sommer 1988, 1989, 1993) because they are an expression of relative growth rates when phytoplankton is nutrient-limited (Hecky and Kilham 1988). Changes in cell biochemical composition brought on by nutrient-deficiency will influence the transfer

of energy and food quality in the food web (Harrison et al. 1990a; Smith 1991; Urabe and Watanabe 1992; Sterner et al. 1993). Phytoplankton nutrient status, through its control of growth rate and cellular composition, influences the accumulation of organic contaminants in the food web (Taylor et al. 1991; Swackhammer and Skoglund 1993) and the responses of phytoplankton to toxic metals (Creed et al. 1990; Twiss and Nalewajko 1992).

Thesis Format

Each chapter in this thesis follows the central theme. Phytoplankton nutrient status measurements are examined along a physical and/or chemical gradient in nature to determine factors controlling phytoplankton growth. In the first paper (Chapter 2), phytoplankton nutrient status is examined in lakes of different size. The lakes, all located in northwestern Ontario, were chosen to be as similar as possible in terms of external nutrient loading and ratios. The size range extends from a 29 ha lake to Lake Superior which is 82,300 km^2 and the world's largest lake in terms of area. The gradient in Chapter 3 is both chemical and physical. Nutrient status measurements were made along transects in a large coastal embayment on the south shore of Nova Scotia. The transects ran from shallow very nearshore sites to deeper sites offshore but still in the embayment. Some of the nearshore sites were sites of aquaculture activity which provided a nutrient supply gradient. Chapter 4 is also coastal marine but the location is Barrow Strait in the Eastern Arctic. The comparison here is stratified and unstratified conditions controlled by melting and

moving pans of ice. In Chapter 5, a transect from the Roseway Bank on Nova Scotia's Continental Shelf across the Continental Slope and Gulf Stream to the mid-ocean gyre of the Sargasso Sea provides a large gradient in physical energy and both nutrient supply and nutrient ratios. Chapter 5 concludes with a comparison of the North Atlantic transect and the Northwestern Ontario Lake Size Study (NOLSS) described in Chapter 2.

Authorship

The NOLSS study (Chapter 2) is a long term multidisciplinary study. I participated in the field work and performed most of the nutrient status measurements, data analysis and interpretation for this paper, but the physical, chemical and photosynthesis data were provided by several of the co-authors. Chapter 2 was published in the Canadian Journal of Fisheries and Aquatic Science, Vol. 51, 1994. Chapter 3 was published in Toxic Phytoplankton Blooms in the Sea edited by T.J. Smayda and Y. Shimizu (1993). Dr. Robinson provided guidance in interpreting the large multivariate set of data from the NOLSS study as well as the Arctic manuscript. Dr. W.G. Harrison, my co-author on the North Atlantic paper, provided guidance during the data collection and made ancillary chemical and physical data available.

Chapter 2

Effects of Lake Size on Phytoplankton Nutrient Status

Abstract

Phytoplankton nutrient status measurements (carbon [C]:phosphorus[P], C:nitrogen[N], C:chlorophyll [chl], N:P, alkaline phosphatase activity, and N debt) were measured for 6 yr in seven remote Canadian Shield lakes and for 2 yr in lakes Nipigon and Superior. These lakes form a logarithmic series in surface area from 29 ha to 8.223 x 10^6 ha (Lake Superior); they all stratify fully during the summer and have water renewal times >5 yr. All lakes were severely P-deficient; however, the large lakes (>2000 ha) were consistently less P-deficient than the small lakes. Chemical factors (total P and dissolved organic C) were good predictors of chl concentrations, but physical factors systematically related to lake size (temperature and mixed depth) were equally good or better predictors of nutrient status. Decreasing mean water column light intensity could not explain decreasing P-deficiency in large lakes. The deeper, more energetic mixed layers in the large lakes apparently led to more efficient within-lake cycling of P, which resulted in decreased P-deficiency. Photosynthesis rates normalized to particulate C were used as an indicator of relative phytoplankton growth rates. These data agreed with the nutrient status indicators in that the small lakes had lower growth rates than the large lakes. Phytoplankton nutrient status and growth rates determine the quality and availability of phytoplankton as food for upper trophic levels, the sensitivity of phytoplankton to toxic elements, and contaminant bioaccumulation in upper trophic levels. When results of experiments or observations in small lakes are applied to large systems, it

should be remembered that large lakes may be more efficient than small ones at recycling nutrients, and may have less nutrient-deficient phytoplankton.

Introduction

Phytoplankton nutrient status measurements have a variety of uses. First, they indicate the specific nutrient or nutrients controlling phytoplankton growth (Healey and Hendzel 1980; Hecky and Kilham 1988; Suttle et al. 1991). Second, they are essential for managing water quality of lakes and controlling nuisance algae (Schindler 1977; Lean 1987; Lohman and Priscu 1992). Third, they can show a lack of nutrient-limitation in situations where factors other than nutrients (e.g. light) control phytoplankton growth (Hecky and Guildford 1984; Guildford et al. 1987; Agusti et al. 1990). Fourth, they can explain competitive interactions of phytoplankton (Van Donk and Kilham 1990; Sommer 1988, 1989, 1993) because they are an expression of relative growth rates when phytoplankton are nutrient-limited (Hecky and Kilham 1988). The nutrient status of phytoplankton is also important functionally because it determines the quality of phytoplankton as food for consumers (Smith 1991; Urabe and Watanabe 1992; Sterner et al. 1993), influences the accumulation of organochlorines in the food web (Swackhamer and Skoglund 1993; Taylor et al. 1991), and determines the responses of phytoplankton to toxic metals (Creed et al. 1990; Twiss and Nalewajko 1992). Therefore, it is important to understand the processes influencing nutrient status.

A primary objective for studying phytoplankton nutrient status along a lake size gradient was to determine whether it is appropriate to apply information from whole ecosystem experimental studies on small lakes such as those in the Experimental Lakes Area (ELA) (Johnson and Vallentyne 1971; Schindler et al. 1990) and from long term ecological research (LTER) sites (Magnuson et al. 1991) to larger lakes of social and economic interest (e.g. Laurentian Great Lakes). Phytoplankton of small, oligotrophic lakes on the Canadian Shield is extremely nutrient-deficient (Healey and Hendzel 1980), whereas the role of nutrients in the Great Lakes is more equivocal (Nalewajko et al. 1981; Harris 1986; Fee et al. 1992). These differences may be a direct function of the size of the system causing differences in physical and chemical conditions. Only by comparing lakes of similar nutrient regimes can the physical effects of lake size be determined.

Conceptual models (Margalef 1978; Legendre and Demers 1984; Harris 1986) state that phytoplankton processes should be increasingly linked to physical processes in lakes of increasing size because large lakes have more vigorous horizontal and vertical water motions and thus produce higher levels of turbulent kinetic energy. An increasing number of physical processes come into play at increasing length scales (Boyce 1974). We examine this observation by determining and comparing phytoplankton nutrient status along a gradient of increasing lake size (28.3 ha - 8.223 x 10^6 ha).

In order to compare lake systems of different sizes, temporal variance must be determined and accounted for by comparative statistical analysis. Measurements

over a range of time intervals can identify relationships or differences among lakes. Temporal events range from short-lived phenomena such as an upwelling event (scale of minutes to days) to longer-term events such as annual hydraulic and nutrient loading. Low frequency events (e.g. El Nino) can only be shown to influence biological processes if the study period is long enough to capture these phenomena. The comparison of factors controlling biological processes on different time scales may lead to important conclusions for lake management. The time scale of sampling used in this study, weeks to 5 yr, neither covered very short time scales, which can be important to phytoplankton, nor long-term events such as decadal climatic variability, but it allowed examination of variability within and between years. The study included some of the warmest years on record as well as average conditions.

During the study, six lakes were sampled 10 times during each open-water season for 6 yr and two large lakes were sampled for 2 yr, producing a total of 400 samples. The lakes were similar with respect to climate, stratification, water residence times (>5 yr), and geology (Canadian Shield) but spanned a considerable range of lake surface areas. The research attempted to capture the natural variability of the study lakes, and the data may provide a benchmark for healthy ecosystems against which suspected perturbations of nutrient cycling in impacted systems can be evaluated.

Methods

Study Area and Design

The nine lakes of the study are located on the Canadian Shield within the north temperate climatic region (Fee and Hecky 1992). Only lakes Nipigon and Superior have permanent human settlements in their basins, but these are few relative to the large size of the lakes. The surface areas of the nine lakes form an approximately logarithmic series from ELA Lake 373 (29 ha) to Lake Superior (8.223×10^6 ha) (Table 2.1).

Field Sampling

The lakes were sampled from ice out (early May in the small ones) to mid October at intervals of ≤3 wk from 1986-1991. Sampling was more frequent immediately after ice out (weekly) and less frequent after stratification in early June (every 3 wk). Samples were usually taken at the deepest part of the lake or, for lakes Nipigon and Superior, at an offshore location chosen on the basis of previous surveys (Fee and Hecky 1992). Integrated whole water samples were taken over 0-3 m, and stored at *in situ* temperatures in the dark for 2-6 h before analyses. Concentrated net plankton samples were collected by taking surface tows with a 10 μm mesh net.

In situ measurements included light and temperature profiles. Light attenuation was measured with a Li-Cor LI-185 underwater quantum sensor (flat

plate, cosine-corrected collector). Daily mean photosynthetically available radiation (PAR) in the mixed layer ($\bar{I}$) was calculated as:

$$\bar{I}=I_s\frac{\int_0^{Z_{mix}} A(z)I(z)dz}{\int_0^{Z_{mix}} A(z)dz} \qquad (2.1)$$

where I_s is the mean solar flux at the surface of the lake during the day (24 h average), Z_{mix} is the mixing depth, I(z) is the fraction of the surface solar radiation that penetrates to depth z, and A(z) is the area of the lake at depth z. I_s was calculated with simulated cloud-free solar data (Fee 1990).

Manual resistance thermometers were used to measure temperature as a function of depth in the NOLSS lakes in 1986 and 1987 and in Lake 373 in all years. A free-falling temperature profiler that measured temperature at depth intervals of ≈0.05 m was used in other lakes and years (R. Brancker Research Ltd., Ottawa, ON). Mixed-layer depths were taken as the maximum rate of change of temperature with depth, and normally exceeded 1.0°C·m^{-1}.

Lab Procedures

Water samples were subdivided for chemical analyses, plankton identification and counting, nutrient status measurements, and photosynthetic rate measurements.

Table 2.1. Morphometric and chemical parameters for the studied lakes. A_0, lake surface area (net water area, not including the area of islands), ha; A_d, area of the terrestial drainage basin (not including the lake area), ha; $(A_d+A_0)/V$, the ratio of total watershed area to lake volume; τ_w, nominal water renewal time, calculated from lake volume, total watershed area, and maps of mean annual runoff, yr; Z_m, maximum depth, m; $\bar{Z}$, mean depth, m; SLD, shoreline development (including islands in shoreline length; not calculated for lakes Nipigon and Superior because of a disparity in map scales); ratio of epilimnion sediment area to epilimnion volulme in midsummer, m^{-1}. The volume of Lake Nipigon was estimated by assuming that its area vs depth curve is the same as Lake Superior's.

	A_0 (ha)	A_d (ha)	$(A_d+A_0)/V$	τ_w (yr)	Z_m (m)	$\bar{Z}$ (m)	SLD	A_e/V_e (m^{-1})
Lake 373	29	54	0.278	13.5	21	10.3	1.54	0.074
Green	89	234	0.474	8.6	19	7.7	2.02	0.081
Orange	167	1,100	0.529	7.8	29	14.4	2.31	0.055
Linge	706	2,980	0.624	6.7	23	8.4	2.84	0.104
Musclow	2,220	32,850	0.821	5.0	46	19.2	3.64	0.032
Sydney	5,750	46,400	0.454	9.1	73	20.0	7.40	0.053
Trout	34,700	71,800	0.226	17.5	49	13.6	10.48	0.059
Nipigon	484,800	2,450,000	0.103	25.6	143	58.5		0.007
Superior	8,223,600	21,000,000	0.024	180.4	403	148.7		0.003

Water samples were analyzed for NO_3, NO_2, NH_4, TDN, (total dissolved nitrogen), TDP (total dissolved phosphorus), SRSi (soluble reactive silicon), air equilibrated pH, conductivity, alkalinity, and DOC (dissolved organic carbon). Unless otherwise specified, chemical analyses were done using the methods of Stainton et al. (1977). Chlorophyll (chl) was determined by filtering 100 mL of water onto a GF/C filter. GF/C filters were chosen to match existing long term data sets. The filter was placed in a glass vial, 10 mL of 95% methanol was added, and the vial was frozen at -10°C in a field freezer and allowed to stand overnight (at least 16 h). The extract was agitated, allowed to settle, and its fluorescence was assayed on a Turner Model 110 fluorometer. The fluorometer was routinely standardized with a chl solution (Sigma Chemicals) the stability of which was verified using an HP scanning spectrophotometer. Chlorophyll was not corrected for phaeopigments. In 1986, chl extracts were not always mixed prior to reading fluorescence; this introduced a serious and inconsistent bias, so data from 1986 are not reported.

Phytoplankton photosynthesis rates per unit volume at different light intensities were measured using the ^{14}C incubator method (Fee et al. 1989). Photosynthesis parameters (P^B_m and α^B) and *in situ* integral photosynthesis were estimated using the computer programs of Fee (1990). P^B_m is the light-saturated rate of photosynthesis per unit of chl, and α^B is the slope of the chl normalized photosynthesis vs light curve as light approaches zero (photosynthetic efficiency). P_{opt} (the non normalized rate of photosynthesis at light levels optimum for

photosynthesis) was normalized to particulate carbon (C) as an independent measure of C turnover and was used as an estimate of relative growth rate.

Phytoplankton nutrient status measurements consisted of four seston composition ratios (C:nitrogen [N], C:phosphorus [P], C:chl, and N:P) and two metabolic indicators (alkaline phosphatase activity[APA] and N debt both expressed per unit chl). During 1987, P debt and $^{32}PO_4$ turnover time were also measured. Particulate C, N, and P samples from both whole water and net samples (net samples were concentrated whole water samples, not dried samples) were filtered onto preignited GF/C filters (Stainton et al. 1977) and kept frozen until analyzed (Stainton et al. 1977). Nutrient composition ratios were calculated on an atom:atom basis for C:N, C:P, and N:P, and an atom:weight basis for C:chl. Because the C:chl ratio changes with nutrient status and is used as an indicator of nutrient status no attempt was made to make a correction for detrital carbon such as Banse (1974).

Alkaline phosphatase activity, an indicator of P-deficiency, was measured fluorometrically (Healey and Hendzel 1979b) using 5 μM ortho-methyl-fluorescein-phosphate as the substrate. Parallel determinations were made of total and soluble activities to distinguish between APA associated with particles and APA in solution; the soluble activity was that passing through 0.2 μm filters. The difference is reported as particulate activity. APA was routinely normalized to chl *a*; however, APA was also normalized to P_{opt} as a biomass-independent nutrient status indicator.

The N debt assay was used in conjunction with particulate C:N ratios to determine N-deficiency. The assay is based on the work of Healey (1977) who

demonstrated that several species of algae took up more ammonium (NH_4^+) in the dark than when N-deficient than when N-sufficient. For the N debt assay, 100 mL of unfiltered sample was enriched with ammonium chloride to yield a final concentration of ≈5 μM N. Ammonium was measured (Stainton et al. 1977) on triplicate subsamples at the beginning and end of the incubation. Samples were incubated in the dark at room temperature (18-24 °C). Dark incubations were done to standardize and it was felt more energy would be available for ammonium uptake in the dark Nitrogen debt was calculated as the nutrient removed over a 24 h period per unit of chl (Healey 1977). Nitrogen debt values for lakes Nipigon and Superior are not reported because of methodological problems with the NH_4^+ analysis. Phosphorus debt was measured in a similar way to N debt except that potassium dihydrogen phosphate was added (final concentration 5 μM). Soluble reactive phosphorus (SRP) was measured on triplicate subsamples passed through GF/C filters (Healey 1975). Phosphorus turnover times were measured using ^{32}P following the method of Lean and Nalewajko (1979). Statistically significant agreement existed among the three P-deficiency indicators (APA, P debt and $^{32}PO_4^{3-}$ turnover times), confirming that all three physiologically based methods agreed on the P nutrient status in these lakes (SJG and LLH, unpubl. data). In subsequent years, P nutrient status was measured using APA per unit chl. Elemental composition of the seston was measured using both whole water and net samples over the duration of the study. Paired t-tests of the ratios indicated that there was no significant difference between the two types of samples (SJG and LLH, unpubl. data). The limits for the

various types and degrees of nutrient-deficiency indicated by both the seston composition ratios and metabolic assays are given in Table 2.2 (Healey and Hendzel 1980).

Data Analysis

Data were ln- or ln+1-transformed to achieve more normal distributions and variances independent of their means and to deal with zero values (N debt data) (Elliott 1983; Hanna and Peters 1991). Bartlett's test (Steel and Torrie 1960) was used to test the hypothesis that variances were homogeneous (HGV) and analysis of variance (ANOVA) was used to test the hypothesis that means were equal. When the assumption of HGV was not met, 0.001 was chosen as the probability below which both hypotheses were rejected. When ANOVA results indicated means were not equal, further comparisons were conducted using Tukey HSD multiple comparison tests (Steel and Torrie 1960). Relative contributions of lakes, years, months, and unexplained variance to the total sums of squares for each variable were calculated from ANOVAs.

Principle components analysis (PCA) was done on ln-transformed, standardized data. The data were standardized because the variables encompassed a wide range of scales. Data were standardized for each variable by subtracting the mean and dividing by the standard deviation (SD). This resulted in all variables having a mean of 0 and an SD of 1. PCA was done on a correlation matrix of the annual means (June 1 - September 30, unless otherwise stated) for each lake. We

Table 2.2. Values indicative of presence or absence or degree of nutrient-deficiency for nutrient status indicators used in this study (from Healey and Hendzel 1980). C, carbon; N, nitrogen; P, phosphorus; chl, chlorophyll *a*; APA, alkaline phosphatase activity.

Indicator	Nutrient	No deficiency	Moderate deficiency	Extreme deficiency
C:N[a]	N	<8.3	8.3-14.6	>14.6
C:P[a]	P	<129	129-258	>258
C:chl[b]	N or P	<4.2	4.2-8.3	>8.3
(APA·chl^{-1})[c]	P	<0.003	0.003-0.005	>0.005
		No deficiency	Deficient	
N:P[a]	P	<22	>22	
N debt[d]	N	<0.15	>0.15	
P debt[e]	P	<0.075	>0.075	

[a] atomic ratio
[b] μmol C:μg
[c] particulate APA, μmol P· μg chl^{-1}· h^{-1}
[d] μmol N· μg chl^{-1}
[e] μmol P· μg chl^{-1}

hypothesized that nutrient status (and other biological variables) are a multivariate function of the physical and chemical variables in a lake. If lakes are ordinated along multivariate axes for physical and chemical variables, then it should be possible to correlate nutrient status variables (and other biological variables) against these axes. The variables used in the PCA were: total phosphorus (TP), total nitrogen (TN), soluble reactive silicon (SrSi), dissolved organic carbon (DOC), alkalinity (Alk), temperature (Temp), light extinction (Ext), and Z_{mix}. Various rotations were tried and the Quartimax rotation was selected because it gave the best separation of variables. Statistical analyses were done using SYSTAT (Wilkinson 1990).

Results

Natural Variability

For all but two of the variables (P^B_m and α^B), the majority of the explained variation was caused by lake-to-lake differences (Table 2.3). Biological variables (except chlorophyll *a*) had higher proportions of unexplained variation than the chemical and physical variables. No consistent increase or decrease in variation was observed among years for seasonal means of biological, chemical, and physical variables with changing lake size (Fig. 2.1).

Plots of the geometric means (±95% confidence intervals [CI]) for the 5 yr of data for each variable and lake against $\log_{10}$ lake size (Fig. 2.2A, B) emphasized trends apparent in Table 2.3. Total nitrogen, TP, SrSi, DOC, alkalinity, extinction,

Table 2.3. Percentages of the total sums of squares for four categories: lake, year, month, and unexplained. APA· chl^{-1} = alkaline phosphatase activity per unit chlorophyll *a*, (μM P· μg chl· h^{-1}); the elemental ratios C:P, C:N, and N:P are molar ratios; C:chl = carbon:chlorophyll *a* (μM:μg); N debt = nitrogen debt per unit chlorphyll *a*, (μM N· μg chl^{-1}); chl = chlorophyll *a*, (μg· L^{-1}), α^B = the slope of the light-limited part of the photosynthesis-light curve normalized to chlorophyll *a* (μg C· μg chl^{-1}· Ein^{-1}· m^2); P^B_m = the maximum rate of light saturated photosynthesis normalized to chlorophyll *a* (μg C· μg chl^{-1}· h^{-1}); Popt· C^{-1} = the maximum rate of light saturated photosynthesis normalized to particulate carbon (μM C· h^{-1}· μM C); TP = total phosphorus (μM); TN = total nitrogen (μM); SRSi = soluble reactive silicon (μM); Alk = alkalinity (μEq· L^{-1}); DOC = dissolved organic carbon (μM); $\bar{I}$ = mean water column light intensity in the mixed layer (mEin· m^{-2}· min^{-1}); Temp = temperature (°C); Z_{mix} = mixed depth (m); Ext = light extinction coefficient (m^{-1}); Secchi = Secchi disk depth (m).

	Lake	Year	Month	Unexplained
Biological				
APA· chl^{-1}	38	15	4	43
C:P	39	4	6	51
C:chl	62	9	0	29
C:N	27	8	5	60
N:P	16	4	1	79
N debt	12	1	5	82
chl	74	7	1	18
α^B	9	25	8	57
P^B_m	5	12	2	81
Popt· C^{-1}	51	2	0	47
Chemical				
TP	69	4	1	26
TN	84	1	0	15
SRSi	90	3	0	15
Alk	100	0	0	0
DOC	92	2	1	5
Physical				
I	43	2	40	15
Temp	40	8	10	42
Z_{mix}	43	7	9	41
Ext	88	1	1	9
Secchi	77	1	6	17

Figure 2.1. Coefficient of variation for seasonal means (June 1 - September 30, 1987-1991) for biological, chemical, and physical variables plotted as a function of lake size. Lakes Nipigon and Superior are not included. Abbreviations as in Table 2.3.

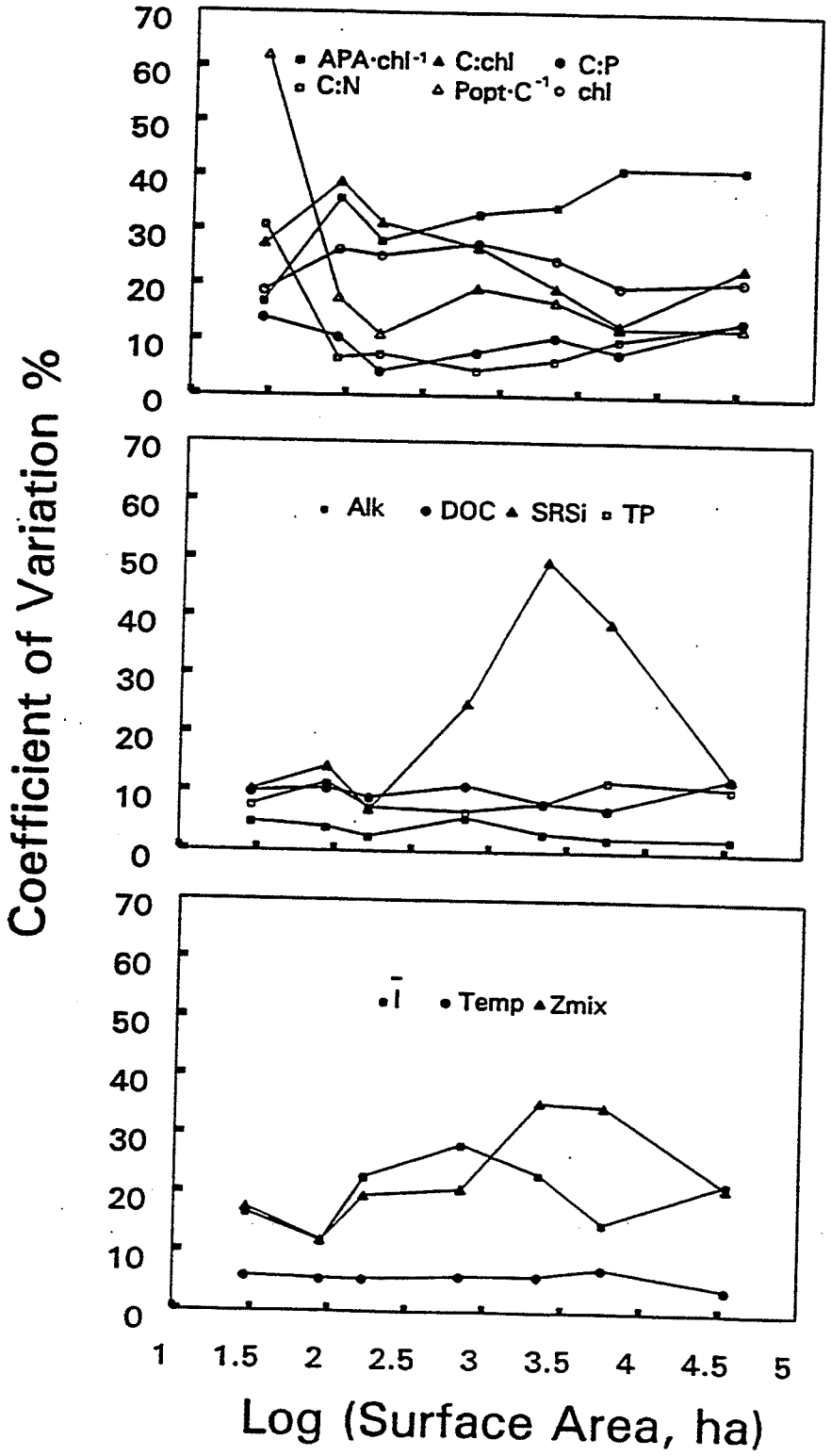

Coefficient of Variation %
APA·chl⁻¹ C:chl C:P
C:N Popt·C⁻¹ chl
Alk DOC SRSi TP
Ī Temp Zmix
0
10
20
30
40
50
60
70
1
1.5
2
2.5
3
3.5
4
4.5
5
Log (Surface Area, ha)

Fig. 1

Figure 2.2. A: Seasonal means and 95% confidence intervals (Cl; vertical bars) for biological variables (June 1 - September 30, 1987-1991) plotted as a function of lake size. Values above dashed lines indicate nutrient deficiency (see Table 2). B: Seasonal means and 95% Cls for chemical and physical variables (June 1 - September 30, 1987-1991) plotted as a function of lake size. Abbreviations as in Table 3.

A

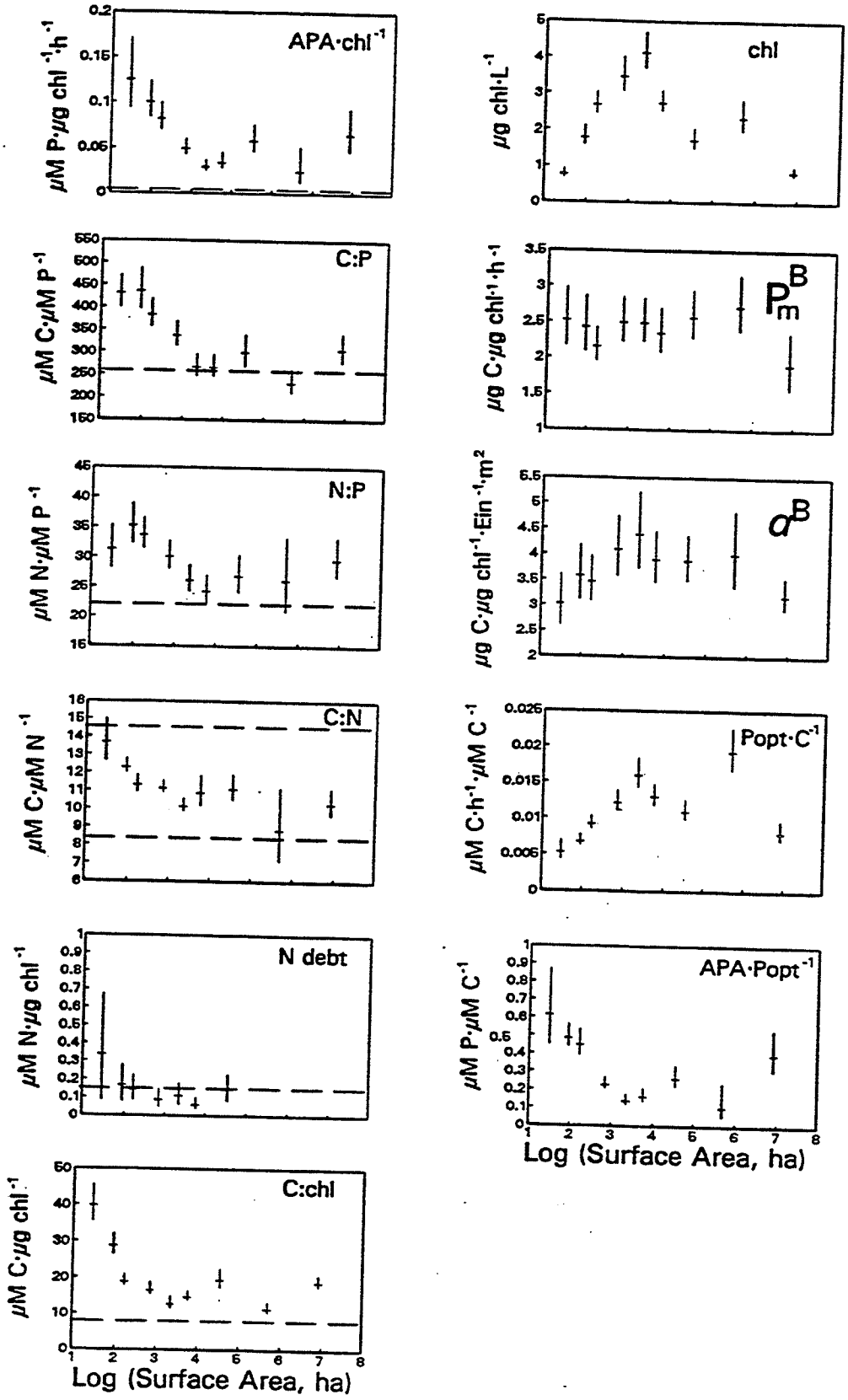

APA·chl⁻¹
μM P·μg chl⁻¹·h⁻¹
chl
μg chl·L⁻¹
C:P
μM C·μM P⁻¹
P_m^B
μg C·μg chl⁻¹·h⁻¹
N:P
μM N·μM P⁻¹
a^B
μg C·μg chl⁻¹·Ein⁻¹·m²
C:N
μM C·μM N⁻¹
Popt·C⁻¹
μM C·h⁻¹·μM C⁻¹
N debt
μM N·μg chl⁻¹
APA·Popt⁻¹
μM P·μM C⁻¹
C:chl
μM C·μg chl⁻¹
Log (Surface Area, ha)
Log (Surface Area, ha)

Fig. 2A

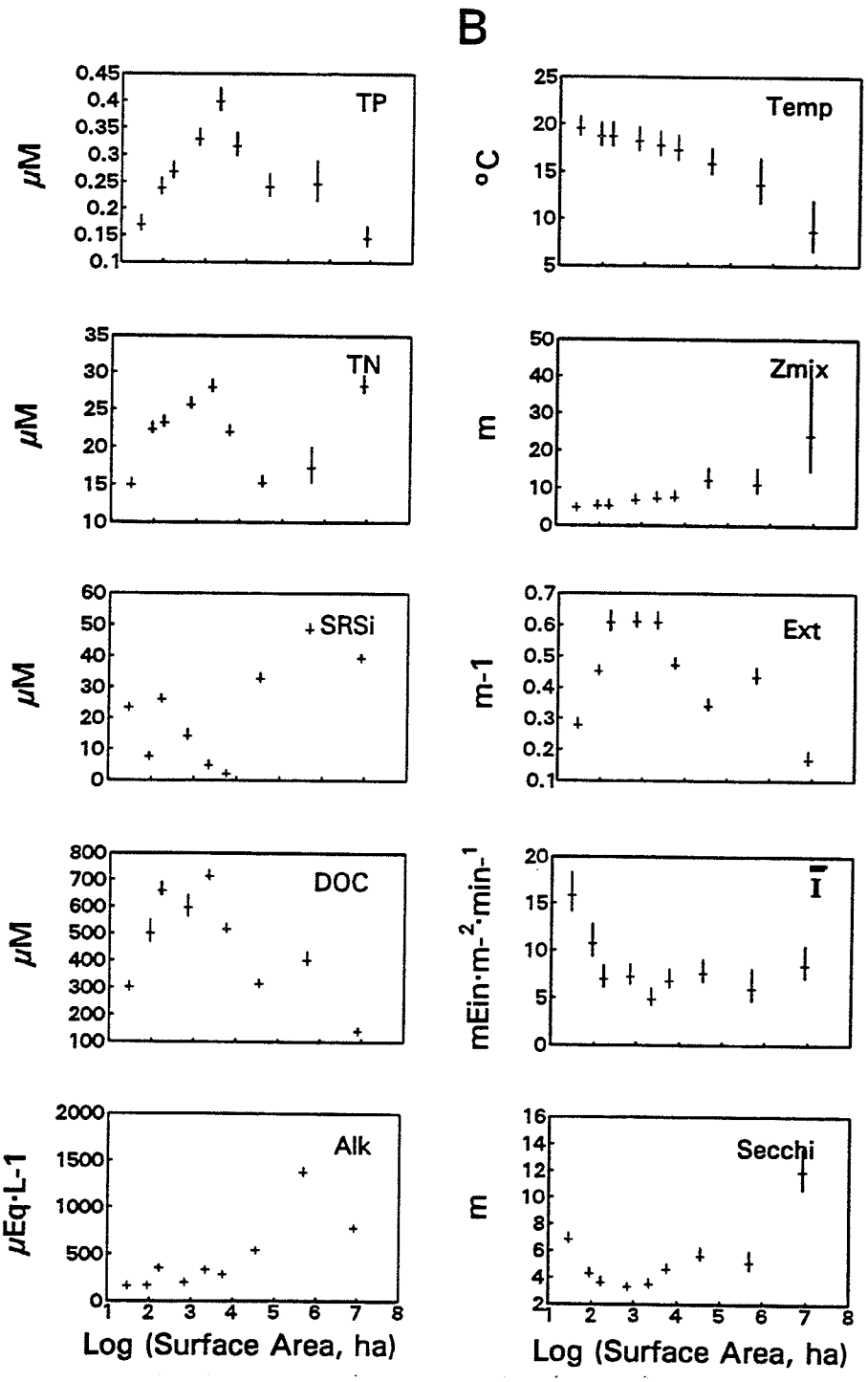

B
TP
µM
Temp
°C
TN
µM
Zmix
m
SRSi
µM
Ext
m-1
DOC
µM
Ī
mEin·m-2·min-1
Alk
µEq·L-1
Secchi
m
Log (Surface Area, ha)
Log (Surface Area, ha)

Fig 2B

Secchi depth, and chlorophyll *a* (Fig. 2.2A, B) have strong lake-to-lake variation and narrow CIs. The remaining variables have wider CIs but, except for P^B_m and α^B, more lake-to-lake than within-lake variation is still evident. The lakes are different from each other for most variables (ANOVA, $P<0.001$; Table 2.4). However, Tukey HSD multiple comparisons for individual variables (not given) indicated no consistent pattern in the lake-to-lake differences.

Phytoplankton Nutrient Status

Nutrient status indicators for P ($APA \cdot chl^{-1}$, C:P, and N:P) indicated that all nine lakes are strongly P-deficient (Fig. 2.2A). Carbon:chl, often used as a general nutrient status indicator (Healey and Hendzel 1980), had a pattern similar to the P nutrient status indicators (Fig. 2.2A). Nitrogen debt and C:N (Fig. 2.2A) indicated that the smallest lake, 373, also bordered on extreme N-deficiency. The remaining lakes were moderately N-deficient according to the C:N ratio but were not usually N-deficient using N debt data, although the spread in the CIs showed that N debt occurred occasionally in all of the lakes. An almost linear relationship appeared to exist between nutrient-deficiency indicators and lake size for the five smallest lakes in the size series (373, Green, Orange, Linge, Musclow) but the relationship became nonlinear as the larger lakes were included (Fig. 2.2A).

Table 2.4. Five year geometric means of biological, chemical and physical variables (June 1 - September 30, 1987-1991). Lake names are abbreviated to their first three letters (see Table 1). Abbreviated variables and their units as in Table 3. HGV = Bartlett's test for homogeneity of variance, ANOVA = analysis of variance.

	373	Gre	Ora	Lin	Mus	Syd	Tro	Nip	Sup	HGV	ANOVA
Biological											
APA· chl^{-1}	0.126	0.102	0.083	0.050	0.030	0.035	0.059	0.026	0.067	0.006	0.000
C:P	434	439	386	340	269	268	302	234	390	0.273	0.000
C:chl	40	29	19	17	13	15	20	12	29	0.000	0.000
C:N	13.8	12.4	11.4	11.2	10.2	11	11.2	8.9	10.4	0.000	0000
N:P	31.5	35.5	33.9	30.3	26.4	24.5	27	26.3	29.8	0.003	0.000
N debt	0.33	0.14	0.13	0.08	0.10	0.05	0.12	NA	NA	0.000	0.007
chl	0.82	1.83	2.73	3.51	4.17	2.79	1.76	2.38	0.89	0.106	0.000
a^B	3.06	3.61	3.50	4.13	4.42	3.93	3.91	4.04	3.22	0.009	0.005
P^B_m	2.55	2.45	2.18	2.52	2.51	2.37	2.6	2.74	1.92	0.082	0.121
$P_{opt}\cdot C^{-1}$	0.006	0.007	0.010	0.012	0.016	0.014	0.012	0.019	0.009	0.000	0.000
Chemical											
TP	0.17	0.24	0.27	0.33	0.40	0.32	0.24	0.25	0.15	0.000	0.000
TN	15.2	22.5	23.4	25.8	28.2	22.2	15.5	17.5	28.5	0.000	0.000
SRSi	23.9	8.1	26.6	14.8	5.2	2.5	33.3	49.0	39.9	0.000	0.000
Alk	176	187	374	220	352	300	562	1395	796	0.007	0.000
DOC	308	507	666	602	719	523	322	407	146	0.000	0.000
Physical											
I	16.06	10.93	7.16	7.4	5.05	6.99	7.77	6.12	8.63	0.875	0.000
Temp	19.70	18.89	18.88	18.39	17.88	17.47	16.01	13.81	8.83	0.000	0.000
Z_{mix}	5.26	5.71	5.78	7.11	7.72	7.89	12.44	11.57	24.37	0.000	0.000
Ext	0.284	0.456	0.613	0.615	0.614	0.478	0.345	0.439	0.174	0.002	0.000
Secchi	7.0	4.4	3.7	3.4	3.6	4.8	5.7	5.2	12.0	0.025	0.000

Chlorophyll a and Photosynthesis

Mean chl *a* concentrations were all in the oligotrophic range (<7.0 $\mu g \cdot L^{-1}$) (Marshall and Peters 1989). Chlorophyll *a* showed a mirror image to the pattern of the P-deficiency indicators (including those not normalized to chl): an almost linear increase with increasing lake size for the five smallest lakes but then a decrease in the larger lakes (Fig. 2.2A). Only the photosynthetic parameters, P^B_m and α^B, didnot vary significantly among lakes. Tests of the hypothesis that no lake-to-lake differences exist in means for each variable indicated that only P^B_m, α^B, and N debt had probabilities >0.005 that their means were equal (Table 2.4). P_{opt} normalized to particulate C and APA normalized to P_{opt} (Fig. 2.2A) exhibited the same distribution over lake size as the nutrient status indicators, i.e. a linear change with size in small systems, and a plateau or reversal at larger sizes.

Chemical Variables

Total P (Fig. 2.2B), like chl *a* and the P nutrient status indicators (Fig. 2A), increased with increasing lake size for the five smallest lakes, but decreased in the larger lakes; Lake Superior had the same mean TP as Lake 373. The mean TN trend was similar to that of TP except that Lake Superior had the highest TN. Green, Musclow, and Sydney lakes had low Si. The DOC trend was similar to TP, whereas alkalinity increased with lake size (Fig. 2.2B).

Physical Variables

Temperature and Z_{mix} were clearly size related (Fig. 2.2B). Light extinction remained relatively constant within each lake (Fig. 2.2B) and was highly correlated with DOC (Fig. 2.3), indicating that DOC is an effective attenuator of PAR in all the lakes. I, which is calculated from extinction and Z_{mix}, was not related to lake size; the smallest (373, Green) and largest (Superior) lakes had the three highest mean water column light intensities (Fig. 2.2B). The lowest mean I occurred in Musclow Lake, which also had the lowest extinction value and highest DOC.

Principle Components Analysis of the Physical Chemical Variables

The first principle components axis (PCA1), which explained 41% of the total variance, primarily contained Ext, TP, and DOC (Fig. 2.4, Table 2.5). PCA2, which primarily contained Alk, Z_{mix}, and Temp explained 33% of the total variance. PCA3 (SrSi) and PCA4 (TN) each explained 11% of the variance. The PCA analysis revealed that different years grouped tightly together for individual lakes (Fig. 2.4), supporting the fact that variation caused by year-to-year differences was much less important than the lake-to-lake differences for the variables measured (Table 2.3).

The highest loadings on PCA1 (Ext, TP, DOC) were essentially chemical variables; although Ext is a physical measurement, Ext is highly correlated to the chemical variable DOC (Fig. 2.3). Two of the three highest loadings on PCA2 (Z_{mix}, Temp) were physical variables. In these lakes, Temp and Z_{mix} were correlated with lake size ($r=0.941$, $P<0.001$, $n=9$ and $r=0.809$, $P<0.01$, $n=9$, respectively), so a

Figure 2.3. Relationship between dissolved organic carbon (DOC) and light extinction in the nine study lakes. Values are seasonal means (June 1 - September 30, 1987-1991). The first character of each symbol is the first letter of the lake name, except for Lake Superior (Su). The letters are followed by the years (86 = 6, 87 = 7, etc.)

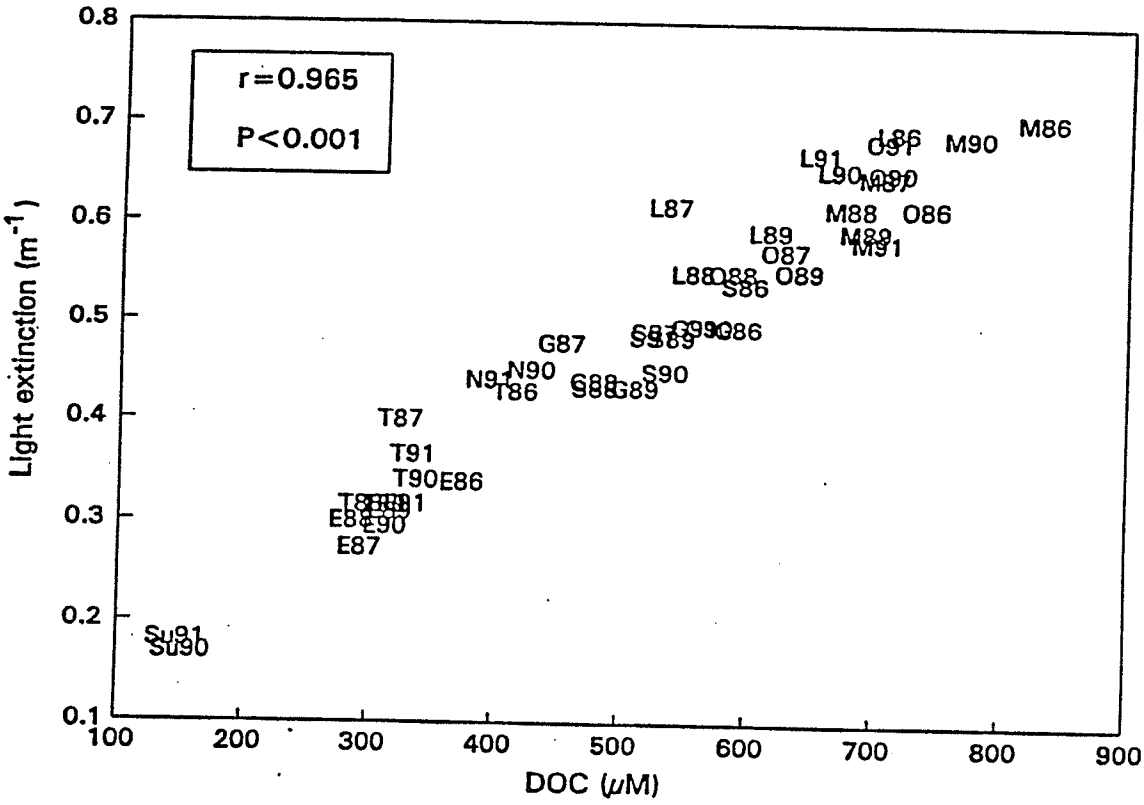

r=0.965
P<0.001
Light extinction (m^{-1})
DOC (μM)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
100
200
300
400
500
600
700
800
900
M86
M90
L91
L87
M88
O86
L89
O87
M91
O89
S86
G87
N90
S90
T87
T91
T90
E86
E87
Su91
Su90

Figure 2.4. Lake-year loadings for the first four axes of the principal components analysis. The first character of each symbol is the first letter of the lake name, except for Superior (Su). The letters are followed by the years (87 = 7, 88 = 8, etc.)

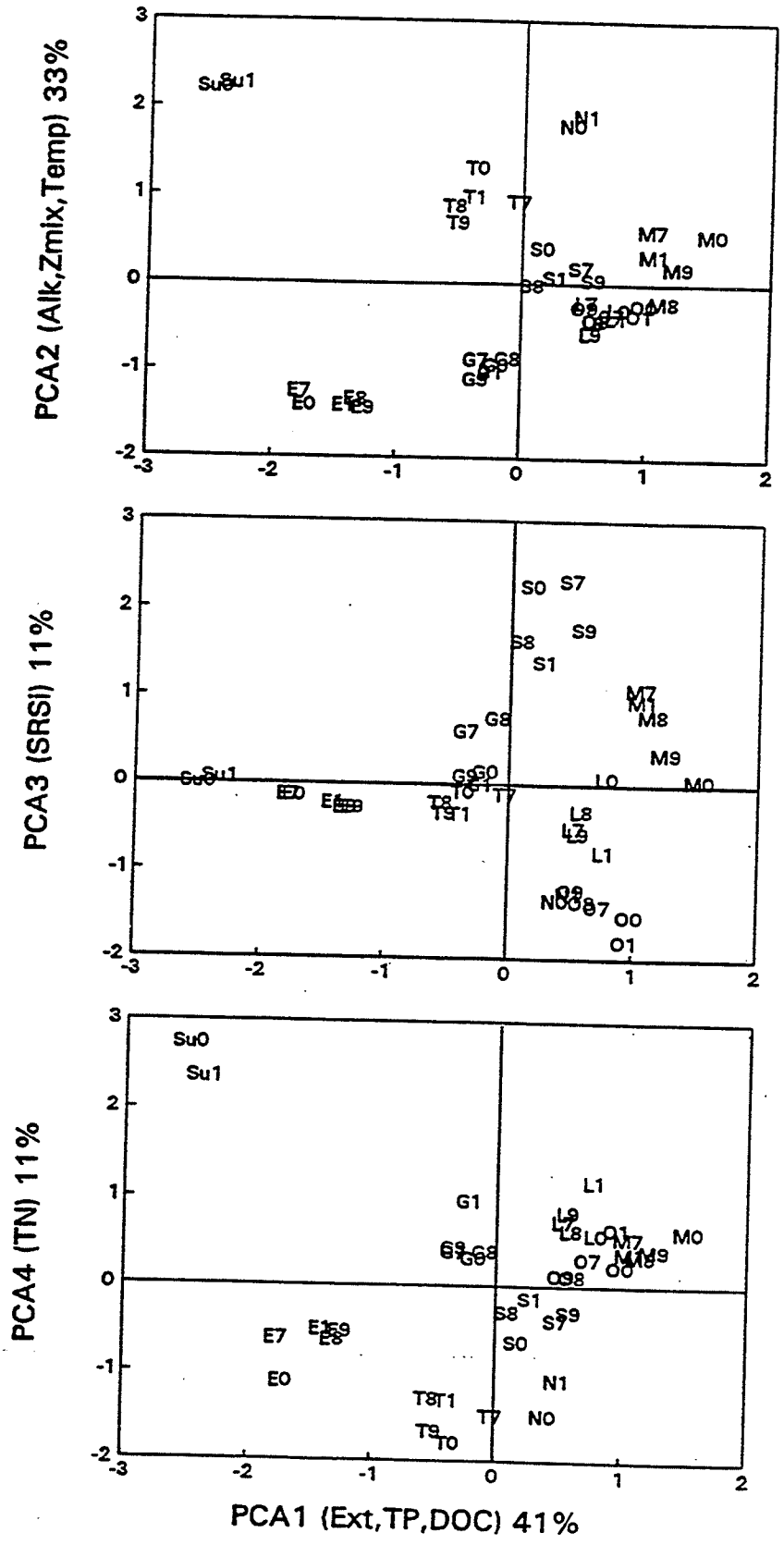

PCA2 (Alk,Zmix,Temp) 33%
PCA3 (SRSI) 11%
PCA4 (TN) 11%
PCA1 (Ext,TP,DOC) 41%

Table 2.5. Principal component (PC) analysis of a correlation matrix of the annual means of eight selected chemical and physical variables from the nine study lakes. Other abbreviations as in Table 2.3.

	PC1	PC2	PC3	PC4
Rotated loadings				
Ext	0.955	-0.225	-0.061	0.098
TP	0.918	0.042	0.277	0.050
DOC	0.913	-0.345	0.021	0.082
Alk	0.037	0.918	-0.247	-0.174
Z_{mix}	-0.289	0.910	0.075	0.061
Temp	0.414	-0.836	0.012	-0.290
SRSi	-0.408	0.240	-0.857	-0.142
TN	0.494	0.105	0.159	0.841
Variance explained by rotated loadings				
	3.254	2.611	0.908	0.864
Percent of total variance explained				
	40.674	32.631	11.345	10.797

good correlation existed between log lake area and PCA2 ($r=0.966$, $P<0.001$). This correlation was strengthened by the fact that alkalinity was higher in the large lakes than in the small ones. Large lakes on the Canadian Shield may be enriched by carbonate minerals; the larger the watershed the higher the probability of encountering glacial deposits that yield carbonate alkalinity (Fee and Hecky 1992).

PCA3 was dominated by SRSi (Fig. 2.4); Green, Musclow, and Sydney lakes had distinctly lower SRSi concentrations than the other lakes (Table 2.4). PCA4 was dominated by TN; Trout Lake, Lake Nipigon, and Lake 373 had the lowest mean TN concentrations, whereas Lake Superior had the highest.

Relationship of Biological to Physical Chemical Variables

If the biological variables are a function of the physical and chemical features of the lakes, then a relationship should be evident between the biological variables and the PCA axes (especially PCA1 and PCA2, which accounted for most [74%] of the physical/chemical variance among lakes). Chlorophyll *a* was highly correlated with PCA1, the largely chemical axis ($r=0.912$). Addition of PCA2, the physical axis, yielded a slightly improved correlation ($r=0.924$). Nutrient status indicators, $APA \cdot chl^{-1}$, C:P, C:N, and C:chl were more highly correlated with the multiple linear combination of PCA1 + PCA2 than with either axis alone (Table 2.6), as were $P_{opt} \cdot C^{-1}$ and $APA \cdot P_{opt}^{-1}$. P^B_m and α^B were not strongly correlated to either or both axes, which is not surprising since they did not exhibit significant lake-to-lake differences.

Discussion

Natural Variability

Most of the variability in the data within the open-water season over the 5 yr studied was caused by lake-to-lake differences rather than yearly or monthly differences (Table 3), despite the fact that the study area experienced hot, dry years (1987, 1988) and extremely wet years (1990, 1991; Fig. 2.5). Hanna and Peters (1991) reported similar results in their study of 16 lake basins located in a uniform climatic and geologic region. Total P and chl *a* variance was much greater among lakes than among times (years, sampling dates) or sampling protocols. The low seasonal variability relative to interlake variability in our study can be partly attributed to the oligotrophic nature of our study lakes (cf. eutrophic lakes, Marshall and Peters 1989).

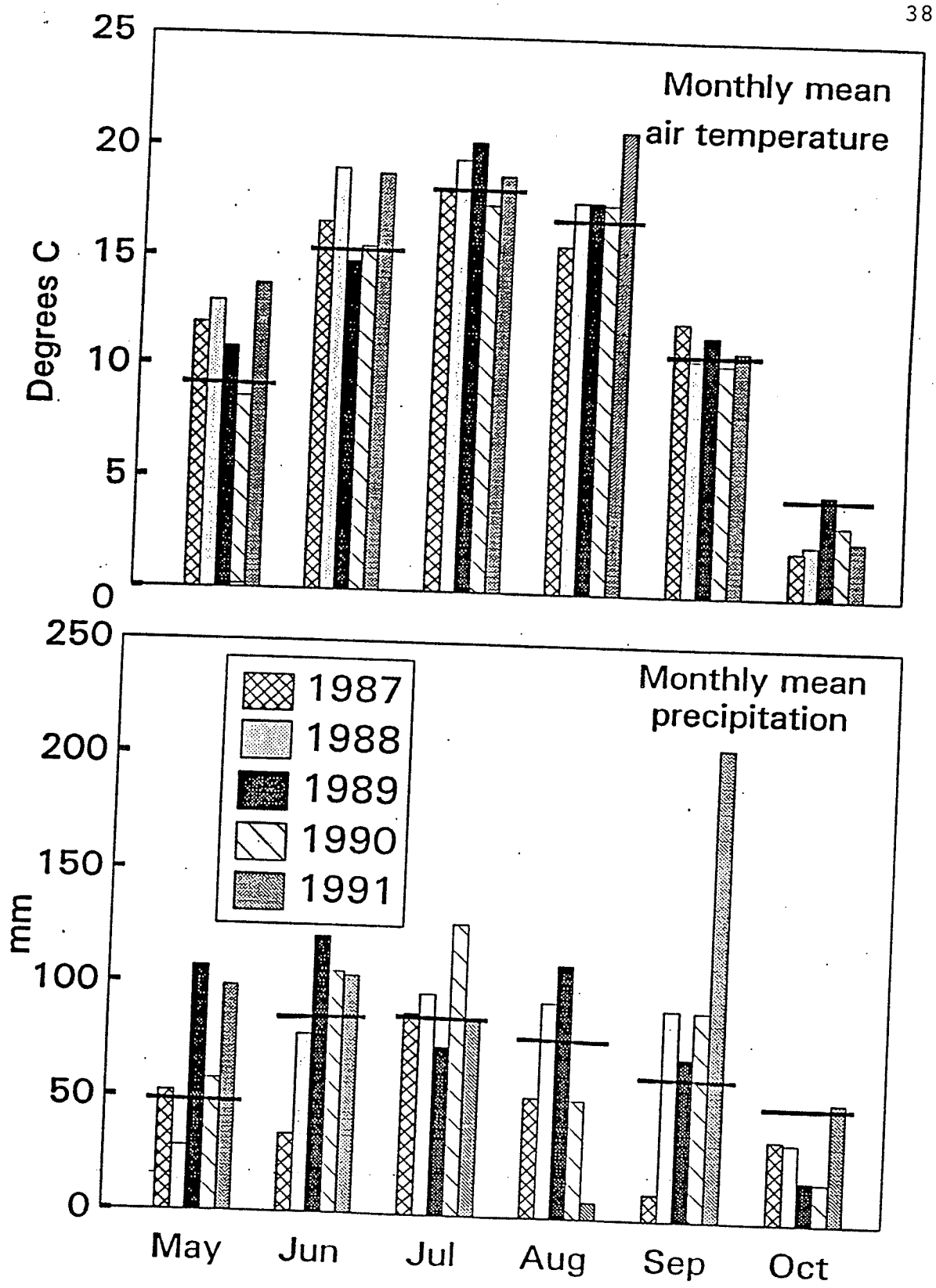
Site replication can be a minor source of variance (Hanna and Peters 1991) but this was not addressed in the study. Low year-to-year variability and significant interlake differences (Table 2.4) indicate that biological variables are annually typical in the lakes, and that few samples are necessary to characterize nutrient status for lakes of this region.

The NOLSS study originally hypothesized that natural interannual variability is an inverse function of size (Fee and Hecky 1992), based on the assumption that large bodies of water would be more buffered than small ones against extreme events. However, the coefficient of variation for nutrient status, and chemical and physical variables showed no tendency to decrease with increasing lake size (Fig.

Table 2.6. Correlation coefficients between the annual means of the biological variables and the scores for each lake year from the principal components (PC) analysis of the physical and chemical variables described in Fig. 2.4 and Table 2.5. Columns 1 and 2 are the simple correlation coefficients between the biological variables and the chemical (PC1) and physical (PC2) axes. Column 3 is the multiple linear correlation coeffieicnt between the biological variables and PC1 + PC2. * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. Abbreviations as in Table 3.

	PC1	PC2	PC1 + PC2
APA · Chl^{-1}	-0.462**	-0.471**	0.705***
C:P	-0.386*	-0.699***	0.799***
C:Chl	-0.623***	-0.606***	0.869***
C:N	-0.426**	-0.633***	0.763***
N:P	-0.202	-0.485**	0.525**
N debt	-0.601***	0.113	0.602***
Chl *a*	0.912***	0.149	0.924***
α^B	0.27	0.124	0.297
P^B_m	0.002	-0.123	0.123
Popt · C^{-1}	0.597***	0.513**	0.787***
APA · $Popt^{-1}$	0.512**	0.482**	0.752***
I	-0.739***	-0.571***	0.934***

Figure 2.5. Monthly mean air temperature (top panel) and monthly mean precipitation (bottom panel) at Red Lake, Ontario for 1987-1991. The solid horizontal line for each month represents the long-term (1950-1981) monthly mean.


Monthly mean
air temperature
Degrees C
25
20
15
10
5
0
Monthly mean
precipitation
1987
1988
1989
1990
1991
mm
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct

2.1), although data from Lakes Nipigon and Superior, the two largest lakes, were incomplete and were not included. Fee et al. (1992) also found no relationship between interannual variability of P^B_m and α^B and lake size.

The biological variables, with the exception of chl *a*, had a high proportion of unexplained variation (Table 2.3), probably because of analytical error and inappropriate sampling scales. Analytical error is high because the biological variables are mostly ratios (to correct for biomass), and errors inherent in the dividend and divisor are included in the quotient. The spatial and temporal scales of tri-weekly sampling at one station are not directly relevant to the scale of phytoplankton cellular processes (Reynolds 1984; Harris 1986) because significant changes can occur on a daily basis over short distances. In spite of the large unexplained variation, all but three of the biological variables were significantly different among lakes (Table 2.4).

Phytoplankton Nutrient Status

All nine lakes were extremely P-deficient, according to the criteria suggested by Healey (1975); inferred growth rates were low (<20% of maximum). APA·chl^{-1} values were >0.005 μM P·μg chl^{-1}·h^{-1}, C:P seston ratios were >258 (except Lake Nipigon: 234), and all N:P seston ratios were >22. The assignment of extreme P-deficient status was based on 5 yr mean values for June 1 - September 30. Within seasons, P-deficiency ranged from none to extreme (Fee et al. 1989). In spite of the extreme P-deficiency in all lakes, consistent differences were evident in the degree of

P-deficiency among lakes. The three smallest lakes were always more strongly P-deficient by all indicators than the remaining larger lakes (Fig. 2.2A).

Similar degrees of P nutrient status were observed from seasonal studies done on epilimnetic samples from other stratified Canadian Shield lakes. Healey and Hendzel (1980) reported extreme P-deficiency in seven lakes in the ELA using similar indicators (APA·chl^{-1}, C:P, N:P seston ratios, P debt). Lean et al. (1987) and Pick (1987), using phosphate turnover times, the phosphate deficiency index (PDI), and total APA, classified offshore station 403 of Lake Ontario as strongly P-deficient throughout the stratified period; they also showed that the smaller (500 ha) Sharpes Bay on Jacks Lake, Ontario, was much more strongly P-deficient than Lake Ontario.

Carbon:nitrogen atomic ratios indicated that all the lakes were moderately N-deficient. Mean N debt values indicated that only Lake 373 was N-deficient. The composition ratios gave a different impression than the metabolic uptake measurement of N status. Composition ratios indicated that N as well as P was in short supply in the lakes. However, C:N composition ratios indicate only moderate N-deficiency and N debt values were rarely in the range indicative of N-deficiency (Table 2.2). Although both N and P may have been in short supply, the phytoplankton may have appeared more P-deficient than N-deficient in these lakes because the uptake processes for these nutrients require energy, which may have been directed toward the more deficient nutrient, P, in these lakes. Co-occurrence of P and N-deficiency as observed in Lake 373 has been reported from other ELA lakes (Healey and Hendzel 1980) and can be expected in natural communities with a

mixture of phytoplankton species. Suttle et al. (1991) used size fractionation techniques and uptake rates of both P and N to conclude that simultaneous N and P-deficiency in oligotrophic Sproat Lake, British Columbia, was caused by the presence of two species: N-deficient *Synechococcus* and a P-deficient diatom. The presence of N_2-fixing cyanobacteria and detection of N_2-fixation are other indicators of N-deficiency. Surprisingly, the lakes that had the highest C:N ratios (373 and Green, which were also the most P-deficient lakes) had the lowest biomass of N_2-fixing cyanobacteria (HJK, unpubl. data). Samples were routinely analyzed for N_2-fixation in these lakes (acetylene reduction method) but detectable fixation in unconcentrated samples was rarely observed. However, maximal rates of N_2-fixation were observed in samples concentrated by a 10 μm net in Linge and Musclow lakes (Fee et al. 1994).

Although we did not conduct nutrient status measurements for Si, it was noted that Si concentrations were routinely <5 μM in Green Lake and <2 μM in Sydney and Musclow lakes. In the larger lakes (Sydney and Musclow), where P was not as strongly limiting as in the smaller lakes, Si was probably an intermittent limiting factor for diatoms (Levasseur et al. 1990).

Relative Growth Rates

Droop (1968, 1970) described the growth rate of nutrient-limited phytoplankton as a function of the internal cell quota of the limiting nutrient using the following general equation:

$$\mu = \bar{\mu}\left(1 - \frac{kq}{Q}\right) \qquad (2.2)$$

where μ is the specific growth rate; $\bar{\mu}$ is the specific growth rate at infinite substrate concentration; Q is the cell quota of the limiting nutrient; and kq is the subsistence quota, Q at $\mu = 0$. This equation expresses the basic theory underlying several nutrient status measurements based on seston composition ratios such as C:P, C:N, and N:P. Application of the theory presumes that the seston ratios are representative of living material. In Canadian Shield lakes with residence times >6 mo, these ratios are representative of living material (Healey and Hendzel 1980; Hecky et al. 1993). Elemental ratios in seston collected on a GF/C filter were compared with those collected with a 10 μm net. Both sets of samples were prefiltered through 200 μm net. The 10 μm net concentrates larger living cells which should have a different ratio than whole-water seston if detritus less than 10 μm has different ratios than living material. The comparison revealed no significant differences between the two types of samples (paired t-test; SJG and LLH, unpubl. data), which agrees with the results of Healey and Hendzel (1980).

As with the composition ratios, the metabolic measurements (APA, P debt, N debt) were calibrated with respect to nutrient-limited cultures and their cell nutrient quotas growing at different growth rates set by the limiting nutrient (Healey 1975; Healey and Hendzel 1979a, 1980). These uptake and activity indicators were directly proportional to the degree of nutrient-deficiency and inversely proportional to growth rate. Thus, lakes 373, Green, and Orange should have low relative growth rates, whereas Musclow Lake and Lake Nipigon should have high relative growth rates, based on the metabolic nutrient status indicators. The metabolic measurements, like the composition ratios of natural samples, represent more than pure phytoplankton. Our APA measurements included phosphatase activity produced by bacteria-sized particles >0.2 μm. Bacterial biomass, especially in the late fall, could be double the phytoplankton biomass (HJK, unpubl. data). Because peaks in bacterial biomass appeared in both large and small lakes, and occurred when APA was generally low, the trends observed in APA were probably not caused by bacterial activity.

The Droop equation predicts that growth rate varies inversely with nutrient status. Relative rates of growth can be estimated from photosynthetic uptake rates (P_{opt}) normalized to particulate C. The $P_{opt} \cdot C^{-1}$ seasonal means had a pattern that was the mirror image of the nutrient status measurements (Fig. 2A). Measurements of $APA \cdot chl^{-1}$ and $P_{opt} \cdot C^{-1}$ were negatively correlated ($r=-0.777$, $n=37$, $P<0.001$, Fig. 2.6). The ratios C:P, N:P, C:chl, and C:N were also significantly negatively correlated to $P_{opt} \cdot C^{-1}$ ($r=-0.544$ to -0.818, $P<0.001$). The agreement of the two independent estimators, $APA \cdot chl^{-1}$ and $P_{opt} \cdot C^{-1}$, allowed inferences to be made about

relative growth rates in the study lakes. The smallest lakes clearly had the lowest relative growth rates, whereas growth rates in the larger lakes were higher although not strictly defined by size.

It is recognized that correlated ratios each containing C cannot be considered truly independent of each other and that measurements normalized to biomass contain nonliving and living particles as discussed above. To neutralize the biomass estimate, we compared the variable $APA \cdot P_{opt}^{-1}$ among the study lakes. $APA \cdot P_{opt}^{-1}$ is not an established nutrient status indicator, but it is useful because it is independent of either chl *a* or suspended C. It is similar in this respect to the PDI of Lean et al (1987). $APA \cdot P_{opt}^{-1}$, had the same pattern as $APA \cdot chl^{-1}$ and other biomass-based nutrient status indicators and was the mirror image of $P_{opt} \cdot C^{-1}$ (Fig. 2.2A). Therefore, the conclusion that nutrient-deficiency is lower and relative growth rates higher in large lakes than in small lakes is independent of the normalization of many of these indicators on biomass.

Chlorophyll - Total Phosphorus

Correlation coefficients between the biological variables and PCA1 (the chemical axis) and PCA2 (the physical axis) demonstrated that chl *a* was readily predicted by the chemical variables. In contrast, the nutrient status and growth rate variables were best predicted by a combination of physical and chemical variables (Table 2.6).

Figure 2.6. Relationship between the maximum rate of light-saturated photosynthesis (P_{opt}) normalized to particulate carbon (C) and alkaline phosphatase activity (APA) normalized to chlorophyll *a* (chl) in the nine study lakes. Values are seasonal means (June 1 - September 30, 1987-1991). The first character of each symbol is the first letter of the lake name, except for Lake Superior (Su). The letters are followed by the years (87 = 7, 88 = 8, etc.).

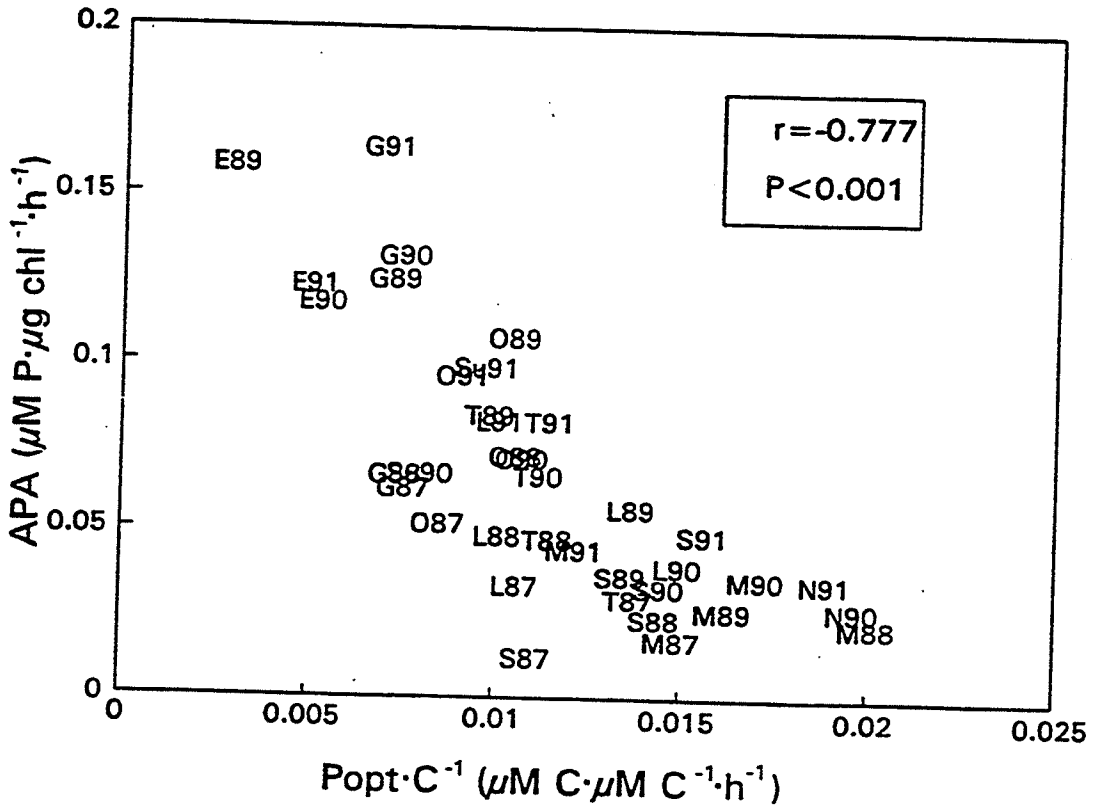

r=-0.777
P<0.001
APA (μM P·μg chl^{-1}·h^{-1})
Popt·C^{-1} (μM C·μM C^{-1}·h^{-1})
0.2
0.15
0.1
0.05
0
0.005
0.01
0.015
0.02
0.025
E89
G91
G90
E91
G89
E90
O89
O91
S91
T89
L91
T91
G88
G87
T90
L89
O87
L88
T88
M91
S91
L90
S89
S90
M90
N91
L87
T87
S88
M89
N90
M87
M88
S87

Fig. 6

In P-limited lakes, a statistically significant correlation usually exists between epilimnetic TP and epilimnetic chl *a* (Sakomoto 1966; Dillon and Rigler 1974; Riley and Prepas 1985; Molot and Dillon 1991). Total P concentration can be predicted from annual TP load and flushing characteristics for the lake and drainage area (Dillon and Rigler 1975; Canfield and Bachmann 1981). These TP-chl *a* and TP-flushing relationships have been used as the basis for managing lakes (Dillon and Rigler 1975; Canfield and Bachmann 1981).

A highly significant correlation existed between TP and chl *a* in the nine lakes of this study (Table 2.7). The C:N and N debt data indicated that N-deficiency occasionally co-occurred with P-limitation in the lakes and I values were sometimes below those reported to limit photosynthesis (Fee et al. 1992), so a multiple stepwise linear regression was done using TN, I, and TP. Prediction of chl in these lakes was improved statistically by including I with TP (Table 2.7) but the increased amount of variance explained by including I was minor.

Physical/Chemical Control of Nutrient Status

The study lakes are P-deficient so it is possible that the chemical axis can predict both chl concentrations and nutrient status indicators equally well. The fact that significant correlations also required inclusion of physical variables suggested that the nutrient status indicators and growth rates were influenced by both chemical and physical variables. If nutrient status was a simple linear function of TP, then Lake Superior would be as severely P-deficient as Lake 373 and Trout Lake would

Table 2.7. Simple and stepwise multiple linear regression equations for the dependence of chlorophyll *a* on total phosphorus (TP) and I. Data were seasonal means for the period June 1 - September 30, 1987-1991, for all lakes except Nipigon and Superior (seasonal means, 1990-1991). Abbreviations as in Table 2.3.

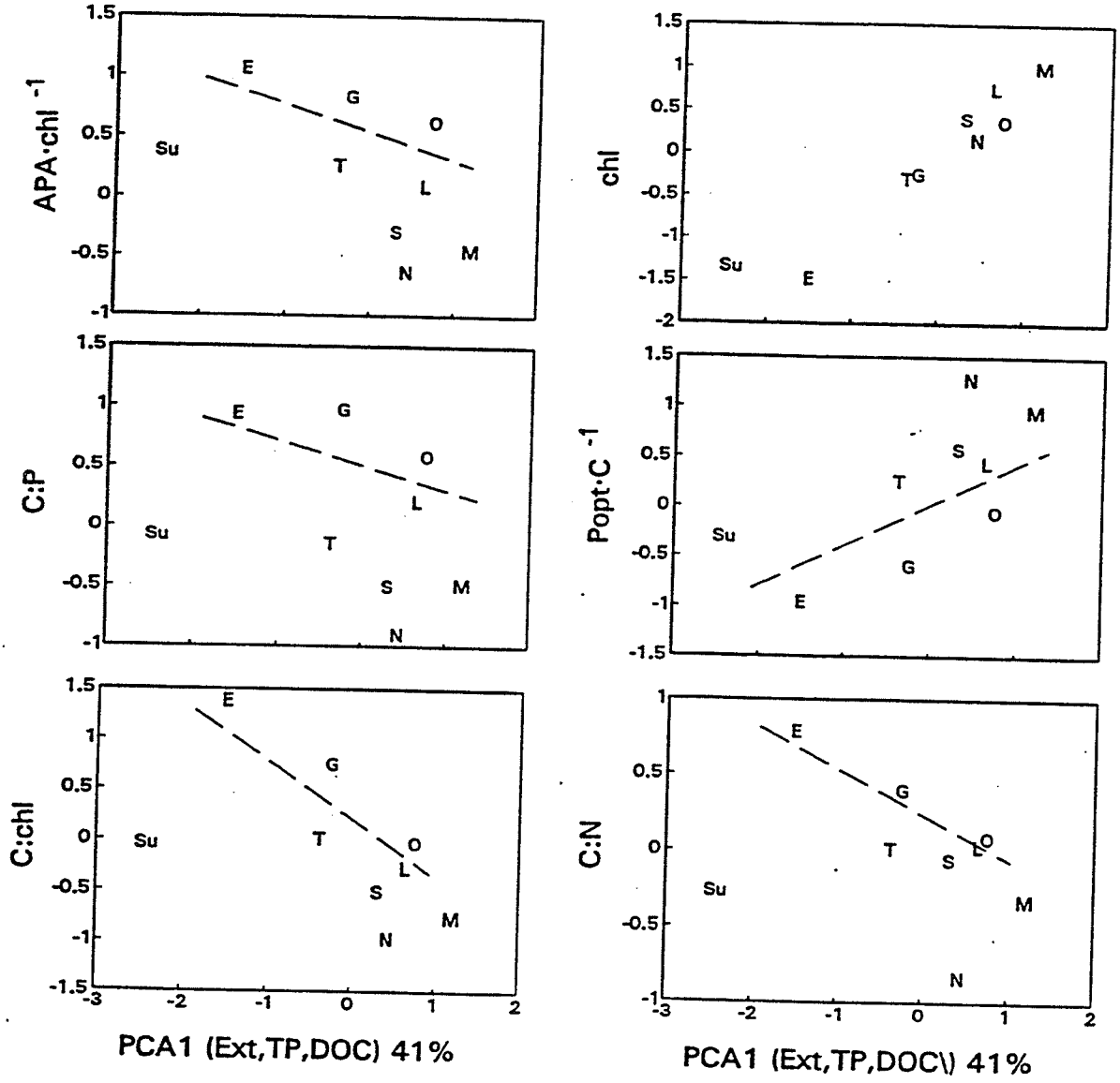
Equation	r^2	n	p
log (Chl *a*) = -1.299 + 1.787 log (TP)	0.876	39	0.001
log (Chl *a*) = -0.626 + 1.437 log (TP) - 0.389 (log)I	0.906	39	0.001

be as severely P-deficient as Green Lake because the two sets of lakes have similar mean TP concentrations (Table 2.4). In fact, the large lakes are not as P-deficient as the small ones (Fig. 2.7). Nutrient status and growth rate estimators for each lake plotted against PCA1 showed that the larger lakes are less nutrient-deficient and have higher phytoplankton relative growth rates than smaller lakes with similar mean TP.

Deep mixing (Sterner 1990) and/or high light extinction (Hecky and Guildford 1984) in certain situations will result in light-deficiency rather than nutrient-deficiency. However, the deep mixed depth in Lake Superior usually did not lead to light-deficiency, nor did the high light extinction coefficient in Musclow Lake. Other, physical effects may explain the low nutrient-deficiency in the large lakes. The thermocline is more stable in the small lakes than in the large ones (Fee et al. 1994). Fee et al. (1994) calculated eddy diffusivity coefficients for the NOLSS lakes and used vertical concentration gradients to show that little or no P is returned from below the epilimnion during the stratified period. Nevertheless, the large lakes have deeper and more turbulent mixed layers than the small lakes, which may result in more efficient retention of particles in the epilimnion (Fee et al. 1994); longer retention leads to improved nutrient recycling. Thus, lakes of different sizes having similar external inputs of P in the spring would have quite different fluxes of recycled P during the summer and, consequently, different degrees of P-limitation.

The fact that a combination of chemical (PCA1) and physical (PCA2) variables correlate significantly with the nutrient status and growth rate variables is an artificial but useful finding. It is artificial because it is not really possible to

Figure 2.7. Nutrient status and growth rate indicators (standardized means) plotted against the first principal components axis (PCA1). Dotted lines have been added to emphasize the separation between the smaller (E = Lake 373, G = Green Lake, O = Orange Lake) and larger lakes (see Table 1 for remaining lakes). Abbreviations as in Table 3; units as in Fig. 2.


APA·chl -1
chl
C:P
Popt·C -1
C:chl
C:N
Su
E
G
T
O
L
S
N
M
PCA1 (Ext,TP,DOC) 41%
PCA1 (Ext,TP,DOC\) 41%

separate chemical and physical variables in these systems. For example, we hypothesized that physical mixing depth influences P cycling, but it could be the cycling of P, rather than mixing depth, that directly influences nutrient status. Nonetheless, for this group of lakes, a combination of physical and chemical variables provided a useful classification because it described the combination of variables that best predicted the biological variables, and it showed that the factors predicting chl (algal biomass) did not account fully for variability in nutrient status (relative growth rate).

Application of Results from Small Systems to Large Systems

We have shown that the TP-chl relationship holds for all the lakes of the study. We have also shown that nutrient status, relative growth rate, and probably trophic performance (Sterner et al. 1993; Hecky et al. 1993) of the study lakes are affected by size-related physical factors. Thus, models constructed to describe processes in large lakes, based on information from studies on small lakes that are highly nutrient-deficient, must take into account differences imposed on lakes of different size by physical factors that affect within-lake nutrient regeneration. Processes known to be dependent on algal growth rates and algal quality include secondary production (Enright et al. 1986; Sterner et al. 1993), sensitivity to toxic metals (Creed et al. 1990; Twiss and Nalewajko 1992), and bioaccumulation of contaminants (Swackhamer and Skoglund 1993; Taylor et al. 1991). Nutrient status analyses yield information about phytoplankton growth rates, and so these analyses

provide a means of scaling models of biological processes that depend on growth rate from small experimental lakes (Johnson and Vallentyne 1971) to large systems, including the Great Lakes where application of theory is most critical.

Chapter 3

Patterns of Nutrient-Deficiency Along an Aquacultural Gradient

Abstract

Physiological phytoplankton nutrient status measurements and physical and chemical measurements were made in St. Margaret's Bay, Nova Scotia along a 9 km transect from an inshore aquaculture site (12 m depth) to an offshore station (53 m depth). Physical measurements, inorganic nutrients (P, N, and Si) and chlorophyll concentrations showed no discernable trend along the transect or with time. Two of the nutrient status measurements, nitrogen debt and silicon demand, consistently differed between stations close to the aquaculture site and those offshore. Stations near the aquaculture site were less N-deficient than the offshore stations and showed Si uptake more frequently. Intensive aquaculture at these sites increased the flux of N to phytoplankton even though ambient inorganic N concentrations were not measurably affected.

Introduction

It has been suggested that toxic marine phytoplankton blooms are increasing globally as a result of changing nutrient supply and nutrient ratios in coastal areas (Smayda 1990), and it has been demonstrated in laboratory experiments that toxin production by some species of marine phytoplankton varies with nutrient supply ratio (Boyer et al. 1987; Anderson et al. 1990; Bates et al. 1991). While it has not been demonstrated in the field that the nutritional status of the phytoplankton affects the occurrence of toxic algal species or toxin production, the situation may be similar to freshwater eutrophication where decreasing N:P supply ratios result in proliferation

of undesirable filamentous blue-green algae. The underlying cause was not clearly understood until whole lake manipulations and sensitive nutrient status measurements showed that N:P supply ratios were critical in determining species occurrence and abundance (Hendzel et al. 1994). While whole system manipulations are not possible in marine systems, the application of sensitive nutrient status indicators is possible (Hecky and Kilham 1988). In this study, measurements of physiological phytoplankton nutrient status and physical and chemical parameters were made along a transect from an inshore aquaculture site to an offshore station. The objective was to determine whether the aquacultural activity, a point source of increased nutrient loading, affected phytoplankton nutritional status on a local scale. The purpose of this study is not to suggest that aquacultural activity causes toxic algal blooms, but to demonstrate the use of methods sensitive to phytoplankton nutrient status that may be useful in understanding the causes of toxic phytoplankton blooms regardless of the source of anthropogenic nutrients.

Methods

Samples were collected at five stations (Table 3.1) in St. Margaret's Bay, Nova Scotia during August and September 1990. (Sharaf et al. 1970; Platt et al. 1970) from 1 m and from below the thermocline, held near in situ temperature for 2 to 10 h and passed through a 200 μm pre-filter to remove large zooplankton before processing. NO_3, NO_2, SRP (soluble reactive P) were measured on filtered seawater stored in the dark at 4°C (up until 2 weeks) until analyzed with an automated method

(Stainton et al. 1977). Stainton et al. (1977) is a freshwater analytical chemistry manual but the principals for nutrient analyses in freshwater are the same as for seawater. NH_4 and SRSi (soluble reactive silicate) were measured on the day of collection using unfiltered seawater (Stainton et al. 1977). TIN (total inorganic nitrogen) is the sum of NO_3, NO_2, and NH_4. Particulate C, N, and P samples filtered onto pre-ignited GF/C glass fibre filters were analyzed (Stainton et al. 1977). GF/C filters rather than GF/F filters were used to allow comparison to previously collected freshwater data sets and to facilitate comparison to the nutrient status indicators used in this study. Particulate silicon samples collected on polycarbonate filters (pore size 0.2 μm) were also analyzed (Stainton et al. 1977). Chlorophyll *a* samples collected onto GF/C filters, extracted in 90% methanol, were determined fluorometrically as in Stainton et al. (1977).

Cell surface alkaline phosphatase activity was measured fluorometrically (Healey and Hendzel 1979b). Parallel determinations were made of total and soluble activities, the soluble activity being that passing through 0.2 μm filters. The difference is reported as particulate activity. N debt was measured by adding a final concentration of 5 μM NH_4Cl to 100 mL of unfiltered seawater and leaving this in darkness at room temperature for 24 h. Triplicate 10 mL samples were removed at the beginning and end and analyzed for ammonium (Stainton et al. 1977). N debt was calculated as the nutrient removed over a 24 h period per unit of chlorophyll *a* (Healey 1977). Silicon demand was measured in the same way, except that uptake was normalized to particulate biogenic silicon.

Table 3.1. Information about stations.

Station	Depth (m)	Distance offshore (km)	Aquaculture activity
MI	15	0.2	mussel strings
AS2	11.5	0.3	salmon pens and mussel strings
AS1	13	0.3	mussel strings
4	48.6	1.8	none
9	52.2	1.7	none

Results and Discussion

Nearshore and offshore stations were similar with respect to surface temperature, transparency and presence or absence of stratification (Table 3.2). TIN, SRP, and SRSi concentrations, usually less than 1 μM (Table 3.2), varied with time generally in the same direction. The stations near the aquaculture sites did not have higher nutrient concentrations. Chlorophyll *a* concentrations were greater at station 9 on September 12 (Table 3.2). Otherwise, there was no pattern.

The nutrient status indicators showed there was a difference between the aquaculture sites and the non aquaculture sites (Table 3.3). Of the three inshore stations (MI, AS1, AS2), the two most closely associated with aquaculture (AS2 and MI) were less N-deficient and more Si-deficient than the other inshore station and offshore stations 4 and 9. Although ambient NH_4 concentrations were not detectable at the sites, the lessened N-deficiency measured at the aquaculture sites suggests a greater rate of N loading from feeding activities or regeneration in that region. This may be due to the large volume of water filtered by the mussels; output from the salmon cages where fish food was added, or regeneration from the sediments. The difference between inshore aquaculture sites and offshore sites may not be related to the aquacultural activities alone, but to differences in offshore and inshore hydrological features. Inshore station AS1 appeared similar hydrologically to AS2 and MI, but the density of mussel strings there was less than at AS2 or MI. This supports the interpretation that the differences in nutrient status were a result of the aquaculture influence rather than proximity to shore.

Table 3.2. Physical and chemical measurements at the stations. Temp is surface temperature, Z_{mix} is mixing depth, Secchi is Secchi disk depth, Ext is the light extinction coefficient, TIN is total inorganic nitrogen, SRP is soluble reactive phosphate, SRSi is soluble reactive silicon, Chl *a* is chlorophyll *a*, C:N is the molar ratio of particulate carbon and nitrogen.

	Date	MI	AS2	AS1	4	9
Temp (°C)	Aug 22	NA	16.4	16.6	16.1	15.9
	Aug 28	19.5	19.5	20.2	19.0	19.2
	Sep 12	17.8	NA	17.3	17.2	17.5
	Sep 26	16.5	NA	15.4	16.0	15.6
Z_{mix} (m)	Aug 22	NA	9.5	4.0	8.5	6.0
	Aug 28	5.0	6.0	4.5	5.0	8.0
	Sep 12	15.0	NA	12.0	48.6	52.0
	Sep 26	11.0	NA	13.0	12.0	14.0
Secchi (m)	Aug 22	NA	NA	11.11	13.0	12.5
	Aug 28	13.0	NA	12.0	14.0	15.0
	Sep 12	9.0	NA	9.8	12.0	10.0
	Sep 26	8.5	NA	12.2	12.5	9.5
Ext (m^{-1})	Aug 22	NA	NA	0.175	0.155	0.182
	Aug 28	0.136	NA	0.159	0.119	0.118
	Sep 12	NA	NA	NA	NA	NA
	Sep 16	0.131	NA	NA	NA	NA
TIN (μM)	Aug 22	NA	0.39	0.32	0.36	0.61
	Aug 28	0.43	0.46	0.29	0.29	0.45
	Sep 12	0.54	0.74	0.57	0.98	0.97
	Sep 26	0.62	0.70	0.40	0.40	0.55
SRP (μM)	Aug 22	NA	0.87	0.81	0.90	1.03
	Aug 28	0.78	0.81	0.78	0.78	0.74
	Sep 12	0.81	0.81	0.81	0.81	0.78
	Sep 26	0.81	0.81	0.81	0.81	0.74
SRSi (μM)	Aug 22	NA	0.68	0.52	0.82	0.55
	Aug 28	0.90	0.77	0.74	0.64	0.61
	Sep 12	1.46	1.12	1.07	0.85	1.20
	Sep 26	2.22	2.43	1.75	1.38	1.49
Chl *a* ($\mu g \cdot L^{-1}$)	Aug 22	NA	0.37	0.29	0.34	0.35
	Aug 28	0.70	0.66	0.70	0.75	0.83
	Sep 12	0.59	0.74	0.42	0.36	1.26
	Sep 26	0.61	0.25	0.47	0.22	0.56
C:N (molar)	Aug 22	NA	11.7	11.7	13.6	13.5
	Aug 28	9.2	13.6	9.8	9.3	9.6
	Sep 12	12.8	13.1	13.1	11.7	13.1
	Sep 26	NA	11.7	9.0	9.6	10.4

Samples strongly N-deficient did not exhibit strong Si uptake and samples exhibiting Si demand were not N-deficient (Fig. 3.1). Particulate C:N ratios at all five stations indicated moderate N-deficiency (Table 3.2). Levasseur et al. (1990) suggested that C:N ratios were not specific for N and reported elevated C:N ratios when physiological assays indicated either Si or N-deficiency.

P-deficiency (i.e. alkaline phosphatase activity), unlike Si-deficiency, was often present in samples exhibiting N-deficiency (Fig. 3.1). It is not uncommon in freshwater to observe indications of both P and N-deficiency in the same sample since different species in the community may be limited by different nutrients (Healey and Hendzel 1980; Hecky and Kilham 1988; Suttle et al. 1991). C:P ratios (not shown) were extremely low (average 60:1 molar ratio), raising the possibility that both mineral and biological forms of P were being measured in the particulate P digests. SRP concentrations did not reflect the substantial biomass change at station 9. This suggests that SRP measurements may also be affected by mineral P at fine grain sizes which passed through the GF/C filters. The definition of clay sized particles is <2.0 μm.

Smayda (1990) has cited many examples of coastal eutrophication and associated changes in nutrient ratios in coastal waters as circumstantial evidence for an increasing occurrence of toxic phytoplankton blooms. Several laboratory studies have shown that toxin production can be related to physiological nutrient status (Boyer et al. 1987; Anderson et al. 1990; Bates et al. 1991). This study has shown that point sources of nutrients (mussel strings and salmon cages) resulted in less

Table 3.3. Presence or absence of N-, Si-, or P-deficiency. Frequency is the number of positive indications of deficiency as a percent of the number of times the measurements were made. NA means no sample.

Station	MI			AS2			AS1			4			9		
Nutrient	N	Si	P	N	Si	P	N	Si	P	N	Si	P	N	Si	P
Depth I															
Aug 22	NA	NA	NA	o	o	o	+	o	+	+	+	o	+	o	o
Aug 28	o	+	+	+	+	NA	+	+	+	o	o	+	+	+	+
Sept 12	o	+	o	o	+	NA	o	o	o	+	o	+	+	o	o
Sept 26	+	o	o	+	o	+	+	+	+	+	o	+	+	o	+
Depth II															
Aug 22	NA	NA	NA	o	o	o	o	o	o	NA	NA	NA	+	+	o
Aug 28	o	+	+	o	+	NA	+	+	+	NA	NA	NA	o	+	o
Sept 12	o	+	+	o	+	NA	o	+	o	NA	NA	NA	+	o	+
Sept 26	+	+	+	+	+	+	+	o	+	NA	NA	NA	+	o	+
Frequency	33	83	67	38	83	50	63	50	63	75	25	75	88	38	63

Figure 3.1. Si demand and alkaline phosphatase activity plotted against N debt for all stations and depths. Points above the arrows are deficient.

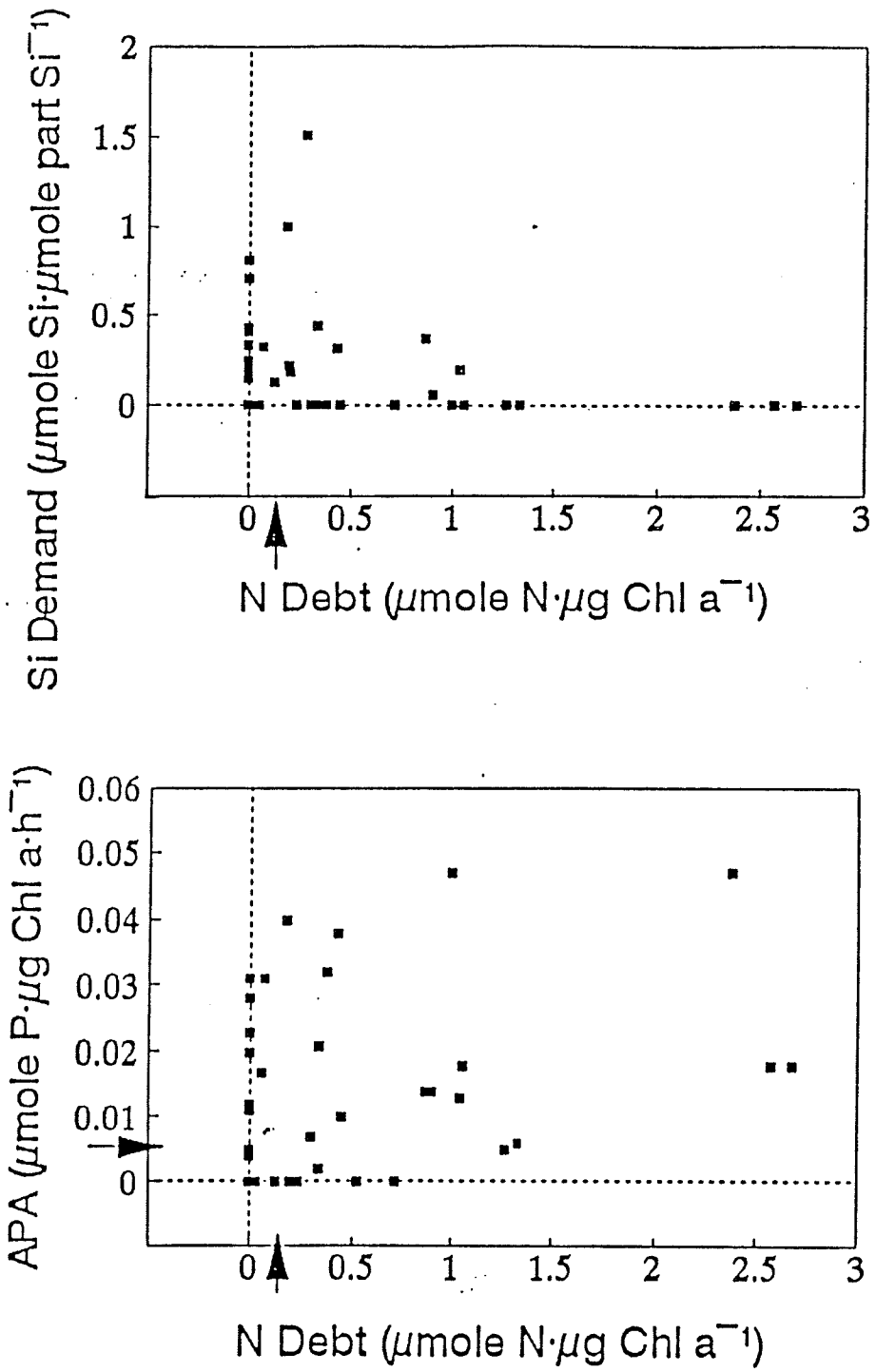


Fig.3.1. Si demand and alkaline phospahatase activity plotted against N debt for all stations and depths. Points above the arrows are deficient.

N-deficient phytoplankton compared to communities away from the nutrient source. However, the difference in nutritional status was only apparent using sensitive physiological assays. Measurements of ambient nutrient concentrations and chlorophyll concentrations did not reveal any spatial pattern. Nutrient status indicators, such as used in this study, have the potential to provide the link between field and laboratory studies to determine the conditions that produce toxic phytoplankton.

Chapter 4

Phytoplankton Nutrient Status in Coastal and Offshore Water in the North Atlantic Compared to Some North Temperate Lakes

Abstract

Nutrient status of phytoplankton in the North Atlantic Ocean varied with nutrient supply ratio and degree of water column stratification in a manner similar to lakes. When TN:TP was high and the water column was stratified, phytoplankton communities exhibited signs of phosphorus deficiency. Along a transect from the Shelf water off Nova Scotia to the Sargasso Sea north of Bermuda during April, the TN:TP ratio increased mainly driven by decreasing TP. Phytoplankton biomass, as indicated by chlorophyll concentration, decreased along the transect and nutrient status measurements indicated no N or P-deficiency in the Shelf and Slope water and severe nutrient-deficiency in the Sargasso Sea water. High rates of alkaline phosphatase activity in the Sargasso Sea indicated phosphorus deficiency in the particulate matter.

Introduction

Phytoplankton nutrient status measurements can indicate what nutrient or nutrients control phytoplankton growth in nutrient-limited systems (Healey and Hendzel 1980; Hecky and Kilham 1988; Suttle et al. 1991). In anthropogenically affected lakes, nutrient status measurements have been used to determine whether to manage watershed inputs of nitrogen or phosphorus or both to control the occurrence of nuisance algae. Similarly, in coastal areas with increasing inputs of nutrients as the result of human activity, nutrient status measurements can be used to determine which of the nutrients is key to controlling excessive blooms of algae such as

Phaeocystis in the North Sea (Joint and Pomroy 1993; Sakshaug and Olsen 1986). In both freshwater and the sea, the occurrence of toxic phytoplankton blooms has been associated with changing nutrient conditions (Smayda 1990; Carmichael 1992). Phytoplankton nutrient status is an important factor in the transfer of energy and food quality in the food web (Sterner et al. 1993; Sterner and Hesson 1994). Nutrient stressed phytoplankton provide a poor ration of food for consumers (Elser and Hassett 1994; Anderson and Hesson 1995).

Historically marine phytoplankton have been considered to be N-deficient (Ryther and Dunstan 1971) and most phytoplankton-nutrient interaction research in marine systems has, until recently, focussed on N (Hecky and Kilham 1988; Price et al. 1994; Karl et al. 1995). However, as global patterns of chlorophyll and nutrients have become available through the development of satellite imagery and cooperative research programs such as JGOFS and GEOSECS (SCOR 1990), it has become apparent that in parts of the ocean, phytoplankton biomass is not solely controlled by N availability. The pattern that is emerging is a dynamic and complex one. Fe is thought to control uptake of N in the equatorial Pacific (Greene et al. 1994; Price et al. 1994) and Southern Ocean (Martin et al. 1991). Silicon has been suggested to be limiting in some coastal areas (Ragueneau et al. 1994) especially those anthropogenically enriched in N and P relative to Si (Smayda 1990). Phosphorus cycling has been examined in coastal Hawaiian waters (Bjorkman and Karl 1994) and grazer control of biomass has been the subject of many studies (Frost 1991; Price et al. 1994).

In freshwater, P is most frequently confirmed as the nutrient limiting phytoplankton growth (Hecky and Kilham 1988). When N limitation exists in freshwater it is linked with changes in loading ratios of N and P. This has been demonstrated experimentally in whole lake manipulations at the Experimental Lakes Area in northwestern Ontario (Schindler 1977; Healey and Hendzel 1980; Hendzel et al. 1994) and in British Columbia (Suttle et al. 1991) and observed in lakes with naturally occurring low N:P ratios (Smith 1983). A shift from P to Si-deficiency has been observed and is correlated with anthropogenic enrichment of P and a resulting decrease in Si:P ratios in the Laurentian Great Lakes (Schelske et al. 1986), and in the Mississippi estuary (Dortch and Whitledge 1992).

In this study, Shelf, Slope and Sargasso Sea waters were collected in order to compare phytoplankton nutrient status measurements along the transect and between the transect and a set of similar data from a series of north temperate Canadian Shield lakes including Lake Superior, the world's largest lake (Guildford et al. 1994). Identical nutrient status measurements and ancillary physical and chemical observations have, for the first time, been made across large gradients of spatial scale (size in the lake study, coastal to deep ocean in the sea), maximizing the range of physical conditions and providing a broad range of nutrient conditions. In particular, the sampling strategy provided a broad range of TN:TP values.

The objective of this paper is to examine the phytoplankton-nutrient status in relation to physical and chemical conditions across the large gradients provided by these two data sets. Nutrient status of phytoplankton growing under nutrient-limited

conditions is an indication of growth rate (Healey and Hendzel 1980). By examining the relationship between nutrient status and physical and chemical conditions across such a wide range of physical and chemical conditions including lakes and the ocean, critical factors which control phytoplankton growth can be determined.

Methods

Study Area

This study was part of a Joint Global Ocean Flux Study (JGOFS) (SCOR 1990) cruise organized by the Biological Oceanographic Division of the Department of Fisheries and Oceans from Bedford Institute of Oceanography in Dartmouth, Nova Scotia. The Canadian Scientific Ship "Hudson" departed Dartmouth on April 3, 1991 and returned on April 20, 1991. The general areas sampled are indicated in Fig. 4.1 and can be divided into three general categories: Shelf water, Slope water and Sargasso Sea water based on their latitudinal and longitudinal coordinates (Fig. 4.1 and Table 4.1).

CTD Profiles

Temperature, salinity and depth measurements were done by CTD (W.G. Harrison (unpublished data). A mixed layer for each profile was estimated by plotting the sigma t profiles and choosing the depth of greatest density change.

Figure 4.1. Sampling locations along the transect from Nova Scotia to the Sargasso Sea (April 4 - April 19, 1991).

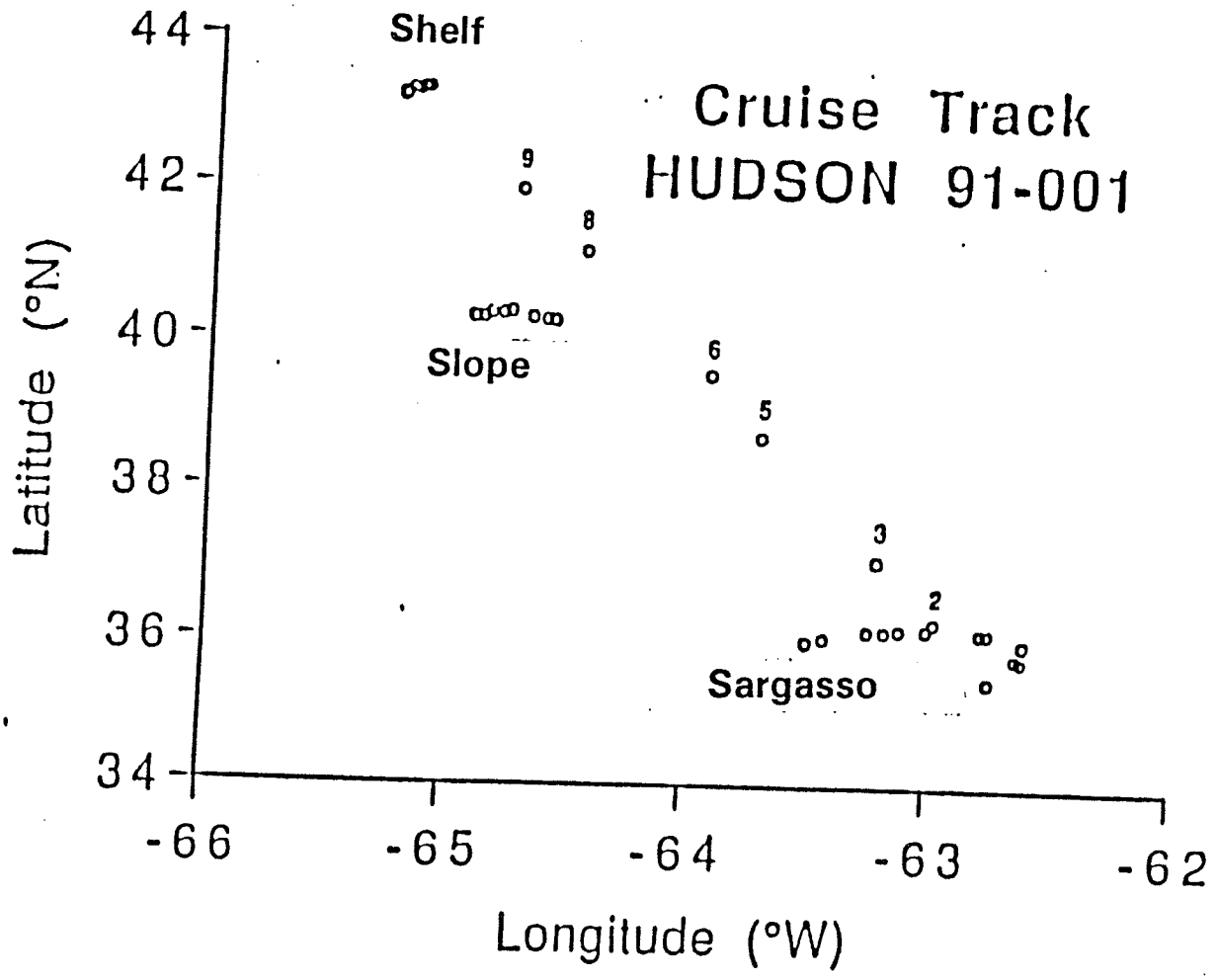

Cruise Track
HUDSON 91-001
Shelf
Slope
Sargasso
9
8
6
5
3
2
44
42
40
38
36
34
-66
-65
-64
-63
-62
Latitude (°N)
Longitude (°W)

Table 4.1. Values indicative of presence or absence or degree of nutrient-deficiency for nutrient status indicators used in this study (from Healey and Hendzel 1980). C, carbon; N, nitrogen; P, phosphorus; chl, chlorophyll *a*; APA, alkaline phosphatase activity.

Indicator	Nutrient	No deficiency	Moderate deficiency	Extreme deficiency
C:N[a]	N	<8.3	8.3-14.6	>14.6
C:P[a]	P	<129	129-258	>258
C:chl[b]	N or P	<4.2	4.2-8.3	>8.3
(APA·chl^{-1})[c]	P	<0.003	0.003-0.005	>0.005
		No deficiency	Deficient	
N:P[a]	P	<22	>22	
N debt[d]	N	<0.15	>0.15	
P debt[e]	P	<0.075	>0.075	

[a] atomic ratio
[b] μmol C:μg
[c] particulate APA, μmol P· μg chl^{-1}· h^{-1}
[d] μmol N· μg chl^{-1}
[e] μmol P· μg chl^{-1}

Chemical Analyses

Dissolved nitrate, phosphate and silicate measurements were made on samples collected by rosette with the CTD profile. Analyses were done using an Alpkem RFA autoanalyzer (Irwin et al. 1990). Data were obtained from B. Irwin (personal communication) and methods are described in Irwin et al. (1990). Water samples for chlorophyll and nutrient status measurements were taken primarily using a pumping system (Herman et al. 1984), although some samples were from the CTD rosette. The depths sampled for nutrient status measurements were usually chosen to coincide with depths chosen for photosynthesis measurements. At each depth, water was collected and filtered onto GF/C filters which were frozen for later analysis of chlorophyll, particulate carbon, nitrogen, and phophorus at the Freshwater Institute, Winnipeg. GF/C filters were used to allow comparisons with existing freshwater data sets and the nutrient status indicators (Table 4.1). A comparison of the results obtained using GF/C filters analyzed at the Freshwater Institute (FWI) and GF/F filters analyzed by the Bedford Institute of Oceanography (BIO) is given in Appendix 1. Linear regression of matched pairs of BIO and FWI data indicated the GF/C filters were missing 20 to 40 % of the particulate material which is not surprising. However, when the larger data sets were used from both Institutes the means for each analysis were quite similar (Appendix 1). Filtrate was kept cool and dark and later analyzed for total dissolved N and P at the Freshwater Institute. Particulate silicate was measured on polycarbonate filters with a pore size of 0.2 μm (Stainton, unpubl. data). Chlorophyll was analyzed as described in Guildford et al. (1994) and

particulate C, N, and P as in Stainton et al. (1977). Total N (TN) and total P (TP) are the sum of the total dissolved and particulate fractions. NO_3 measured at the FWI and BIO were highly correlated (Appendix 1) but the FWI values were lower. SRSi was higher at the FWI (Appendix 1). In this paper the BIO nutrient data are presented because they are more complete. The chlorophyll and particulate are all FWI analyzed data.

Nutrient Status Measurements

Phytoplankton nutrient status measurements consisted of five seston composition ratios (C:N, C:P, C:chl, C:Si and N:P) and three metabolic indicators (alkaline phosphatase activity [APA] and N debt both expressed per unit chl, and Si demand expressed per unit of suspended Si). Nutrient composition ratios were calculated on an atom:atom basis for C:N, C:P, C:Si and N:P, and an atom:weight basis for C:chl.

Alkaline phosphatase activity, an indicator of P-deficiency, was measured fluorometrically (Healey and Hendzel 1979b) using 5 μM ortho-methyl-fluorescein-phosphate as the substrate. Parallel determinations were made of total and soluble activities to distinguish between APA associated with particles and APA in solution; the soluble activity was that passing through 0.2 μm filters. The difference normalized to chlorophyll is reported as particulate activity.

The N debt assay was used in conjunction with particulate C:N ratios to determine N-deficiency. The assay is based on the work of Healey (1977) who

demonstrated that several species of algae took up more ammonium (NH_4^+) in the dark when N-deficient than when N-sufficient. For the N debt assay, 100 mL of unfiltered sample was enriched with ammonium chloride to yield a final concentration of ≈5 μM N. Ammonium was measured (Stainton et al. 1977) on triplicate subsamples at the beginning and end of the incubation. Samples were incubated in the dark at room temperature (18-24°C). Nitrogen debt was calculated as the NH_4^+ removed over a 24 h period per unit of chl (Healey 1977). Silicate demand (using sodium silicate) was measured in plastic test tubes but otherwise in a similar way to N debt, except uptake was normalized to suspended silicate. Values indicative of presence or absence or degree of nutrient-deficiency for the nutrient status indicators are given in Table 4.1. Unlike the N debt assay, the Si demand assay has not been tested on laboratory cultures of algae grown at different growth rates in nutrient-limited continuous culture. Therefore, the Si demand results can only be examined for their relative values. It is assumed that as the ratio increases the diatoms will be more Si-limited. However, Parslow et al. (1984) found that severely Si deficient cells experienced a lag before they could take up Si. The 24 h incubation for the Si demand assay may not be long enough for severely Si-deficient cells. The particulate C:Si ratio is also used as an indicator of Si-deficiency.

The maximum rate of photosynthesis (B. Irwin, unpubl. data) was obtained from ^{14}C uptake experiments on water samples incubated at different light intensities and *in situ* temperatures in a shipboard incubator (Irwin et al. 1990).

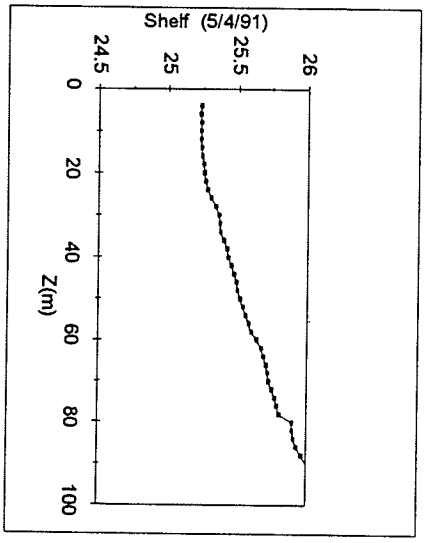
Results

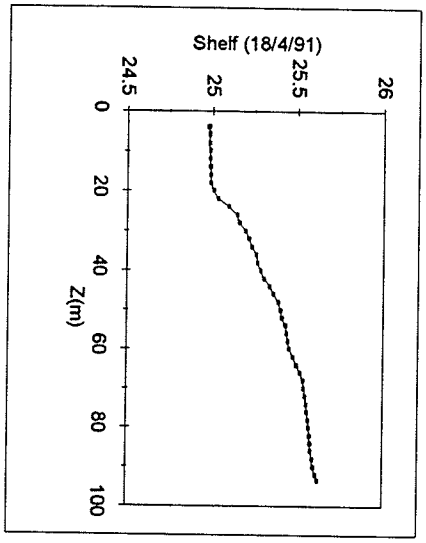
The Physical Chemical Environment

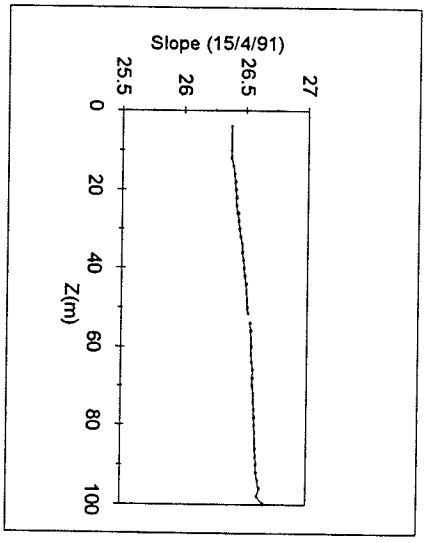
Density stratification is an important water column physical feature as it affects both the light environment and nutrient supply to the phytoplankton through its definition of mixing depth and isolation of nutrient rich deep water. Although all three locations were quite dynamic with respect to density profiles, representative profiles (Fig. 4.2) illustrate the basic patterns. The Shelf and Slope water were only weakly stratified according to the σ_t profiles (Fig. 4.2), although on the return visit to the Shelf water there appeared to be a slightly stronger density gradient in the 20-30 m range (Fig. 4.2). The Sargasso Sea water was clearly stratified on arrival on station during April 9, but strong winds began to erode the density gradient almost immediately (Fig. 4.2).

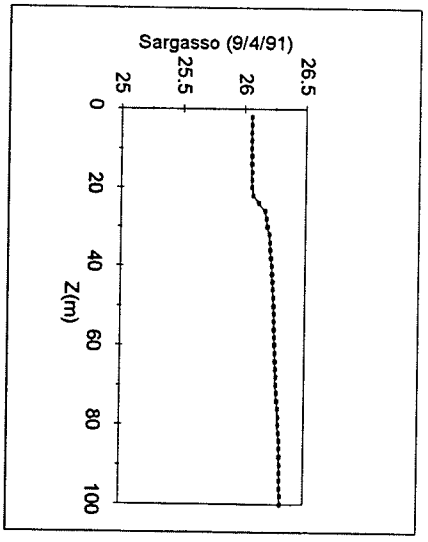
Mean temperature, salinity and phosphate concentration in the upper mixed layers were significantly different in the Shelf water, Slope water and Sargasso Sea ($p<0.001$, Fig. 4.3a, b, c). Nitrate and silicate concentrations were not significantly different in the Shelf and Slope water, but concentrations in the Sargasso Sea were significantly lower than either of these sites ($p<0.001$, Fig. 4.2d, e). The highest variability was observed in the nitrate and silicate concentrations in the Shelf water. The variability was due to vertical variability within the mixed layer rather than variability between profiles at the same location. The TN:TP ratio increased from the Shelf to Sargasso transect, driven mainly by the decreasing TP concentrations (Fig. 4.3f, Table 4.2).

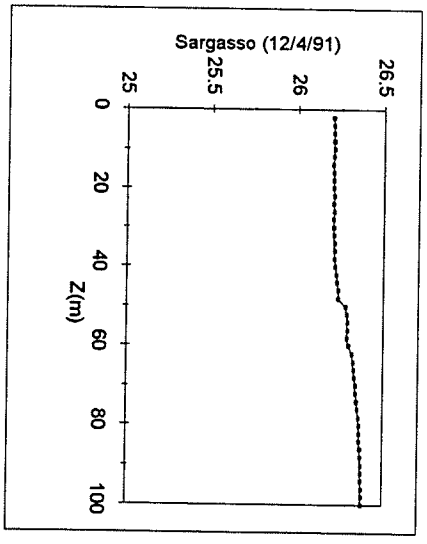
Figure 4.2. Representative σ_t profiles from the Shelf, Slope and Sargasso Sea.


Shelf (5/4/91)
24.5
25
25.5
26
0
20
40
60
80
100
Z(m)


Shelf (18/4/91)
24.5
25
25.5
26
0
20
40
60
80
100
Z(m)


Slope (15/4/91)
25.5
26
26.5
27
0
20
40
60
80
100
Z(m)


Sargasso (9/4/91)
25
25.5
26
26.5
0
20
40
60
80
100
Z(m)


Sargasso (12/4/91)
25
25.5
26
26.5
0
20
40
60
80
100
Z(m)

Biological Variables

Chlorophyll and the nutrient status indicators, particulate C:N, C:chl, and alkaline phosphatase activity, were significantly different in the Sargasso Sea water as compared to the Shelf and Slope water (Fig. 4.4). Particulate C:chl, a non-specific indicator of phytoplankton nutrient-deficiency, alkaline phosphatase activity, an indicator of phosphorus deficiency and particulate C:N, an indicator of nitrogen deficiency, all increased along the onshore to offshore transect (Fig. 4.4). In the Sargasso Sea, the mean C:P, also an indicator of P-deficiency, was greater than the Slope or Shelf water, but because of the large range in values, the difference in C:P ratios at the three sites was not considered significant (Fig. 4.4). Particulate N:P (Fig. 4.4), used in freshwater as a P-deficiency indicator, had a similar range (5-15) at all three areas and would not imply P-deficiency for phytoplankton by the criterion of Healey and Hendzel (1980) (Table 4.1). Particulate C:Si was high in the Slope water (Fig. 4.4).

Variability in the N debt and Si demand assays was high (Table 4.2). There were no clear trends in the N debt data either within or between stations. At each of the three sites, we observed uptake of NH_4^+ on one occasion and release on the remaining 2 to 4 times that samples were measured for N debt. At both the Shelf station (Y) and the Sargasso Sea station (S), samples exhibiting NH_4^+ uptake also had the highest C:N particulate values measured there (Table 4.2).

Silicon was taken up by phytoplankton in the Shelf water samples (Table 4.2). Values were highest on the last day, on the shelf, and coincided with high N

Figure 4.3. Means for chemical and physical variables in the upper mixed layer at the Shelf, Slope and Sargasso Sea sampling locations. TN:TP = total nitrogen:total phosphorus, NO_3^- = nitrate, PO_4^{3-} = phosphate, and SRSi = soluble reactive silicate. Bars represent $\pm$ one standard deviation (data in Appendix 1).

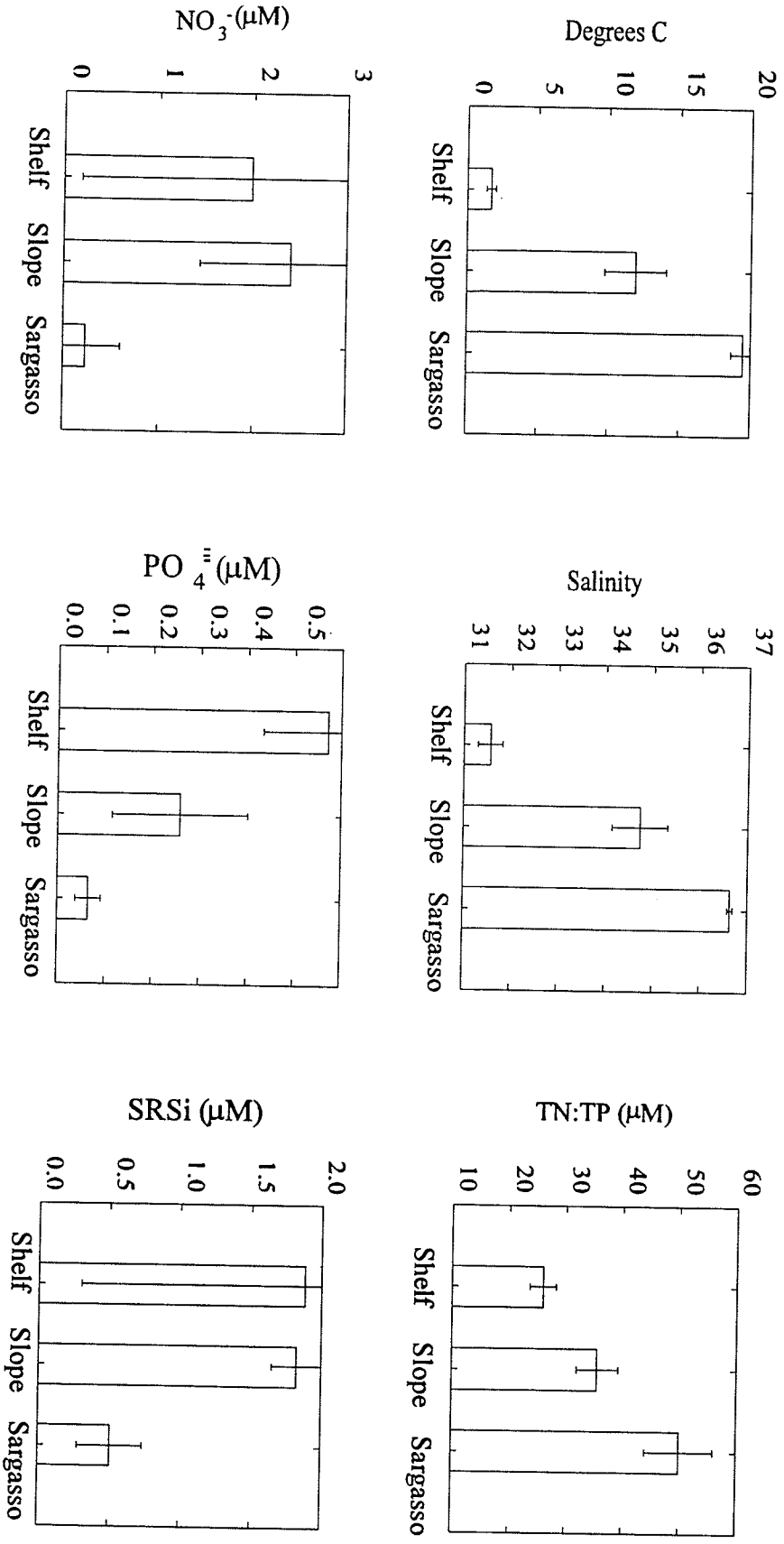

Degrees C
0
5
10
15
20
Shelf
Slope
Sargasso
NO_3^- (µM)
0
1
2
3
Shelf
Slope
Sargasso
Salinity
31
32
33
34
35
36
37
Shelf
Slope
Sargasso
$PO_4^{\equiv}$ (µM)
0.0
0.1
0.2
0.3
0.4
0.5
Shelf
Slope
Sargasso
TN:TP (µM)
10
20
30
40
50
60
Shelf
Slope
Sargasso
SRSi (µM)
0.0
0.5
1.0
1.5
2.0
Shelf
Slope
Sargasso

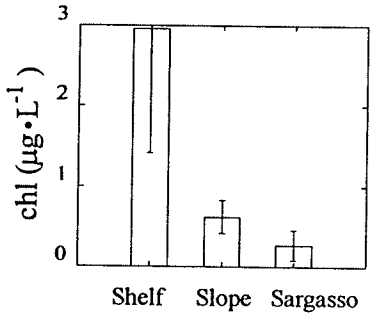
Table 4.2. Summary of upper mixed layer chemical and biological data collected along the Shelf, Slope, Sargasso Sea transect from April 4-19, 1991. Z = depth (m); Lat = latitude; Long = longitude; TN:TP = total nitrogen, total phophorus atomic ratio; chl = chlorophyll *a* ($\mu g \cdot L^{-1}$); C:N, C:P. N:P, C:Si = particulate carbon, nitrogen, phophorus, silicon atomic ratios; C:chl = particulate C:chl ($\mu mol \cdot \mu g^{-1}$); APA = alkaline phosphatase activity ($\mu mol\ P \cdot \mu g\ chl^{-1} \cdot h^{-1}$); N debt = nitrogen debt ($\mu mol\ N \cdot \mu g\ chl^{-1}$); Si demand = silicon demand ($\mu mol\ Si \cdot \mu mol\ particulate\ Si^{-1}$); $P_{opt} \cdot C^{-1}$ = light-saturated rate of photosynthesis normalized to particulate carbon ($\mu mol \cdot \mu mol^{-1} \cdot h^{-1}$).

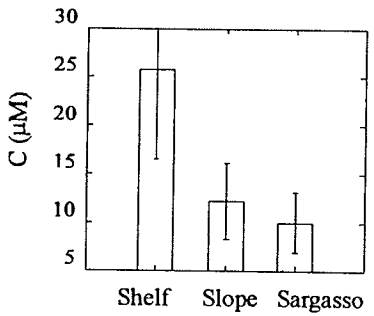
Z	Lat	Long	TN:TP	Chl	C:N	C:P	N:P	C:chl	C:Si	APA	N debt	Si demand	$P_{opt} \cdot C^{-1}$
Shelf April 4-7, 1991													
20	4321	6510	27	5.64	7.0	85	12	5	5	0.000	NA	0.003	0.033
40	4321	6510	28	4.76	8.0	121	15	5	4	0.001	-0.069	0.046	0.033
10	4320	6510	27	3.32	8.1	93	12	9	13	0.002	-0.384	-0.028	0.036
1	4320	6510	21	3.07	7.7	82	11	10	9	0.000	-0.439	0.097	0.027
10	4320	6510	25	4.54	7.5	89	12	7	8	0.001	-0.111	0.230	0.032
30	4320	6510	26	2.99	7.4	67	9	7	8	0.000	-0.426	0.021	0.031
1	4316	6514	26	2.99	10.4	90	9	12	10	0.002	0.319	0.214	NA
5	4316	6514	22	3.4	10.0	107	11	13	11	0.002	0.096	0.313	NA
Shelf April 18-19, 1991													
5	4319	6513	30	0.82	6.7	70	10	19	13	-0.001	NA	-0.036	NA
20	4319	6513	28	1.23	7.2	68	9	14	11	-0.001	-0.094	0.088	0.006
60	4319	6513	26	1.06	8.2	62	8	9	4	0.005	NA	0.118	NA
1	4320	6510	28	1.32	6.3	81	13	16	10	NA	NA	NA	NA
25	4320	6510	25	1.36	6.8	45	7	9	5	NA	NA	NA	NA
35	4320	6510	25	1.13	7.8	41	5	6	2	NA	NA	NA	NA

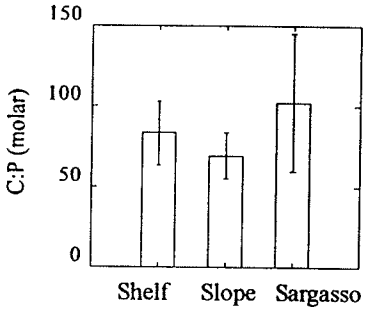
Table 4.2. Cont'd.

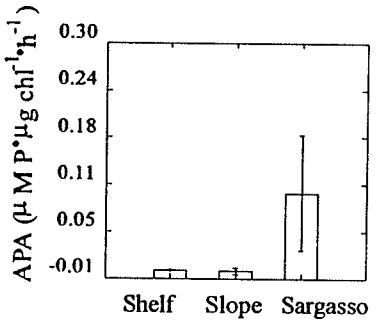
Z	Lat	Long	TN:TP	Chl	C:N	C:P	N:P	C:chl	C:Si	APA	N debt	Si demand	P_{opt}·C^{-1}
Slope April 15-17, 1991													
20	4015	6435	33	1.07	7.8	89	11	19	43	0.001	2.085	0.239	0.014
40	4015	6435	33	0.77	6.6	78	12	19	30	-0.001	1.323	0.406	0.011
10	4022	6445	32	0.51	7.1	72	10	23	27	-0.001	NA	NA	0.007
30	4022	6445	41	0.44	8.2	72	9	27	30	-0.009	NA	NA	0.022
50	4022	6445	40	0.57	6.4	62	10	18	47	0.001	NA	NA	0.013
10	4194	6428	34	0.48	8.3	78	9	26	16	0.004	-0.792	NA	NA
30	4194	6428	36	0.58	7.4	62	8	17	16	0.004	-0.466	NA	NA
Sargasso Sea April 9-14, 1991													
1	3601	6330	53	0.10	15.2	168	11	108	16	0.090	6.370	-0.217	0.008
20	3601	6330	52	0.06	14.6	129	9	208	29	0.250	2.133	-0.856	0.010
40	3601	6330	49	0.17	11.7	103	9	59	20	0.212	-0.671	-0.698	0.010
30	3610	6311	41	0.10	10.6	129	12	83	11	0.130	-22.60	0.159	NA
70	3610	6311	53	0.31	9.5	78	8	24	8	0.063	-7.742	0.171	NA
30	3609	6245	53	0.05	10.5	78	7	150	8	0.200	-6.400	NA	NA
50	3609	6245	53	0.1	11.7	95	8	92	3	0.065	-15.90	NA	NA
80	3609	6245	46	0.13	13.1	78	6	58	9	0.000	-12.92	NA	NA
30	3547	6237	50	0.46	15.8	198	13	42	8	0.097	NA	NA	NA
60	3547	6237	64	0.53	10.0	78	8	19	12	0.059	NA	NA	NA
80	3547	6237	54	0.47	11.7	78	7	21	18	0.041	NA	NA	0.013
10	3843	6342	44	0.17	12.8	71	6	54	10	0.100	NA	NA	0.012
50	3843	6342	42	0.54	9.7	65	7	15	12	0.016	NA	NA	0.020
75	3843	6342	45	0.4	11.7	58	5	19	19	0.011	NA	NA	0.011

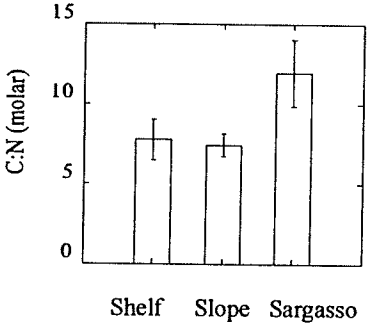
Figure 4.4. Means for biological variables in the upper mixed layer at the Shelf, Slope and Sargasso Sea sampling locations. chl = chlorophyll *a*, C = particulate carbon, C:P = particulate C:particulate phosphorus, APA = alkaline phophatase activity normalized to chl, C:N = particulate C:particulate nitrogen, C:chl = particulate C:chl, N:P = particulate N:particulate P, C:Si = particulate C:particulate silicon. Bars represent $\pm$ one standard deviation (data in Appendix 1).

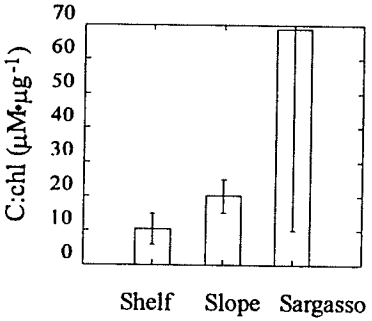

chl (µg•L-1)
3
2
1
0
Shelf
Slope
Sargasso

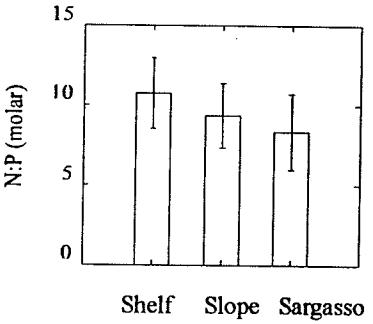

C (µM)
30
25
20
15
10
5
Shelf
Slope
Sargasso

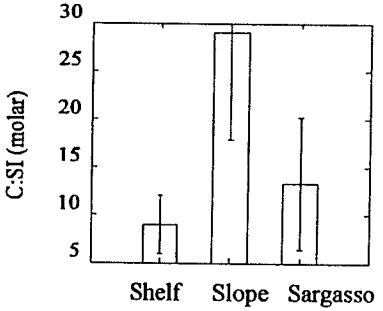

C:P (molar)
150
100
50
0
Shelf
Slope
Sargasso


APA (µ M P•µg chl-1•h-1)
0.30
0.24
0.18
0.11
0.05
-0.01
Shelf
Slope
Sargasso


C:N (molar)
15
10
5
0
Shelf
Slope
Sargasso


C:chl (µM•µg-1)
70
60
50
40
30
20
10
0
Shelf
Slope
Sargasso


N:P (molar)
15
10
5
0
Shelf
Slope
Sargasso


C:SI (molar)
30
25
20
15
10
5
Shelf
Slope
Sargasso

debt and general indicators of nutrient-deficiency. In the Slope water, Si demand was only measured once and it was high relative to other samples (Table 4.2). This area also had the highest C:Si particulates ratios. Release of Si during a Si demand experiment was observed in one of the Sargasso Sea profiles.

Discussion

Shelf Water: No Nutrient-Deficiency

Ambient nutrient concentrations (Fig. 4.2), composition ratios (C:N, C:P, N:P, C:chl, C:Si), APA and N debt assays (Table 4.2), as well as high chlorophyll concentrations (Table 4.2), all indicate no nutrient-deficiency in the Shelf water during the first three days on station. Unless light or some other physical factor such as temperature is limiting phytoplankton growth, lack of nutrient-deficiency is an indication that phytoplankton are growing at or near their maximum growth rates for those conditions. Another indicator of carbon turnover sometimes used as a surrogate for relative growth rate is the rate of photosynthesis at optimum light (P_{opt}) normalized to particulate C. P_{opt}:C ratios in Shelf water were higher than the P_{opt}:C ratios in Slope or Sargasso waters (Table 4.2) where nutrient status indicators also suggested lower growth rates. The good agreement between the nutrient status indicators and the P_{opt}:C ratios is consistent with the interpretation that phytoplankton at the Shelf station was not nutrient-limited and was growing at a relatively high rate. On day 4 at the Shelf station, ambient NO_3 was low and NH_4^+ became undetectable (W.G. Harrison unpublished data) and this coincided with an observed increase in the

particulate C:N ratio and dark uptake of NH_4^+ and silicate in the N debt and Si demand bioassays. These changes indicated that phytoplankton were becoming more nutrient deficient. On the return to the Shelf water at the end of the cruise, nutrients were readily detectable and nutrient status measurements indicated no nutrient-deficiency. However, chlorophyll concentrations were only 30% of the earlier concentrations (Table 4.2). The water column was more stably stratified on the return visit (Fig. 4.2). Sinking losses of slower growing diatoms (Waite et al. 1992) or increased grazing (Legendre et al. 1993) or advection may explain these low chlorophyll but nutrient sufficient conditions (refs).

Slope Water: Silicon Deficiency

Nutrient status measurements for N and P indicated Slope water phytoplankton was neither N nor P-deficient (Fig. 4.4, Table 4.2). Chlorophyll was low and P_{opt}:C was low compared to Shelf water (Table 4.2). Nitrate, silicon and phosphate were all well above detection levels (Fig. 4.3). The Slope water was distinctly different from the Shelf and Sargasso Sea water because of low silicon relative to nitrate (Fig. 4.3) and the particulate C:Si ratio was high relative to the Shelf and Sargasso stations (Fig. 4.4). High C:Si particulate ratios in the Slope water (Fig. 4.4) may be an indication that either few silica containing organisms were present in the particulate matter or that diatoms were silicon-deficient. Inspection of the preserved water sample showed very thinly silicified and slightly curved or bent *Navicula* type cells were present in the plankton however it is not clear whether they

were dominant or rare (H.J. Kling, pers. comm.). In culture, C:Si ratios in this range (30-40) would be indicative of extreme silicon deficiency (Paasche 1980; Brzezinski 1985; Ragueneau et al. 1994). The silicate demand assay (Table 4.2) for Slope water was high compared to Shelf and Sargasso Sea water. Recently, evidence for the enrichment of coastal areas in N relative to Si (Officer and Ryther 1990; Smayda 1990; Dortch and Whitledge 1992) supports the hypothesis that growth by diatoms in these coastal areas may be silicon-limited (Guildford 1993). In our data set the ratio of NO_3 to SRSi was higher in the Slope water than the Shelf water. The phenomenon of silicate limitation of nitrate demand may not be confined to coastal areas.

Sargasso Sea: Phosphorus Deficiency

Physical and chemical data (Fig. 4.3) and nutrient status measurements (Fig. 4.4, Table 4.2) confirm the oligotrophic, nutrient-deficient nature of the Sargasso Sea microplankton relative to the Slope and Shelf water at this time of year (April). The alkaline phosphatase results indicate severe P-deficiency and the elevated particulate C:N ratios indicate N-deficiency (Table 4.2). P-deficiency measurements in the oligotrophic Equatorial Pacific ocean were reported by Perry (1972) and Perry and Eppley (1981) and reports of P-deficiency in the anthropogenically affected Mediterranean (Hernandez et al. 1995) and coastal areas of China (Harrison et al. 1990b) are becoming more common.

The reason the Sargasso Sea microplankton may be strongly P-deficient while the Slope and Shelf waters are never P-deficient may be the result of loss of P

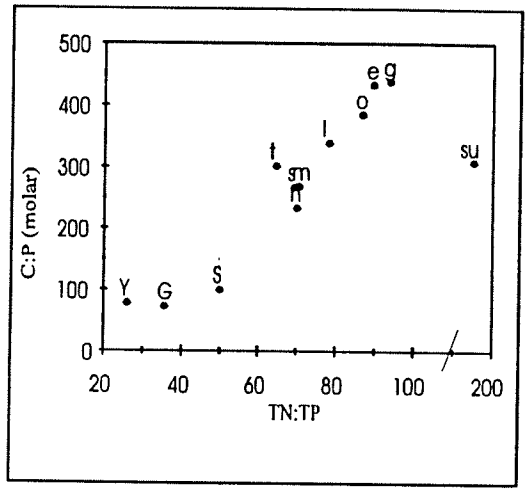
relative to N along the transect from the coast to deep ocean. Although both phosphate and nitrate become low in the Sargasso Sea relative to Shelf and Slope water, the ratio of TN:TP is much higher in the Sargasso Sea samples (Table 4.2, Fig. 4.3). N may be mineralized and returned to solution more readily than P in the upper layers of the ocean or N_2 from fixation may be a source of external N input (Carpenter and Roman 1991; Karl et al. 1995). P may be lost as the result of carbonate sedimentation as documented for the coastal ocean by Jensen et al. (1995).

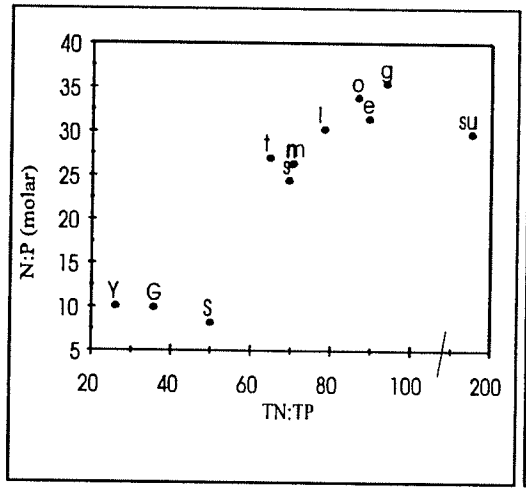
APA, C:chl, C:N, taken in aggregate, indicate P and N-deficiency in the Sargasso Sea in April. Low P_{opt}:C also is consistent with low relative growth rates as indicated by the nutrient status measurements. A high TN:TP ratio in combination with high APA suggests P-deficiency. However, there is some evidence that the nutrient status measurements may represent a P-deficient heterotrophic community rather than a P-deficient autotrophic community. The alkaline phosphatase activity in the Sargasso Sea may be primarily bacterial rather than algal. Bacteria have been shown to be better competitors then algae for PO_4 at low concentrations when organic carbon is available to sustain bacterial growth (Currie and Kalff 1984; Bjorkman and Karl 1994) and bacteria as well as algae can synthesize the enzyme alkaline phosphatase to cleave PO_4 from organic compounds (Cembella et al. 1984). In P-deficient, oligotrophic lakes, high rates of APA are generally accompanied by elevated particulate C:P and C:chl ratios. In the Sargasso Sea, the C:chl ratios were very high relative to the Slope and Shelf water and are in the range that in algal culture would indicate highly nutrient-deficient conditions and low growth rates

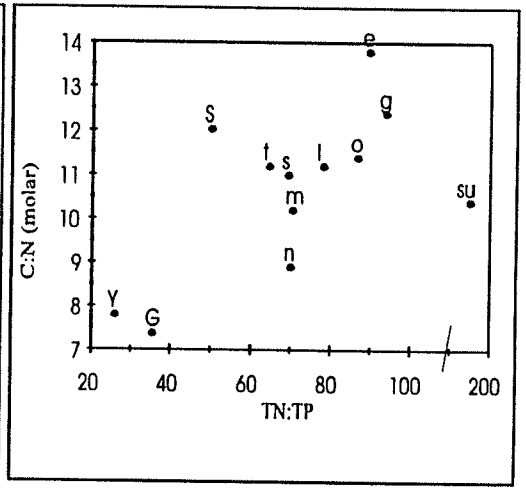
(Table 4.2). However, high C:chl would also occur if a significant portion of particulate material on the filter were non-photosynthetic. The C:chl ratio was extremely high in the Sargasso Sea (higher than in P-deficient lakes (Fig. 4.5) but the Shelf and Slope means for C:chl were not different from lakes (Fig. 4.5). The C:P ratio in the Sargasso was lower than in lakes (Fig. 4.5). Bacteria have more stable C:P ratios (Kirchman 1994; Wehr et al. 1994) and their dominance in samples would explain these ratios. The main response bacteria have to P-deficiency is enzymatic whereas algae can shift their composition considerably.

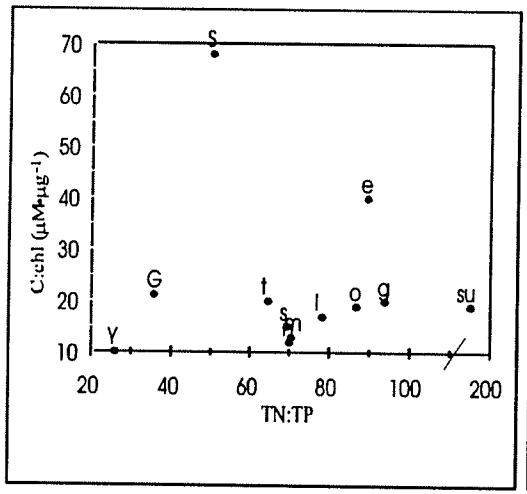
The C:P ratios in the upper 50 m of the Sargasso Sea were 50% higher than the Shelf or Slope water upon arrival on station (Table 4.2). After two days of stormy weather and deepening of the mixed layer (Fig. 4.2) the C:P ratios were lower, similar to those from the Slope and Shelf water, and in the range expected for P sufficient algae (Table 4.1). C:N ratios in the Sargasso Sea water (Table 4.2) were greater than those in Slope and Shelf waters ($p<0.001$) and were in the range expected for N-deficient algae (Table 4.1). During the first day on station, the water column was most strongly stratified and uptake of NH_4^+ was observed in the N debt bioassay. As stratification weakened due to the stormy weather, release of NH_4^+ was observed in N debt assays. One explanation could be that the bacteria were substrate-limited, near steady state growth rate, and in equilibrium with the nutrient-deficient algae while the water column was strongly stratified. It has been calculated

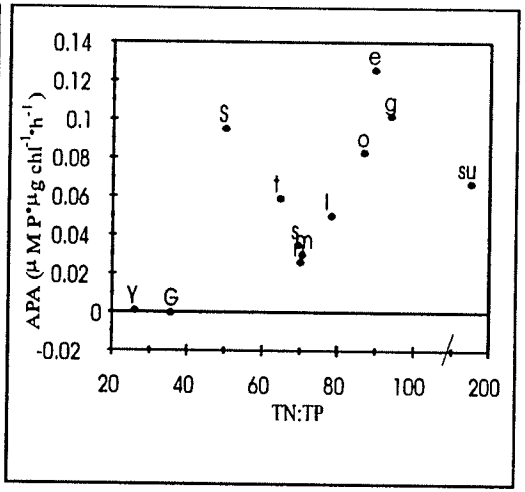
Figure 4.5. Mean biological variables plotted against the TN:TP (molar) ratio for the three marine locations and nine lakes on the Canadian Shield. $P_{opt} \cdot C^{-1}$ = photosynthesis at optimum light normalized to particulate C, Y = Shelf, G = Slope, S = Sargasso Sea, lower case letters refer to lakes in the NOLSS study described in Table 2.1 (Chapter 2). Other abbreviations as in Fig. 4.4.

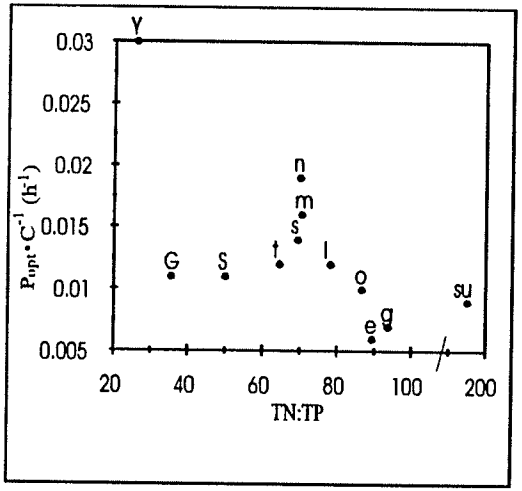

C:P (molar)
TN:TP
500
400
300
200
100
0
20
40
60
80
100
200
Y
G
S
t
sm
n
l
e
g
o
su


N:P (molar)
TN:TP
40
35
30
25
20
15
10
5
20
40
60
80
100
200
Y
G
S
t
m
s
l
o
e
g
su


C:N (molar)
TN:TP
14
13
12
11
10
9
8
7
20
40
60
80
100
200
Y
G
S
t
s
l
o
e
g
m
n
su


C:chl (µM•µg-1)
TN:TP
70
60
50
40
30
20
10
20
40
60
80
100
200
S
G
t
l
o
g
e
su
Y
sm


APA (µM P•µg chl-1•h-1)
TN:TP
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
20
40
60
80
100
200
e
g
S
o
t
l
su
Y
G
sm


Popt•C-1 (h-1)
TN:TP
0.03
0.025
0.02
0.015
0.01
0.005
20
40
60
80
100
200
Y
n
m
s
G
S
t
l
o
e
g
su

that the bacteria in this type of oligotrophic stratified situation must be growing slowly or phototrophs would completely disappear through nutrient competition (Fuhrman et al. 1989). With weakening of stratification and injection of nutrients, the P-limited bacteria would grow but release excess N which would be consistent with the N debt assay results. This scenario would also explain the initially high C:P ratios followed by lower C:P ratios. Bacteria have more stable stoichiometry than algae (Fuhrman et al. 1989; Kirchman 1994; Wehr et al. 1994). Given the capacity of bacteria to outcompete phytoplankton for P when organic substrates are available, it can be inferred that phytoplankton would also be P-limited in the Sargasso and have little capacity to store N.

Comparisons Between Marine and Freshwater

Data for the marine stations are the average of the values from all profiles at each station (mixed layer only) over a few days at most. Although most of the variables are significantly different between at least two of the stations, much longer data sets would be required to determine whether the values at each site are representative of annual values. In April there was a gradient from coastal to offshore with increasing water column stability, decreasing nutrient concentrations, decreasing biomass, increasing TN:TP ratio, increasing nutrient-deficiency and slower carbon turnover. The values that will be compared from freshwater are mixed layer means for each lake (five years of open water data). Lake-to-lake variation was much greater than variation due to seasonal or annual variation in the NOLSS data

set (Guildford et al. 1994 - Chapter 2). The gradients observed in the lake data were basically correlated with lake size. As lake size increased water column stability decreased, and phytoplankton nutrient-deficiency decreased while carbon turnover increased (Guildford et al. 1994 - Chapter 2; Fee et al. 1994).

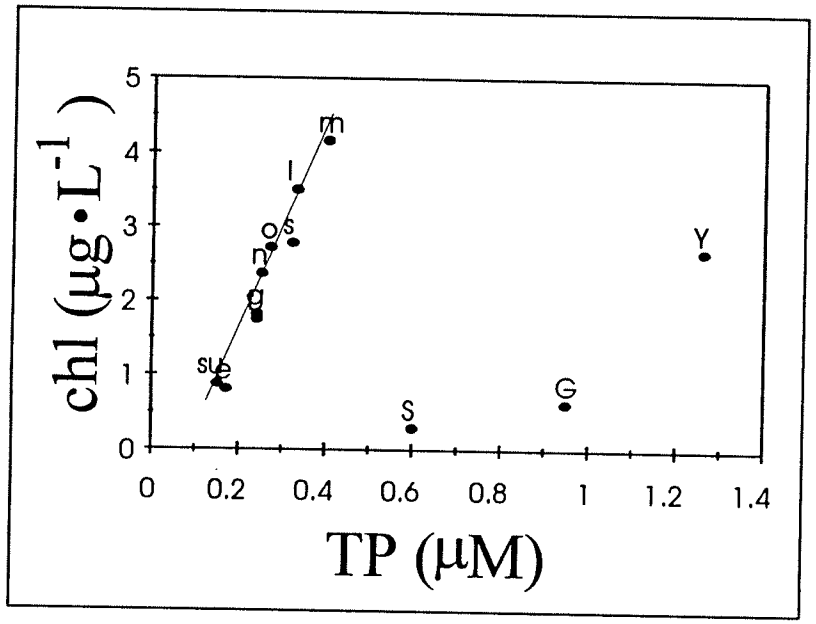
In most nutrient-limited lakes, chlorophyll concentration can be predicted from total nutrient pools (Molot and Dillon 1991). Chlorophyll concentration in the NOLSS study lakes were highly correlated to both TN and TP (Fig. 4.6) with the average chlorophyll-TP relationship being the same as that observed by Dillon and Rigler (1974) in many lakes. Using the same approach, chlorophyll in the three marine sites had little relation to TN (Fig. 4.6) and although there is a relationship between chlorophyll and TP (Fig. 4.6) compared to the lake data it appears that some factor other than or as well as P controls chlorophyll concentration. Since chlorophyll concentration is not always related to algal population growth rates, which can be affected by light, grazing, sinking and dilution, nutrient status measurements (used as indicators of relative growth rates in nutrient-deficient conditions) may be more meaningful for comparing marine and freshwater data.

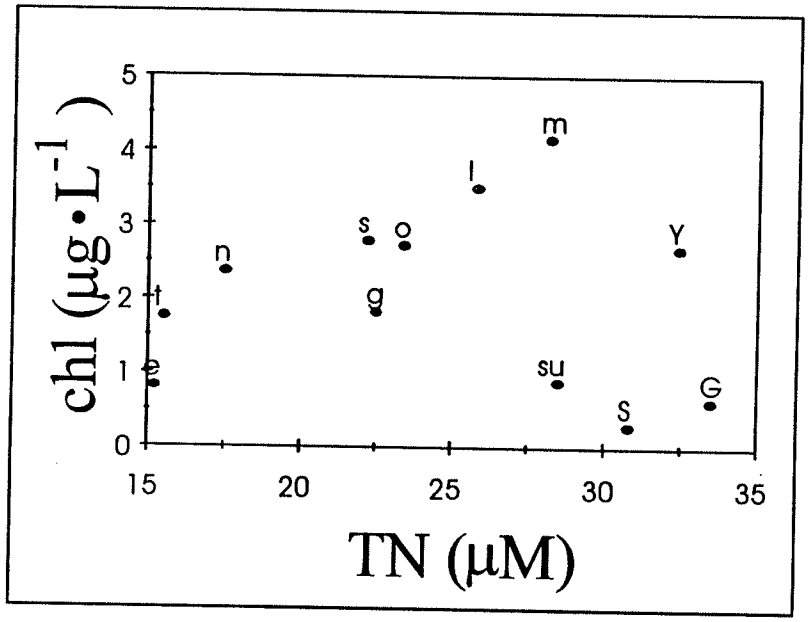
TN:TP is important in lakes as a predictor of whether N or P will be deficient (Healey and Hendzel 1980; Hendzel et al. 1994). When the marine data from this study are combined with the Northwestern Ontario Lake Size Study (NOLSS) data the TN:TP ratio ranges from a low of 25 in the Shelf water to a high of 200 in Lake Superior (Fig. 4.5). The particulate C:P ratio is often used in lakes as an indication of P-deficiency (Healey and Hendzel 1980; Hecky et al. 1993; Guildford et al. 1994 -

Chapter 2). If Superior is not included (it has anomalously high nitrate), then an almost straight line relationship exists between the TN:TP ratio and particulate C:P in the NOLSS lakes (Fig. 4.5a), indicating that at high TN:TP the particulate material will be highly P-deficient as indicated by high particulate C:P ratios. This relationship from freshwater would predict that the C:P ratios from the marine stations in this study would be much lower because TN:TP ratios are much lower and this is indeed what was observed in the April sampling (Fig. 4.5a). The mean C:P ratio in the Sargasso samples was slightly greater than in Slope or Shelf water, but as discussed above, the average of the C:P ratios in the Sargasso was not significantly different than the Slope or Shelf water. However, C:P ratios were higher than at other stations before the water column destabilized due to stormy weather. It is possible that the TN:TP values in the Sargasso are near a transition point with values above 50 tending to P-deficiency given stable physical conditions and adequate light. There is a similar relationship in lakes with particulate N:P, indicating P-deficiency, increasing as the TN:TP ratio increases. In steady state culture, N:P ratios greater than 22 indicate P-deficiency (Healey 1975). As with the C:P ratio, the relationship with TN:TP in lakes would predict no P-deficiency in the three marine stations (Fig. 4.5b).

The particulate C:N ratio is used fairly frequently as an indicator of N-deficiency in both freshwater and the sea (Goldman et al. 1979; Hecky et al. 1993; Smith et al. 1995). Values in culture greater than 8.3 indicate moderate N-deficiency and values greater than 14.6 indicate severe N-deficiency in five

Figure 4.6. Mean chlorophyll *a* (chl) plotted against total phosphorus (TP) and total nitrogen (TN). Abbreviations as in Fig. 4.5. The solid line is the chl-TP relationship of Dillon and Rigler (1974).


chl (µg•L-1)
TP (µM)
0
1
2
3
4
5
0
0.2
0.4
0.6
0.8
1
1.2
1.4
su
e
g
n
o
s
l
m
S
G
Y


chl (µg•L-1)
TN (µM)
0
1
2
3
4
5
15
20
25
30
35
t
e
n
g
s
o
l
m
su
S
G
Y

freshwater algal species (Healey and Hendzel 1979a). When particulate C:N ratios for the three marine stations and the NOLSS study lakes are plotted against the TN:TP ratio, the C:N ratio increases as the TN:TP ratio increases which is not what would be expected if TN:TP was the main controlling factor. N is clearly not deficient in the Shelf and Slope water even though the amount of nitrogen is low relative to P. In the Sargasso and in all but one of the lakes, the C:N ratio indicates some degree of N-deficiency. In the lakes it is the smaller, strongly stratified lakes that are most N-deficient and in the sea it is the Sargasso which is more stable than either the Slope or Shelf water that is N-deficient. High water column stability results in nutrient loss through sedimentation and eventually can impose both N and P-deficiency on the microbial community.

C:chl is used as a general indicator of nutrient-deficiency (Healey and Hendzel 1980) with high ratios indicating nutrient-deficiency, but also as an indicator of light-deficiency with low ratios of C:chl indicating light-deficiency (Laws and Bannister 1980). In the NOLSS study lakes, the C:chl ratio increased as the TN:TP ratio increased in basically the same pattern as the C:P and N:P ratios. The Sargasso samples had extremely high C:chl ratios indicating extreme nutrient-deficiency, or a high relative abundance of non-autotrophs. The Slope water had C:chl ratios in the same range as the strongly P-deficient lakes (Fig. 4.5). As discussed above, Si may be indirectly affecting the C:chl ratio by reducing N uptake and chlorophyll synthesis in the Slope water. The C:chl ratio (and other conceptual ratios) in the Shelf water indicate no nutrient-deficiency.

When the marine and freshwater data for APA are compared, the Sargasso groups with the P-deficient lakes (Fig. 4.5) and although there is not a linear relationship between APA and TN:TP as seen for the C:P ratio, as the TN:TP ratio approaches or exceeds 50 indications of P-deficiency emerge (Fig. 4.5).

Nutrient status indicators are useful for inferring relative growth rates in natural phytoplankton populations that are nutrient-stressed. When phytoplankton is strongly nutrient stressed, growth rates must be low relative to maximum growth rates for the ambient light and temperature environment. When nutrient status measurements indicate no nutrient-deficiency, growth rates will be higher than in nutrient stressed populations unless some physical factor such as light or temperature replaces nutrient-deficiency. Of course, the measurements used in this study focussed on the macronutrients N, P and Si. No assay was available for micronutrients such as Fe which can control growth rates in culture (Harrison and Morel 1986) and in nature (Price et al. 1994). The maximum rate of photosynthesis normalized to particulate carbon is sometimes used to infer carbon turnover in natural populations. When P_{opt}:C values in the NOLSS and marine study are compared, the Shelf station appears to have much higher carbon turnover than the Slope, Sargasso or any of the lakes. This high carbon turnover is consistent with the nutrient status data, i.e. no nutrient-deficiency on the Shelf and some degree of nutrient-deficiency in all the other stations both marine and freshwater. In the NOLSS study, there was a significant correlation between decreasing carbon turnover and increasing nutrient-deficiency as indicated by APA and C:chl. When the three

marine stations are superimposed on this freshwater relationship between APA as an indicator of P-deficiency and P_{opt}:C as an indicator of carbon turnover, the Shelf and Sargasso points fit remarkably well with the study lakes (Fig. 4.7). The Slope station is an exception, but as discussed previously, the carbon turnover in Slope water may be low because of Si-deficiency. When P_{opt}:C is plotted against the general nutrient-deficiency indicator C:chl, the marine and freshwater points fall on the same line (Fig. 4.8).

A comparison of three different oceanic and several freshwater regimes shows a common dependence of carbon turnover on nutrient status. In both studies, processes related to phytoplankton growth were examined along a strong physical chemical gradient. In both studies, it was clear that physical stability and nutrient supply were both important factors in determining the nutrient status of phytoplankton. In the marine study along the coastal to offshore gradient, the water column was more stable away from the coast in the Sargasso Sea and nutrient supply was much lower and in different ratios than the upwelling Shelf region. The combination of more stable water column and low nutrient supply leads to strong nutrient-deficiency and low rates of carbon turnover. In the group of lakes which were chosen to be similar in geology, climate and long water renewal times (>5 yr) but wide ranging in terms of size (0.29-82,300 km^2), water column stability decreased with increasing lake size and nutrient supply to phytoplankton increased with increasing lake size.

Figure 4.7. Mean photosynthesis at optimum light normalized to particulate carbon ($P_{opt} \cdot C^{-1}$) plotted against alkaline phosphatase activity normalized to chlorophyll *a* (APA). Abbreviations as in Fig. 4.5.

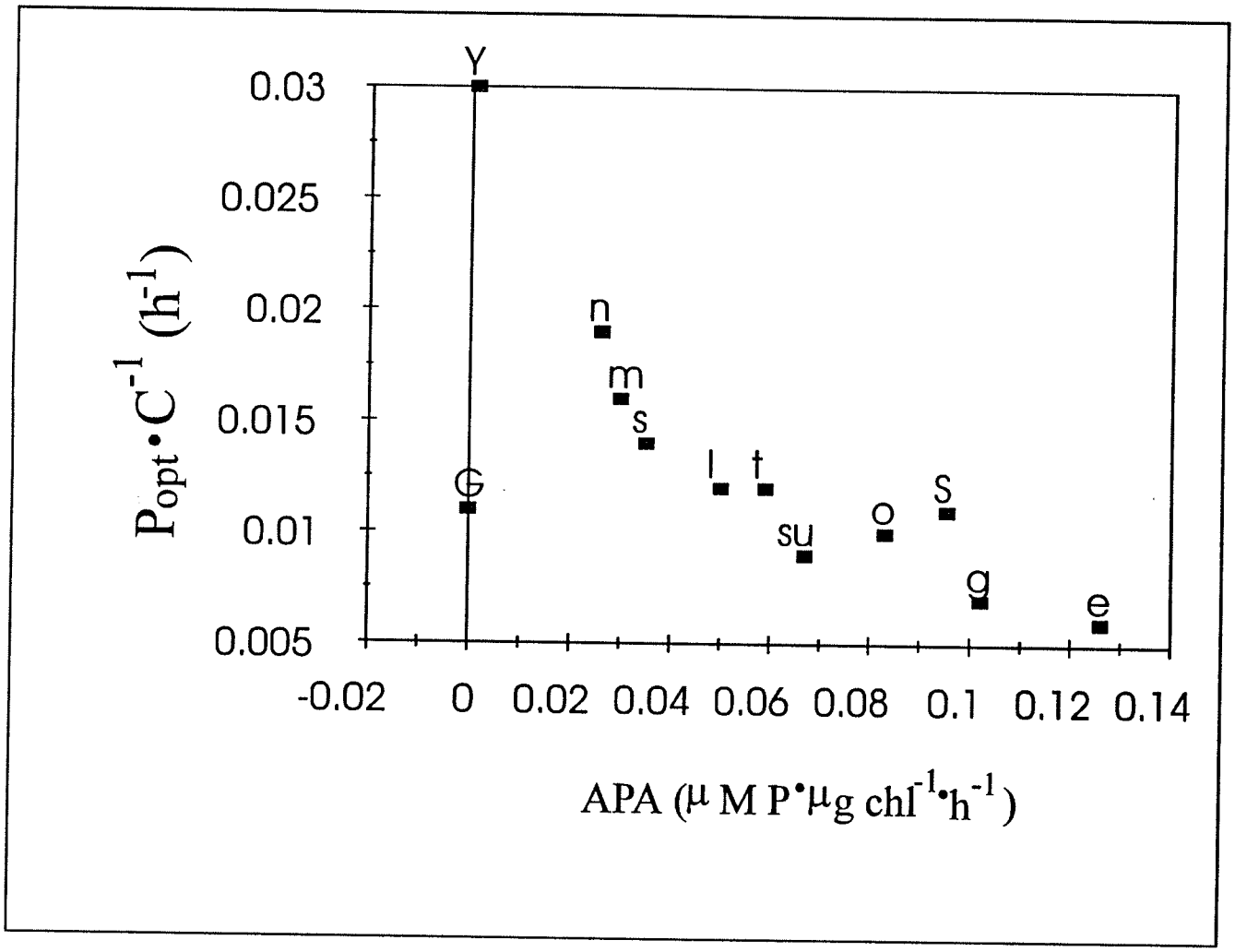
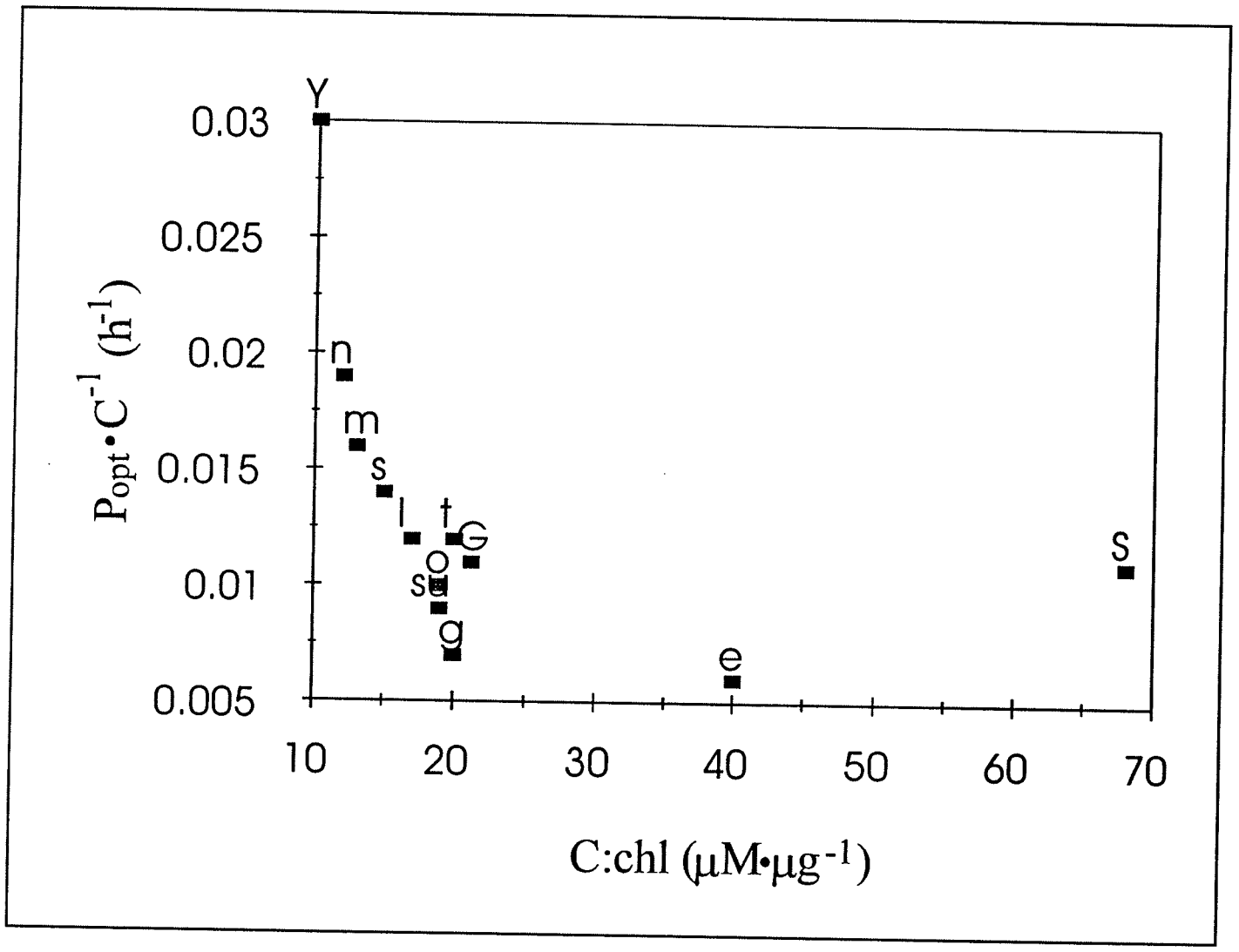

Y
0.03
0.025
0.02
0.015
0.01
0.005
n
m
s
l
t
G
su
o
S
g
e
-0.02
0
0.02
0.04
0.06
0.08
0.1
0.12
0.14
$P_{opt} \cdot C^{-1}$ (h^{-1})
APA (μ M P $\cdot \mu$g $chl^{-1} \cdot h^{-1}$)

Figure 4.8. Mean $P_{opt} \cdot C^{-1}$ plotted against C:chl for the three marine locations and nine lakes on the Canadian Shield. Abbreviations as in Fig. 4.5 and Fig. 4.4.


Y
n
m
s
l
t
G
o
s
g
e
S
0.03
0.025
0.02
0.015
0.01
0.005
10
20
30
40
50
60
70
$P_{opt} \cdot C^{-1}$ (h^{-1})
C:chl ($\mu M \cdot \mu g^{-1}$)

Physical stability increases along the coastal to offshore ocean transect. Distance from the continental land mass also affects the external supply of nutrients to the ocean as well as internal supply of nutrients from deep mixing. Thus, it is not surprising that surface waters in the open ocean stations have much lower nutrient concentrations than coastal or Slope waters. What is surprising is that the ratio of TN to TP in the Sargasso Sea water is so much higher than in coastal waters. In the open ocean away from land masses, an important source of external nutrient supply is rainwater. The TN:TP atomic ratio of rainwater over the NOLSS study lakes was 80 (Fee et al. 1994). Similar data are not readily available for rainwater at ocean sites. However, recently it has been suggested that dissolved organic N in rain may be an important source of N to the oceans (Cornell et al. 1995; Galloway et al. 1995) and data in Duce et al. (1991) and Paerl (1993) indicate the ratio of total N to total P for the oceanic rain may also be high. When offshore oceanic surface waters are stable and isolated from deep ocean waters, this high TN:TP input would tend to push the microplankton toward P-deficiency, which is what we found.

Chapter 5

The Importance of Stratification to the Balance Between Phytoplankton, Nitrogen and Light-Deficiency in the Northwest Passage (Barrow Strait)

Abstract

In Barrow Strait (Canadian Eastern Arctic) nutrient status indicators (particulate C:N, N debt) showed that N was severely limiting phytoplankton growth and carbon turnover in the upper 10 m of stratified waters. Below 10 m in stratified water columns and at all depths in unstratified water columns, we found either moderate or no N-deficiency. *In situ* NO_3 concentration was not a good predictor of the presence of N-deficiency. We found no consistent indication of Si or P-deficiency although rates of alkaline phosphatase activity were surprisingly high. Carbon turnover at optimum light in samples taken from below the stratified layer or from unstratified water columns was generally greater than that in samples from the severely N-deficient mixed layer. However, light extinction and photosynthetic light response data indicate that phytoplankton below the stratified layer was not growing at optimum rates. At one location, N-deficiency was replaced by light-deficiency followed by N-deficiency again within 10 days. Both light and N are important factors to consider when modelling phytoplankton growth in the Barrow Strait and in similar Arctic waters where the mixture of ice and open water creates a dynamic environment with respect to stratification and mixing. The high frequency with which environmental conditions fluctuate in the Barrow Strait may contribute to high productivity.

Introduction

There are several valid reasons to study the controlling factors of phytoplankton growth in the Arctic Ocean. Firstly, how much CO_2 that contributes to increasing greenhouse gases is biologically fixed by the world's oceans? Secondly, are levels of primary productivity in the short Arctic spring and summer adequate to support the seasonally high abundance of consumers? Thirdly, will changes in nutrient status brought on by anthropogenic influences such as increased nutrient loading or climate change affect the quantity and/or quality of consumers of primary productivity given that in freshwater the growth rate of consumers is demonstrably linked to the quality or nutrient status of the food ration (Thompson and Harrison 1992; Sterner and Hesson 1994)? Fourthly, transfer of organic contaminants to higher levels in the food web has been demonstrated to be related to phytoplankton growth rates in the Laurentian Great Lakes (Taylor et al. 1991; Swakhammer and Skoglund 1993). Since it has already been demonstrated that organic contaminants from industrial areas of the world are found in anomalously high concentrations in top levels of the Arctic food web (Muir et al. 1988), it is important that this relationship be examined in the Arctic.

Although there is general consensus that phytoplankton growth in open waters of the Arctic Ocean is primarily controlled by nutrient-limitation after the spring bloom due to shallow stratification (Smith and Sakshaug 1990; Harrison and Cota 1991), there has been little opportunity to observe the spatial and temporal extent of that nutrient-limitation. Most observations have been based on oceanographic cruises

where it is difficult to obtain data at one location over more than a few days. This study tries to provide a slightly longer term and more continuous snapshot of local variability in space (both horizontally and vertically) and time. Because the data contain indicators of phytoplankton growth rates as well as measurements of chemical and physical parameters, the study should be useful for expansion of models of Arctic productivity based on the premise that nutrient-limitation driven by stratification controls primary productivity (Slagstad and Stole-Hansen 1991). Wallace et al. (1995) note that Arctic water has a lower N:P ratio than Atlantic water and speculate that N-deficiency observed along the east coast of North America is the result of the low N:P ratios originating in the Arctic Ocean. In this study, the TN:TP ratio of Barrow Strait water is compared to some other marine and freshwater systems where we also have TN:TP ratios and nutrient status measurements.

This study seeks to understand the relationships between physical parameters (light and temperature profiles), chemical parameters (ambient nutrient concentrations) and biological parameters of phytoplankton nutrient status (composition ratios, N, P and Si uptake and alkaline phosphatase activity) and photosynthesis. Phytoplankton nutrient status is an indicator of phytoplankton growth rate (Healey and Hendzel 1979; Dortch et al. 1985).

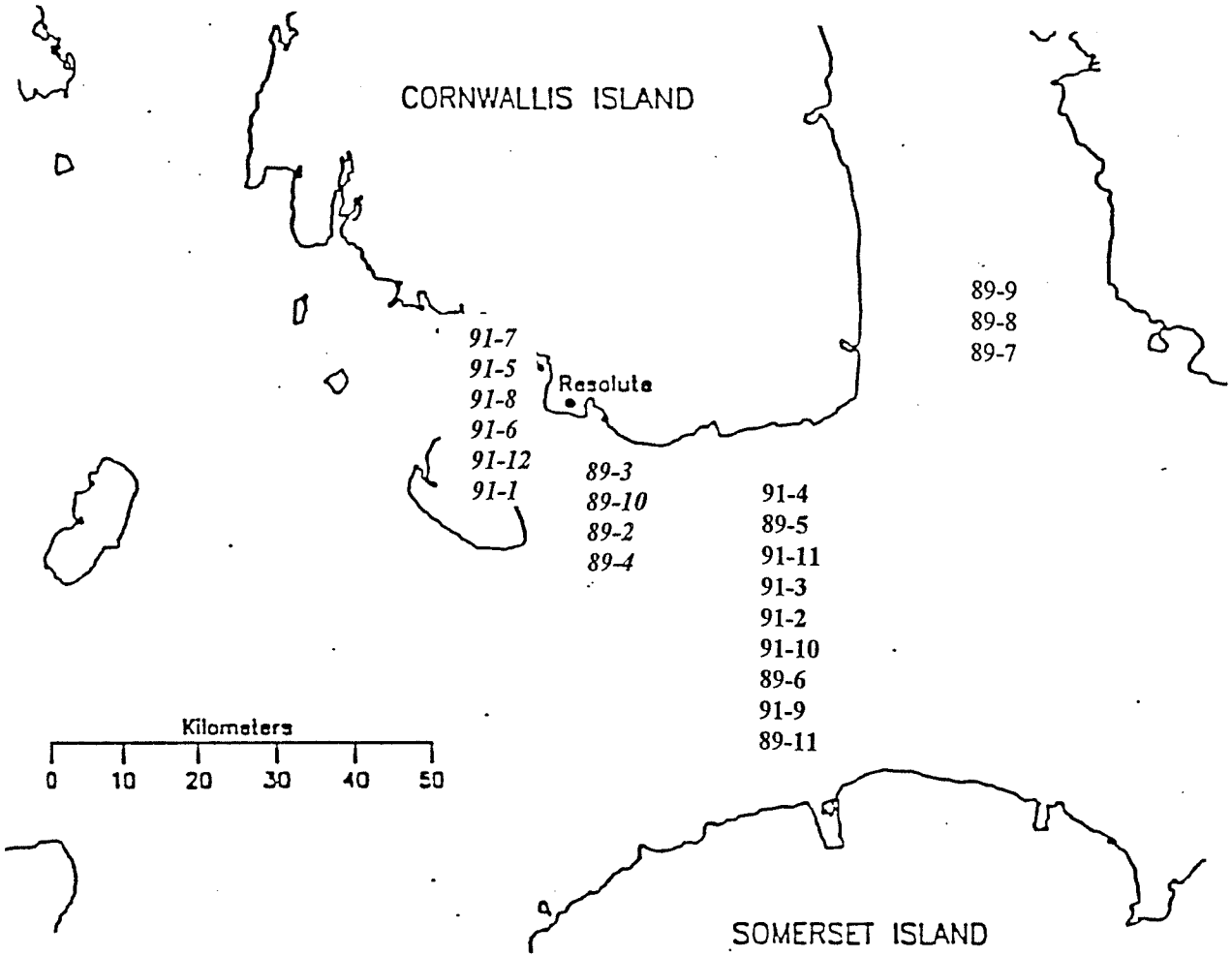
Methods

Study Area and Field Sampling

Barrow Strait is located at a central part of the Northwest Passage in the Canadian Eastern Arctic. Cornwallis Island lies to the north and Somerset Island to the south. The water is Arctic Ocean surface water that flows mainly west to east (Cota et al. 1987) although the movement of water does become complex especially nearshore as a result of tides and basin morphometry (Welch et al. 1992). The passage is open from late July to mid-September but it is never totally ice-free. The mean percentage of open water in the Barrow Strait during August is 70% (Welch et al. 1992).

August sampling trips were made in 1989 and 1991. Each year samples were collected over a 2-wk period (Fig. 5.1). The goal was to make physical, chemical and biological measurements during the time when phytoplankton would have reached or passed its spring bloom phase to determine factors controlling phytoplankton growth. Sampling was usually done from an open boat and the samples were returned to the lab at South Camp of the Department of Fisheries and Oceans near Resolute (Fig. 5.1) for immediate analysis. In 1989, temperature and conductivity measurements were made at 1 m intervals using a Hydrolab 4041 water quality meter and in 1991 temperature was measured using a free falling temperature profiler that measured temperature at depth intervals of 0.05 m (R. Brancker Research Ltd., Ottawa, ON). *In situ* light attenuation was measured with a Li-Cor LI-185 underwater quantum sensor (flat plate, cosine corrected collector). In 1989,

Figure 5.1. Map of the Barrow Strait, N.W.T. showing the general location of sampling sites in 1989 and 1991. Station numbers in italics indicate stations on the north side of Barrow Strait. Plain bold numbers indicate stations in the middle and southern side of Barrow Strait. Plain numbers indicate a transect across Wellington Channel.


CORNWALLIS ISLAND
Resolute
91-7
91-5
91-8
91-6
91-12
91-1
89-3
89-10
89-2
89-4
91-4
89-5
91-11
91-3
91-2
91-10
89-6
91-9
89-11
89-9
89-8
89-7
Kilometers
0 10 20 30 40 50
SOMERSET ISLAND

samples were collected from 10 and 30 m at each station and in 1991 from 5 and 15 m.

Irradiance data were used to calculate the vertical light extinction coefficient (k) (Hutchinson 1957), light at a given depth (I_z) and mean water column light intensity ($\bar{I}$). Light at a given depth was calculated as follows:

$$I_z = I_s e^{-kz} \quad (5.1)$$

where I_z is the solar irradiation that penetrates to depth z, I_s is the mean solar flux at the surface of the water, k is the vertical light extinction coefficient (Hutchinson 1957). Mean water column light intensity was calculated as follows:

$$\bar{I} = I_s \frac{1-e^{-kz}}{kz} \quad (5.2)$$

Lab Procedures

Water samples were subdivided for chemical analyses, plankton identification and counting, nutrient status measurements, and photosynthetic rate measurements. Unless otherwise specified, chemical analyses were done using the methods of Stainton et al. (1977). Chlorophyll (chl) was determined by filtering 100 mL of water onto a GF/C filter. Each filter was placed in a glass vial, 10 mL of 95% methanol was added, and the vial was frozen at -10°C and allowed to stand overnight (at least 16 h). The extract was agitated, allowed to settle, and its fluorescence was

assayed with a Turner Model 110 fluorometer. The fluorometer was routinely standardized with a chl solution (Sigma Chemicals) the stability of which was verified using an HP scanning spectrophotometer.

Phytoplankton photosynthesis rates per unit volume at different light intensities were measured using the ^{14}C incubator method (Fee et al. 1989). Photosynthesis parameters (P^B_m, α^B, and, I_k) were estimated using the method of Fee (1990). P^B_m is the light-saturated rate of photosynthesis per unit of chl, and α^B is the slope of the chl normalized photosynthesis vs light curve as light approaches zero (photosynthetic efficiency). I_k is the light at which photosynthesis is saturated and is calculated from P^B_m/α^B. P_{opt} (the volumetric rate of photosynthesis at light levels optimal for photosynthesis) was normalized to particulate carbon (C) as an independent measure of C turnover and was used as an estimate of relative growth rate. In 1991, a "photosynthetron" type incubator (Lewis and Smith 1983) was used instead of the "Fee type" incubator. ^{14}C uptake using this type of incubator was highly variable especially at low irradiance. We have confidence in the P^B_m data from 1991 but the α^B data are not reported.

Nutrient Status Measurements

Phytoplankton nutrient status measurements consisted of five seston composition ratios (C:N, C:P, C:chl, C:Si and N:P) and four metabolic indicators (alkaline phosphatase activity [APA], N debt, P debt, expressed per unit chl, and Si demand expressed per unit of particulate Si). Nutrient composition ratios were

calculated on an atom:atom basis for C:N, C:P, C:Si and N:P, and an atom:weight basis for C:chl.

Alkaline phosphatase activity, an indicator of P-deficiency, was measured fluorometrically (Healey and Hendzel 1979b) using 5 μM ortho-methyl-fluorescein-phosphate as the substrate. Parallel determinations were made of total and soluble activities to distinguish between APA associated with particles and APA in solution; the soluble activity was that in filtrate passing through 0.2 μm filters. The difference normalized to chlorophyll is reported as particulate activity.

The N debt assay was used in conjunction with particulate C:N ratios to determine N-deficiency. The assay is based on the work of Healey (1977) who demonstrated using several species that algae took up more ammonium (NH_4^+) when N-deficient than when N sufficient. For the N debt assay, 100 mL of unfiltered sample was enriched with ammonium chloride to yield a final concentration of ≈5 μM N. Ammonium was measured (Stainton et al. 1977) on triplicate subsamples at the beginning and end of the incubation. Samples were incubated in the dark at room temperature (the room was unheated). Nitrogen debt was calculated as the nutrient removed over a 24 h period per unit of chl (Healey 1977). Phosphorus debt was measured in a similar way to except that potassium dihydrogen phosphate was added (final concentration 5 μM). Soluble reactive phosphorus (SRP) was measured on triplicate subsamples passed through GF/C filters (Healey 1975). Silicate demand was also measured in a similar way except that sodium silicate was added (final concentration 5 μM). Soluble reactive silicate (SRSi) was measured on triplicate

subsamples. Uptake was normalized to particulate silicate rather than chlorophyll in order to be specific to silicified phytoplankton. Values indicative of presence or absence or degree of nutrient-deficiency for the nutrient status indicators are given in Table 5.1. Unlike the N debt and P debt assays, the Si demand assay has not been tested on laboratory cultures of algae grown at different growth rates in nutrient-limited continuous cultures. Therefore, the Si demand results can only be examined in a relative manner.

Data Analysis

The data set is small and some of the variables had a high degree of variance. To preserve the actual values without showing each value, we use box plots (Wilkinson 1990) which give a median and range. Tests of significance for differences due to sampling year, location or depth were conducted using ANOVA (Wilkinson 1990).

Results

General

All data are presented in Table 5.3. Figure 5.1 indicates the sampling sites.

Variability

Variability due to year, location and depth is presented in Table 5.2. Sampling stations were grouped into stratified and unstratified based on temperature

Table 5.1. Values indicative of presence or absence or degree of nutrient-deficiency for nutrient status indicators used in this study (from Healey and Hendzel 1980). C, carbon; N, nitrogen; P, phosphorus; chl, chlorophyll *a*; APA, alkaline phosphatase activity.

Indicator	Nutrient	No deficiency	Moderate deficiency	Extreme deficiency
C:N[a]	N	<8.3	8.3-14.6	>14.6
C:P[a]	P	<129	129-258	>258
C:chl[b]	N or P	<4.2	4.2-8.3	>8.3
(APA·chl^{-1})[c]	P	<0.003	0.003-0.005	>0.005
		No deficiency	Deficient	
N:P[a]	P	<22	>22	
N debt[d]	N	<0.15	>0.15	
P debt[e]	P	<0.075	>0.075	

[a] atomic ratio
[b] μmol C:μg
[c] particulate APA, μmol P· μg chl^{-1}· h^{-1}
[d] μmol N· μg chl^{-1}
[e] μmol P· μg chl^{-1}

profiles (Fig. 5.2) or if temperature profiles were unavailable, conductivity measurements at the two sampling depths (Table 5.3). At stations classified as unstratified, depth was never a significant source of variability (Table 5.2). At stations classified as stratified, depth was a significant source of variability for nine of the 17 variables measured (Table 5.2). There was a significant difference in SRP by year (Table 5.2), with concentrations being lower in 1989. This was also apparent in TN:TP ratios (Table 5.3).

Stratification

Presence or absence of stratification varied temporally and spatially, however, no pattern could be discerned. In both years, stratification in offshore water on the northern side of Barrow Strait (Fig. 5.1) was observed to disintegrate following stormy weather. Stratification appeared to set up quickly as a result of a combination of calm weather and melting ice pans. The depth of the stratified layer was usually about 10 m (Fig. 5.2) and in stratified water columns conductivity in the upper mixed layer was lower than in the deeper layer (Fig. 5.2, Table 5.3) reflecting the influence of melting ice.

Light

Light extinction measurements were made at some stations each year (Table 5.3). Using a calculated value for cloudless surface light available at Tuktoyuktuk in the Western Arctic (Fee et al. 1989), average hourly light at different depths in the

Figure 5.2. Representative temperature profiles from the Barrow Strait to illustrate stratified and unstratified conditions. Temperature is in degrees Celsius on the upper horizontal axis. The heavy bars are specific conductance measurements from 5 and 15 m samples. Values ($\mu S \cdot cm^{-1}$) are on the lower horizontal axis.

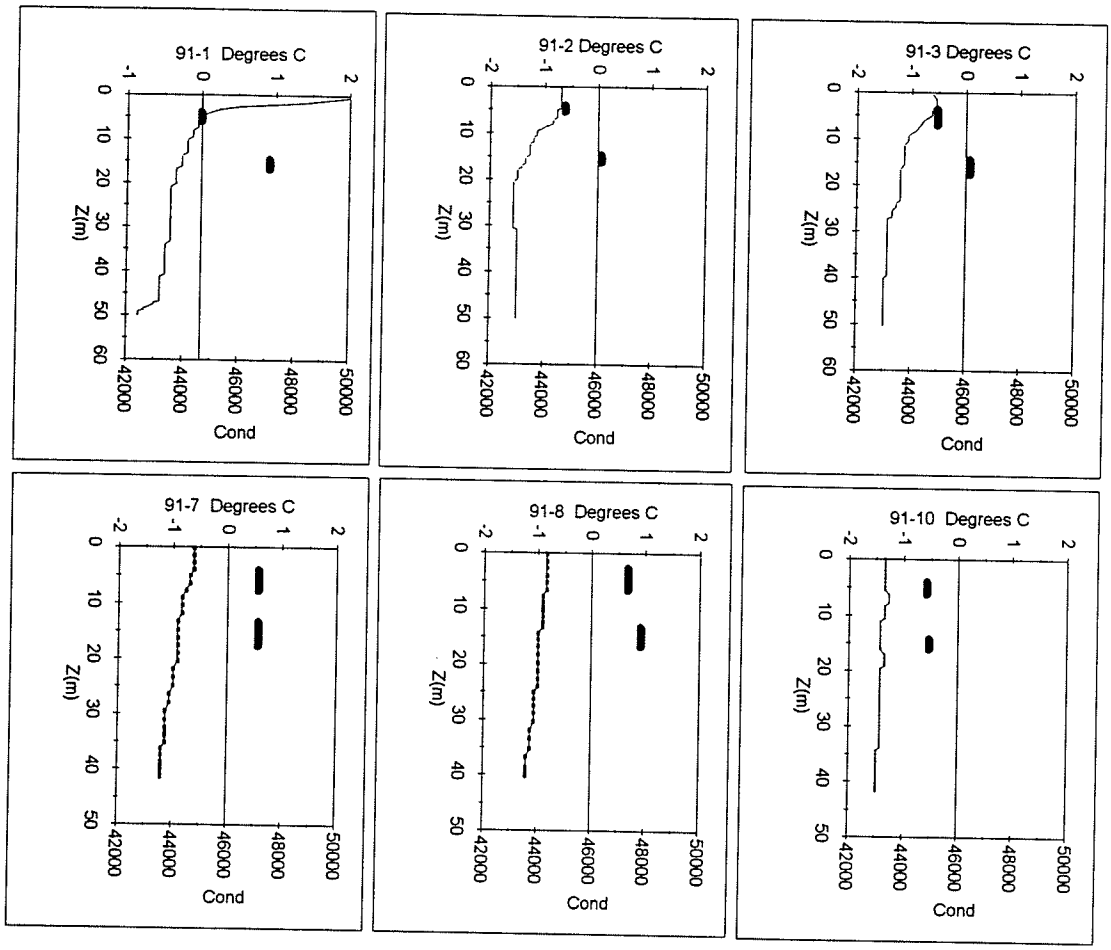

91-1 Degrees C
91-2 Degrees C
91-3 Degrees C
91-7 Degrees C
91-8 Degrees C
91-10 Degrees C
Z(m)
Cond

Table 5.2. Analysis of variance (ANOVA) of variables for three categories: year, location and depth. Samples were classified as stratified or unstratified. NO_3^- = nitrate; SRSi = soluble reactive silicate; SRP = soluble reactive phophorus; Cond = conductivity; chl = chlorophyll *a*; Part. C = particulate carbon; C:N, C:P, N:P, C:Si = particulate carbon, nitrogen, phosphorus, silicon atomic ratios; N debt = nitrogen debt normalized to chl; APA = alkaline phosphatase activity normalized to chl; P_m^B = light saturated rate of photosynthesis normalized to chl; α^B = slope of the light-limited part of the photosynthesis-light curve normalized to chl; I_k = the light intensity at which photosynthesis is saturated. * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$, ns = not significant, nv[1] = no variance due to single year of data.

	Stratified			Unstratified		
	Year	Location	Depth	Year	Location	Depth
Chemical						
NO_3^-	ns	ns	**	ns	ns	ns
SiO_3	ns	ns	ns	*	ns	ns
SRP	**	ns	**	***	ns	ns
Cond	ns	ns	***	ns	***	ns
Biomass						
chl	ns	ns	***	*	***	ns
Part. C	ns	ns	ns	***	ns	ns
Nutrient status						
C:N	ns	ns	***	ns	ns	ns
N debt	ns	***	ns	ns	ns	ns
C:chl	ns	ns	***	ns	ns	ns
C:P	***	*	ns	ns	ns	*
N:P	ns	ns	ns	ns	ns	ns
APA	ns	ns	**	ns	ns	ns
C:Si	nv[1]	*	ns	nv[1]	ns	ns
S demand	nv[1]	ns	ns	nv[1]	*	ns
Photosynthesis						
P_m^B	nv[1]	ns	*	nv[1]	ns	ns
α^B	nv[1]	*	ns	nv[1]	ns	ns
I_k	nv[1]	ns	*	nv[1]	ns	ns

Table 5.3a. Summary of physical, chemical, and photosynthesis data collected in 1989 and 1991. Sta = station (year - sta no.); Z = depth (m); S = stratification (1 = stratified, 2 = unstratified); Exr = light extinction coefficient (m^{-1}); Cond = specific conductance at 25°C ($\mu S \cdot cm^{-1}$); NO_3 = nitrate (μM); SRP = soluble reactive phosphorus (μM); SRSi = soluble reactive silicate (μM); TN:TP = total nitrogen:total phosphorus (atomic); PC = particulate carbon (μM); Chl = chlorophyll *a* ($\mu g \cdot L^{-1}$); PBM = light saturated rate of photosynthesis normalized to chl ($\mu gC \cdot h^{-1} \cdot \mu g\ chl^{-1}$); α^B = slope of the light-limited part of the photosynthesis-light curve normalised to chl ($\mu g\ C \cdot \mu g\ chl^{-1} \cdot Einstein^{-1} \cdot m^2$); I_k = the light intensity at which photosynthesis is saturated ($mEinstein \cdot m^{-2} \cdot min^{-1}$); $P_{opt} \cdot C^{-1}$ = light- saturated rate of photosynthesis normalized to PC ($\mu M\ C \cdot h^{-1} \cdot \mu M\ C^{-1}$).

Sta	Date	Z	S	Ext	Cond	NO_3	SRP	SRSi	TN:TP	PC	Chl	PBM	α^B	I_k	P_{opt}/C
89-2	Aug 13	5	1		42857	0.143	0.39	1.36	18	52	0.33				
89-2	Aug 13	10	1		45542	0.143	0.65	2.21	17	38	0.50				
89-2	Aug 13	30	1		48127	4.286	1.06	7.71	16	81	4.30				
89-3	Aug 15	5	1	0.150	45144	0.071	0.55	0.79	19	113	1.58				
89-3	Aug 15	30	1		48127	5.143	1.13	13.50	15	33	2.00				
89-4	Aug 17	10	2	0.221	46934	0.071	0.71	1.39	16	64	3.60	1.92	9.14	3.49	0.0090
89-4	Aug 17	30	2								2.4	1.12	8.11	2.29	
89-5	Aug 17	10	1	0.160							0.87	1.90	7.8	4.04	
89-5	Aug 17	30	1								5.3	1.84	9.85	3.10	
89-6	Aug 17	10	1	0.151	44249	0.071	0.48	1.68	18	41	0.48	5.18	12.72	6.76	0.0051
89-6	Aug 17	30	1								4.7	1.14	7.83	2.42	
89-7	Aug 17	10	2	0.237	47332	0.071	0.55	1.11	15	78	4.50				
89-7	Aug 17	30	2								3.9				
89-8	Aug 18	10	1	0.160	46337	0.071	0.42	1.39	17	48	0.75	2.49	15.81	2.61	0.0032
89-8	Aug 18	30	1		47928	0.071	0.71	0.79	15	71	7.80	2.09	17.74	1.96	0.0192
89-9	Aug 18	10	1	0.177	46735	0.071	0.55	5.71	16	63	1.08	4.56	20.53	3.69	0.0066
89-9	Aug 18	30	1		48127	3.071	1.03	1.04	15	44	3.50	1.57	12.89	2.02	0.0104
89-10	Aug 21	10	2		46337	0.214	0.58	1.21	17	68	1.59	2.58	8.47	5.06	0.0051
89-10	Aug 21	30	2		46636	0.071	0.58	6.00	15	53	4.90	2.83	12.03	3.91	0.0220
89-11	Aug 21	10	1		44249	0.071	0.87	16.50	14	27	0.42	2.99	6.69	7.42	0.0039
89-11	Aug 21	30	1		46536	5.286	1.29	3.93	14	26	0.44	1.48			0.0021

Table 5.3a. Cont'd.

Sta	Date	Z	S	Ext	Cond	NO_3	SRP	SRSi	TN:TP	PC	Chl	PBM	α^B	I_k	P_{opt}/C
91-1	Aug 2	5	1	0.098	44640	0.143	0.94	3.00	27	28	0.19	2.63			0.0015
91-1	Aug 2	15	1		47120	0.214	1.06	7.89	22	43	3.16	4.43			0.0275
91-2	Aug 2	5	1	0.183	44739	0.143	0.97	1.39	23	49	0.88	2.05			0.0031
91-2	Aug 2	15	1		46128	0.071	1.06	3.75	21	63	2.23	2.69			0.0079
91-3	Aug 2	5	1	0.200	44938	0.143	1.03	4.11	21	51	0.77				
91-3	Aug 2	15	1		46128	0.071	1.03	4.00	21	60	2.32				
91-4	Aug 2	5	1	0.204	45334	0.143	0.97	2.86	23	32	0.37				
91-4	Aug 2	15	1		46922	0.143	1.10	4.71	21	48	3.07				
91-5	Aug 10	5	1		44045	0.071	0.94	3.54	25	24	0.40	3.76			0.0052
91-5	Aug 10	15	1		46426	0.143	1.03	4.64	23	33	2.04	3.92			0.0205
91-6	Aug 10	5	1		44541	0.071	0.94	3.79	22	28	0.60	2.92			0.0051
91-6	Aug 10	15	1		47120	1.571	1.23	9.50	20	40	3.46	2.89			0.0208
91-7	Aug 12	5	2		47120	1.786	1.19	8.61	20	26	2.51	3.98			0.0323
91-7	Aug 12	15	2		47914	4.786	1.29	12.64	20	22	2.65	2.26			0.0231
91-8	Aug 12	5	2		47318	2.571	1.26	8.89	21	28	2.04	2.79			0.0168
91-8	Aug 12	15	2		47814	4.714	1.42	12.18	19	23	2.13	2.35			0.0185
91-9	Aug 15	5	2	0.118	44541	0.143	1.03	2.46	21	33	0.70				
91-9	Aug 15	15	2		45136	0.143	1.00	3.50	22	30	1.37	1.97			0.0075
91-10	Aug 15	5	2	0.151	44838	0.071	0.97	2.00	22	36	1.35				
91-10	Aug 15	15	2		44938	0.071	0.97	4.07	22	33	1.40	4.29			0.0150
91-11	Aug 15	5	1		45037	0.071	1.00	2.29	22	36	0.94				
91-11	Aug 15	15	1		46029	0.143	1.06	6.00	21	35	3.28	1.70	13.1	2.15	0.0133
91-12	Aug 15	5	2		46426	0.071	1.00	4.11	22	50	2.84				
91-12	Aug 15	15	2		46922	0.143	1.06	5.14	21	35	3.28	1.91	17.29	1.83	0.0149

Table 5.3b. Summary of nutrient status data collected in 1989 and 1991. Sta = station (year-sta no.); Z = depth (m); S = stratification (1 = stratified, 2 = unstratified); C, N, P, Si = particulate carbon, nitrogen, phosphorus, silicon atomic ratios; chl = chlorophyll *a*; N debt = nitrogen debt (μM N μg chl^{-1}); P Debt = phosphorus debt (μM P μg chl^{-1}); Si demand = silicon demand (μM Si μM particulate Si^{-1}); Tot APA = total alkaline phosphatase activity (μM P h^{-1}); Sol APA = soluble APA (μM P h^{-1}); Part APA = particulate APA (μM P μg chl h^{-1}).

Sta	Date	Z	S	C:N	C:P	C:chl	N:P	C:Si	N Debt	P Debt	Si Demand	Tot APA	Sol APA	Part APA
89-2	Aug 13	5	1	15.4	160	157	10.4		0.424	0.000		0.018	0.012	0.018
89-2	Aug 13	10	1	12.2	129	75	10.6		0.000	0.000		0.010	0.015	-0.010
89-2	Aug 13	30	1	9.7	209	19	21.6		0.000	0.000		0.022	0.013	0.002
89-3	Aug 15	5	1	13.2	249	71	18.8		0.000	0.000		0.042	0.030	0.008
89-3	Aug 15	30	1	9.7	115	17	11.8		0.000	0.004		0.036	0.031	0.002
89-4	Aug 17	10	2	10.6	124	18	11.8		0.245					
89-4	Aug 17	30	2											
89-5	Aug 17	10	1						0.495					
89-5	Aug 17	30	1											
89-6	Aug 17	10	1	11.9	181	85	15.2		0.769					
89-6	Aug 17	30	1											
89-7	Aug 17	10	2	12.5	150	17	12.0		0.117					
89-7	Aug 17	30	2											
89-8	Aug 18	10	1	16.5	166	64	10.1		1.233			0.006	0.003	0.004
89-8	Aug 18	30	1	9.3	129	9	13.9		0.041			0.005	0.001	0.001
89-9	Aug 18	10	1	15.4	176	58	11.5		0.482			0.000	0.000	0.000
89-9	Aug 18	30	1	9.7	171	13	17.7		0.000			0.015	0.008	0.002
89-10	Aug 21	10	2	16.6	174	42	10.5		0.716	0.009		0.010	0.001	0.006
89-10	Aug 21	30	2	9.2	116	11	12.7		0.151	0.061		0.024	0.005	0.004
89-11	Aug 21	10	1	14.4	207	63	14.4		0.000	0.000		0.019	0.002	0.040
89-11	Aug 21	30	1	13.4	267	59	19.9		0.000	0.000		0.000	0.000	0.000

Table 5.3b. Cont'd.

Sta	Date	Z	S	C:N	C:P	C:chl	N:P	C:Si	N Debt	P Debt	Si Demand	Tot APA	Sol APA	Part APA
91-1	Aug 2	5	1	12.0	176	149	14.6	12.2	0.000		0.049	0.022	0.018	0.021
91-1	Aug 2	15	1	8.9	101	13	11.4	5.2	0.149		0.200	0.032	0.027	0.002
91-2	Aug 2	5	1	13.2	139	56	10.5	6.5	3.080		0.075	0.025	0.022	0.003
91-2	Aug 2	15	1	12.5	140	28	11.2	6.5	0.315		0.032	0.028	0.024	0.002
91-3	Aug 2	5	1	15.1	143	66	9.5	6.6	4.282		0.017	0.029	0.026	0.004
91-3	Aug 2	15	1	12.4	133	26	10.8	5.5	1.194		0.052	0.029	0.024	0.002
91-4	Aug 2	5	1	11.4	123	86	10.8	5.2	4.908		0.027	0.027	0.022	0.014
91-4	Aug 2	15	1	10.6	123	15	11.6	2.5	1.082		0.007	0.024	0.048	-0.008
91-5	Aug 10	5	1	8.7	125	61	14.4	14.1	0.000		0.000	0.062	0.050	
91-5	Aug 10	15	1	8.9	126	16	14.1	9.4	0.000		0.000	0.102	0.075	0.013
91-6	Aug 10	5	1	11.7	110	47	9.4	9.6	0.000		0.000	0.061	0.046	0.025
91-6	Aug 10	15	1	8.1	124	12	15.3	6.2	0.000		0.058	0.065	0.048	0.005
91-7	Aug 12	5	2	7.4	100	10	13.6	4.2	0.000		0.033	0.078	0.041	0.015
91-7	Aug 12	15	2	7.8	112	8	14.4	ERR	0.000			0.070	0.047	0.009
91-8	Aug 12	5	2	7.8	146	14	18.8	7.2	0.000		0.058	0.053	0.034	0.009
91-8	Aug 12	15	2	7.9	78	11	9.8	4.4	0.000		0.084	0.062	0.038	0.011
91-9	Aug 15	5	2	14.7	144	46	9.8	3.7	0.387		0.000	0.078	0.030	0.069
91-9	Aug 15	15	2	9.5	103	22	10.8	4.6	0.420		0.000	0.040	0.030	0.007
91-10	Aug 15	5	2	10.0	111	27	11.1	5.6	0.853		0.007	0.052	0.030	0.016
91-10	Aug 15	15	2	10.1	115	24	11.3	5.8	0.629		0.000	0.061	0.036	0.018
91-11	Aug 15	5	1	11.7	139	38	11.9	7.1	1.478		0.000	0.093	0.068	0.027
91-11	Aug 15	15	1	6.9	109	11	15.7	4.9	0.124		0.027	0.078	0.045	0.010
91-12	Aug 15	5	2	9.1	119	18	13.1	7.0	0.179		0.039	0.051	0.039	0.004
91-12	Aug 15	15	2	7.4	90	11	12.2	5.1	0.000		0.055	0.056	0.044	0.004

water column for four different light extinction values was calculated (Table 5.4). Mean water column light intensity was calculated using the same surface irradiance and different mixed depths (Table 5.4).

Chemistry

There were patterns with depth for NO_3 and SRSi in the stratified samples (Fig. 5.3). NO_3 was detectable but less than 0.2 μM at 5, 10 and 15 m. There was a gradual increase with depth for SRSi. There was no pattern with depth for SRP in either the stratified or unstratified samples and no pattern for NO_3 or SRSi in the unstratified samples (Fig. 5.3). Conductivity increased with depth in stratified water columns (Fig. 5.4), but was more uniform in the well mixed water columns (Fig. 5.4), although at 5 m there was a wide range in the values. The molar ratio of TN:TP was on average 20 (Table 5.3).

Biomass

Chlorophyll was on average less than 1.0 $mg \cdot m^{-3}$ at 5 and 10 m and increased 4x at 15 and 30 m (Fig. 5.5) at stratified stations. Particulate carbon was uniform at all four depths at stratified stations (Fig. 5.5). At unstratified stations there was no pattern for either chlorophyll or particulate carbon (Fig. 5.5).

Table 5.4a. Selected light related data for some stations sampled in 1989. Sta = station (year-no.); Ext = light extinction coefficient (m^{-1}); $I_z(10)$ and $I_z(30)$ = light intensity at 10 and 30 m calculated using equation 1 (mEinstein·m^2·min^{-1}). Surface light was the average cloudless surface light for Tuktoyuktuk, N.W.T. on Aug. 10, 1986 (29.8 mEinstein·m^2·min^{-1}) (Fee et al. 1988). $I_k(10)$ and Ik(30) = saturating light intensities from light response curves for samples taken from 10 and 30 m (mEinstein·m^2·min^{-1}). $I_z/I_k(10)$ and (30) are the ratios of light at depth compared to light required to saturate photosynthesis for a sample from that depth.

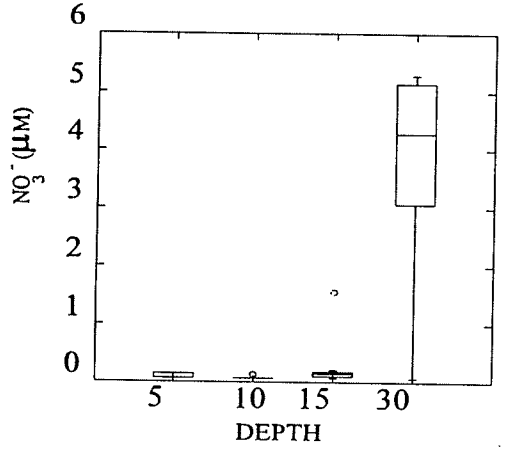
Sta	Ext	$I_z(10)$	$I_z(30)$	$I_k(10)$	$I_k(30)$	$I_z/I_k(10)$	$I_z/I_k(30)$
89-4	0.221	3.28	0.04	3.49	2.29	0.94	0.02
89-5	0.160	6.03	0.25	4.04	3.10	1.49	0.08
89-6	0.151	6.60	0.32	6.76	2.42	0.98	0.13
89-8	0.160	6.03	0.25	2.61	1.96	2.31	0.13
89-9	0.177	5.09	0.15	3.69	2.02	1.38	0.07

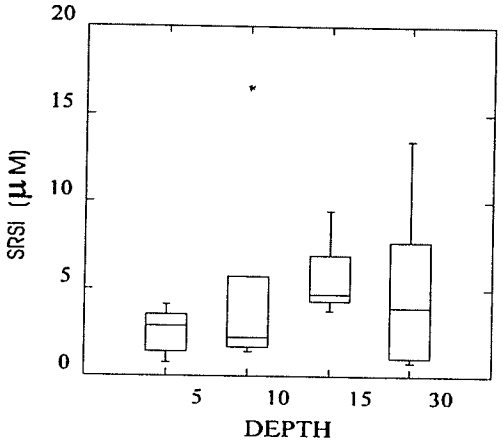
Table 5.4b. I = mean water column light intensity (mEinstein·m^2·min^{-1}) calculated for water columns of various mixed depths (Z_{mix}) (m) using equation 2. Surface light as in Table 5.4a.

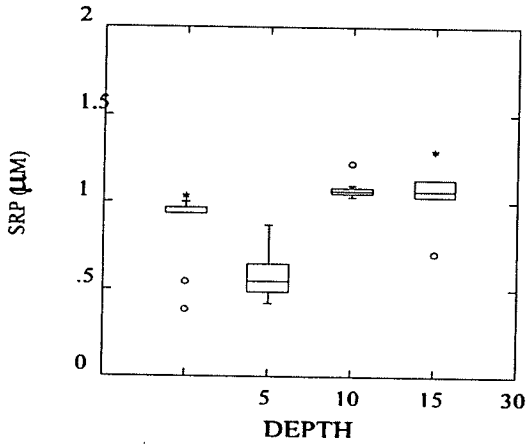
Z_{mix}	$\bar{I}$
10	14.36
20	8.49
30	5.81
40	4.38
50	3.51
60	2.92
70	2.50
80	2.20
90	1.95
100	1.76

Figure 5.3 Nitrate (NO_3^-), soluble reactive silicon (SRSi) and soluble reactive phosphate (SRP) in the Barrow Strait during August 1989 and 1991. Data are plotted as box plots of the combined values at each depth in stratified and unstratifed water columns. The central horizontal line is the median, the lower and upper edges of the box comprise the interquartile range within which 50% of the values occur. The bars extending above and below the the boxes can represent a range around the median 1.5 times the interquartile range or they indicate the maximum and minimum values (if they are less than 1.5 times the interquartile range). Values beyond 1.5 times the interquartile range are indicated by an asterisk (*) and values 3 times the interquartile range by open circles (o). When only one line is plotted, this represents the median without enough data points to calculate the distribution.

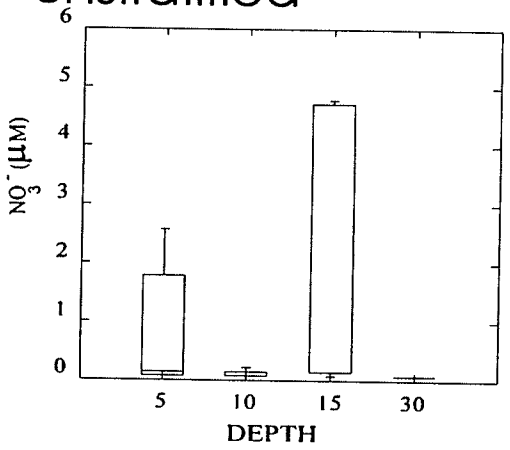
Stratified

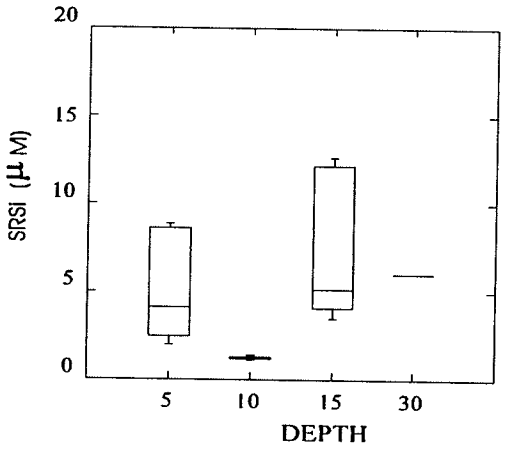






Unstratified





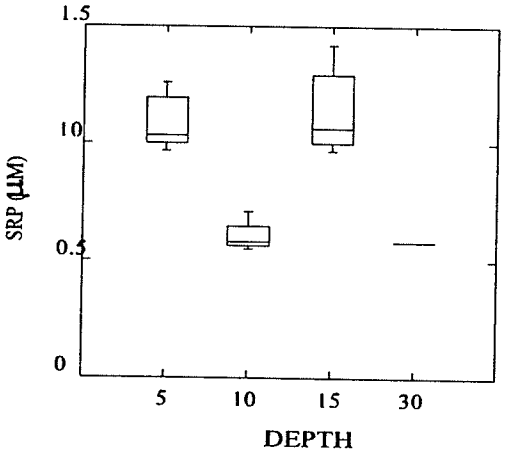
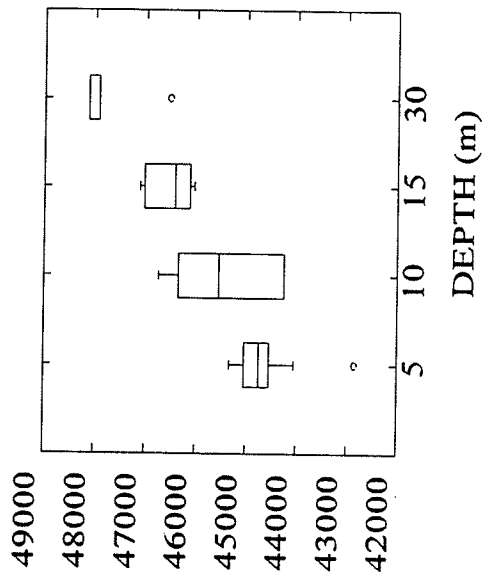


Figure 5.4. Specific conductance (cond) in the Barrow Strait during August 1989 and 1991. Data are plotted as box plots of the combined values at each depth in the stratified and unstratified water columns. See Fig. 5.3 for a description of box plots.


Cond (μS·cm-1)
49000
48000
47000
46000
45000
44000
43000
42000
5
10
15
30
DEPTH (m)

Cond (μS·cm-1)
49000
48000
47000
46000
45000
44000
43000
42000
5
10
15
30
DEPTH (m)

N-deficiency

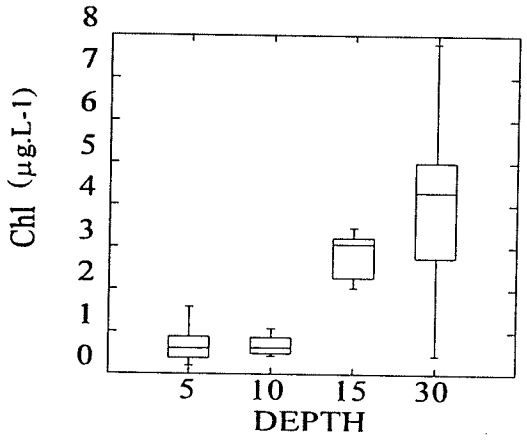
The upper mixed layer at stratified stations was clearly N-deficient with a gradient of decreasing N-deficiency with depth within the layer. At these stations, phytoplankton from the 5 and 10 m samples was moderately to severely N-deficient according to N nutrient status indicators particulate C:N ratio and N debt (Fig. 5.6). Samples taken from 15 and 30 m at the stratified stations and from all four depths at the unstratified stations exhibited either moderate or no N-deficiency (Fig. 5.6). Particulate C:chl (Fig. 5.6) was high (median value 60 $\mu M \cdot \mu g^{-1}$) at 5 and 10 m at the stratified stations and about 10 $\mu M \cdot \mu g^{-1}$ in the deeper water and in the well mixed water columns (Fig. 5.6). High C:chl values may indicate a general nutrient-deficiency while low C:chl values may indicate light-deficiency (Smith et al. 1995).

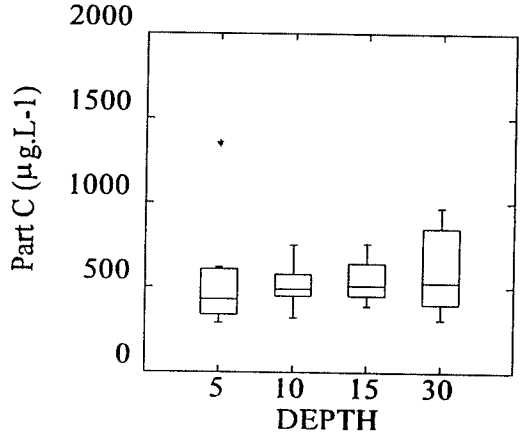
P-deficiency

Several different methods were used to assess P-deficiency. Based on ambient SRP (Fig. 5.3), it was not expected that phytoplankton would exhibit indications of P-deficiency. In none of the P-deficiency indicators was there any pattern with depth in either stratified or unstratified samples. C:P particulate ratios were within the range found for some moderately P-deficient phytoplankton (Healey and Hendzel 1980) (Fig. 5.7). Particulate N:P ratios were less than 15 which is well below the value of 22 which is suggested to indicate the onset of P-deficiency (Healey and Hendzel 1979a). Samples incubated overnight in the dark with added P never assimilated this added PO_4 (Table 5.3). Surprisingly, however, rates of

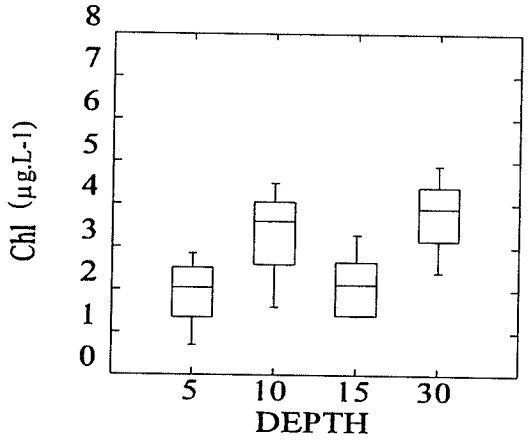
Figure 5.5. Chlorophyll *a* (chl) and particulate carbon (part C) in the Barrow Strait during August 1989 and 1991. Data are box plots of the combined values at each depth in the stratified and unstratified water columns. See Fig. 5.3 for a description of box plots.

Stratified





Unstratified



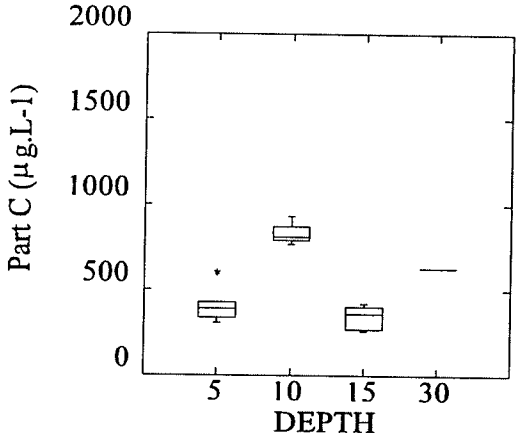
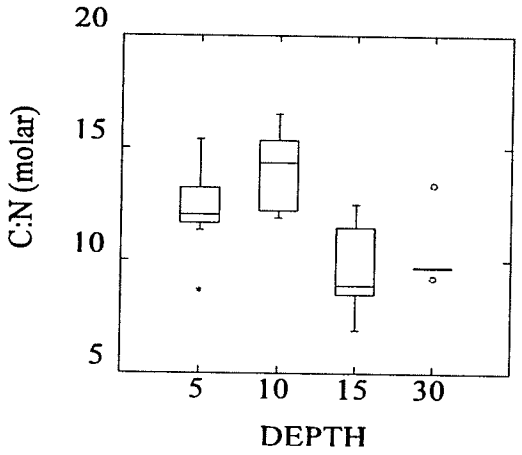
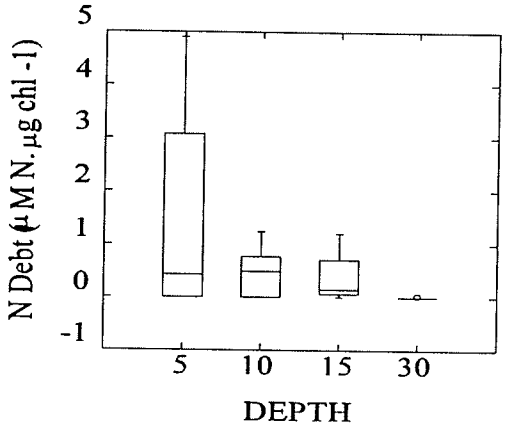
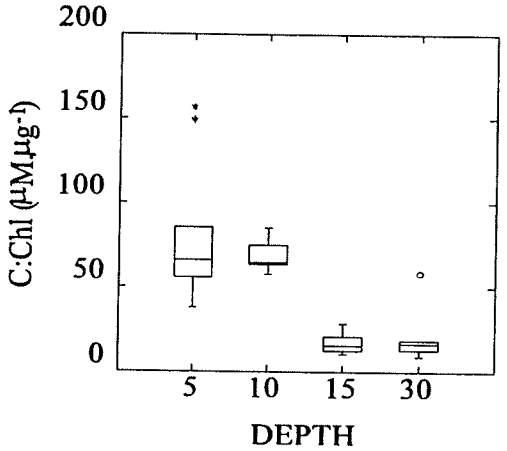


Figure 5.6. Nitrogen-deficiency measurements in the Barrow Strait during August 1989 and 1991. Data are box plots of the combined values at each depth in the stratified and unstratified water columns. See Fig. 5.3 for a description of box plots. C:N = particulate C:particulate nitrogen, N debt = nitrogen debt, C:chl = particulate C:chlorophyll *a*. alkaline phosphatase activity were similar to those rates exhibited by P-deficient algae in culture and in lakes (Fig. 5.7).

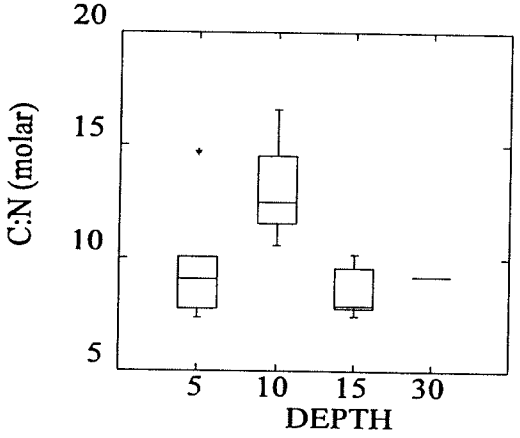
Stratified

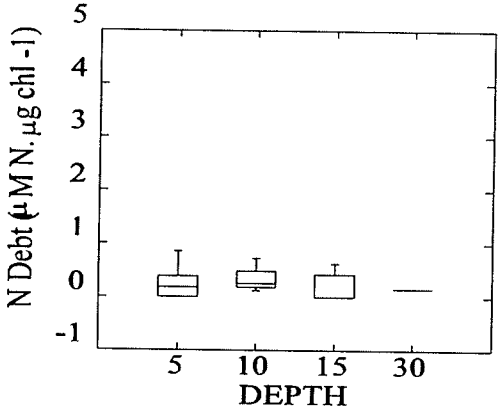


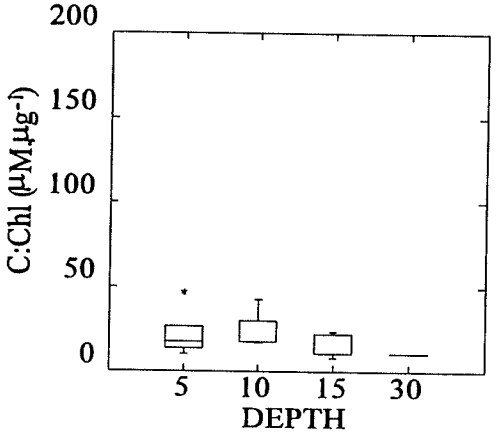




Unstratified







Si-deficiency

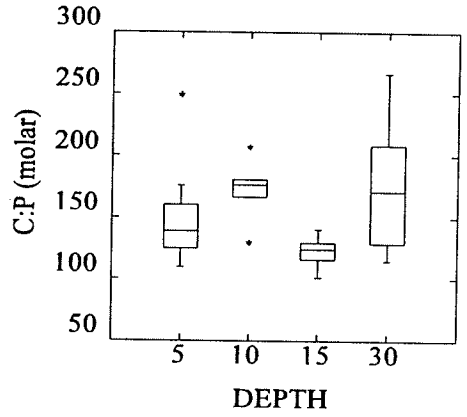
SRSi concentrations were at times less than 2 μM in the 5 and 10 m samples (Fig. 5.3) and appeared to increase gradually with depth. C:Si ratios from 5 m were greater than those from 15 m, but the differences were not statistically significant because of the wide ranges in the 5 m samples (Fig. 5.8). Uptake of Si in the dark normalized to particulate Si (Fig. 5.8) did not suggest any biological pattern with depth or stratification.

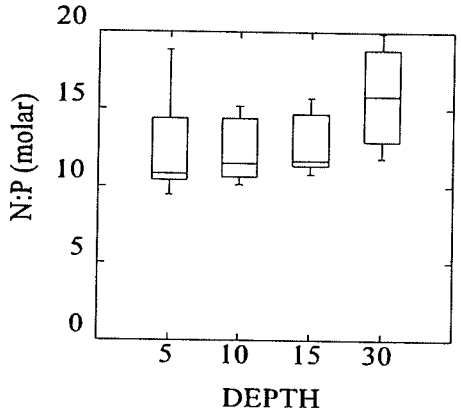
Photosynthesis

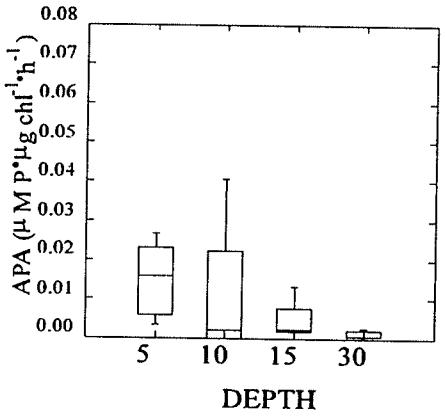
P^B_m, I_k and P_{opt}:C were all significantly different with depth in the stratified samples (Fig. 5.9, Table 5.2). α^B did not differ with depth, although the number of samples was small and the range very large (Fig. 5.9). For the samples where light extinction measurements, P^B_m, and α^B were available, I_k values for those days were compared to calculated light available at the depth the samples were taken from (i.e. 10 or 30 m) (Table 5.3). The calculated light available at 10 m was usually adequate to saturate photosynthesis (0.94-2.3x) but the calculated light available at 30 m was a very small proportion of that required to saturate photosynthesis (0.02-0.13x) (Table 5.4).

Figure 5.7. Phophorus-deficiency measurements in the Barrow Strait during August 1989 and 1991. Data are box plots of the combined values at each depth in the stratified and unstratified water columns. See Fig. 5.3 for a description of box plots. C:P = particulate C:particulate phosphorus, N:P = particulate N:particulate P, APA = alkaline phophatase activity normalized to chl.

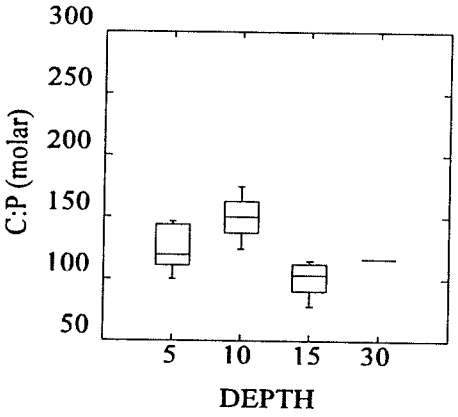
Stratified

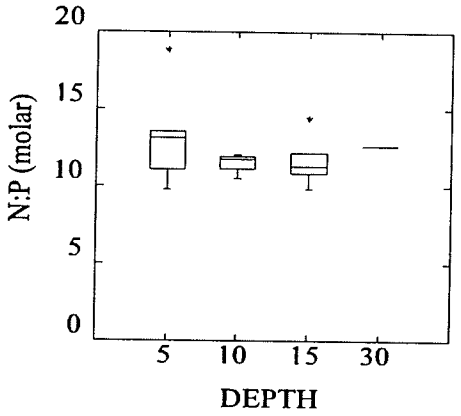






Unstratified





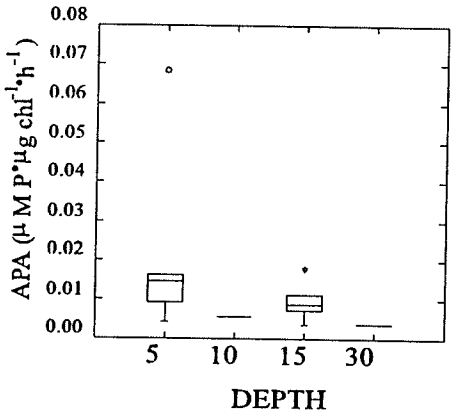
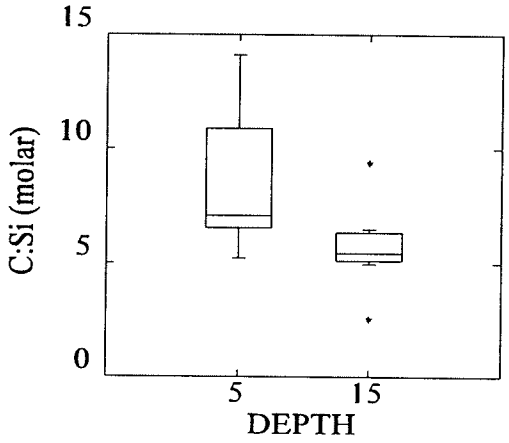
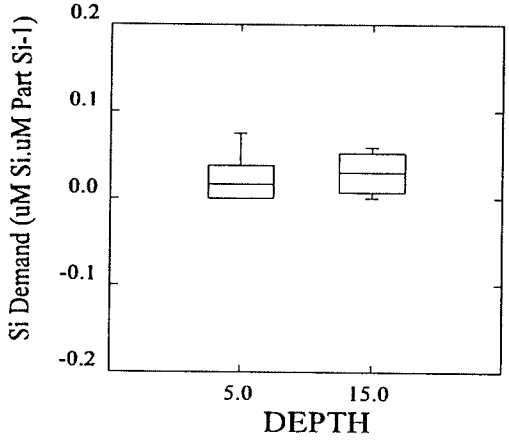


Figure 5.8. Silicon-deficiency measurements in the Barrow Strait during August 1989 and 1991. Data are box plots of the combined values at each depth in the stratified and unstratified water columns. See Fig. 5.3 for a description of box plots. C:Si = particulate C:particulate silicon, Si demand = silicon demand.

Stratified





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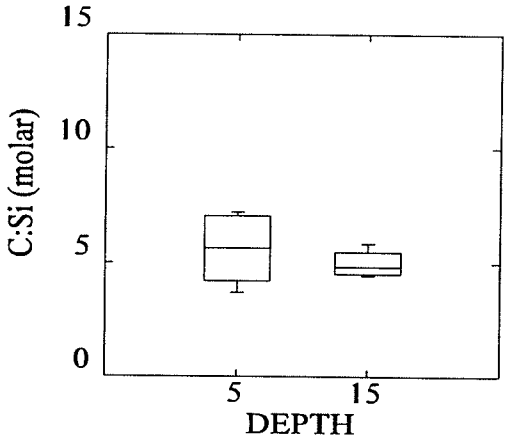


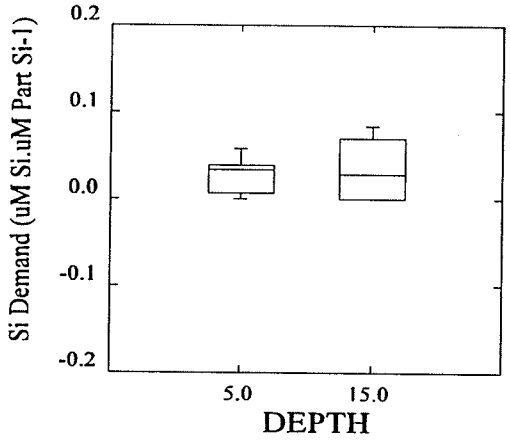
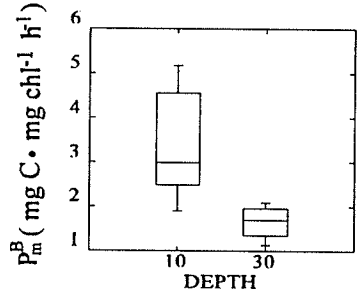
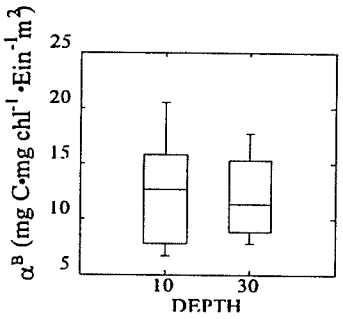
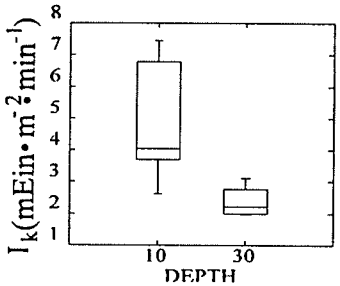


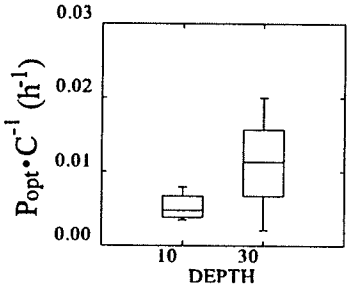
Figure 5.9. Photosynthesis related measurements in the Barrow Strait during August 1989. Data are plotted as box plots of the combined values at each depth in the stratified and unstratified water columns. See Fig. 5.3 for a description of box plots. P^B_m = photosynthesis at optimum light normalized to chl, α^B = the slope of the light-limited part of the photosynthesis-light curve normalized to chl, I_k is the light intensity that saturates photosynthesis, $P_{opt} \cdot C^{-1}$ = the light saturated rate of photosynthesis normalized to particulate C.

Stratified

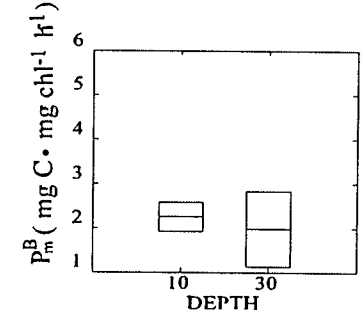


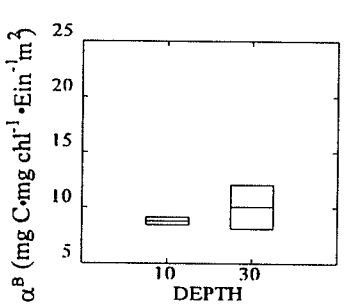


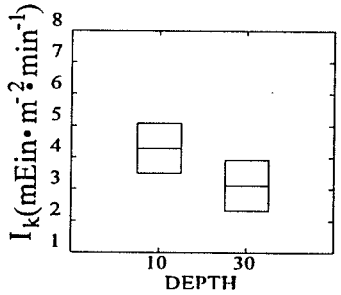


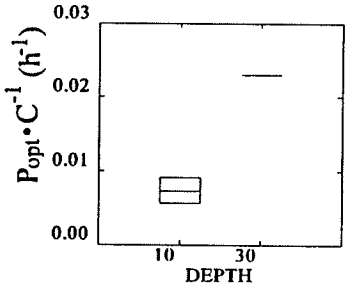


Unstratified









Discussion

Frequency of Stratification

Arctic phytoplankton are thought to be more nutrient-limited than Antarctic phytoplankton (Smith and Sakshaug 1990; Harrison and Cota 1991) and the nutrient-deficiency is a result of the shallow halocline formed by melting sea ice which prevents the resupply of nutrients to the upper mixed layer. It follows from these observations that the frequency with which stratification is set up and eroded will likely have a major influence on phytoplankton growth rates (Sakshaug and Slagstad 1991; Stole-Hansen and Slagstad 1991). Because of the expensive nature of oceanographic cruises, however, most studies examine spatial rather than temporal variability in stratification.

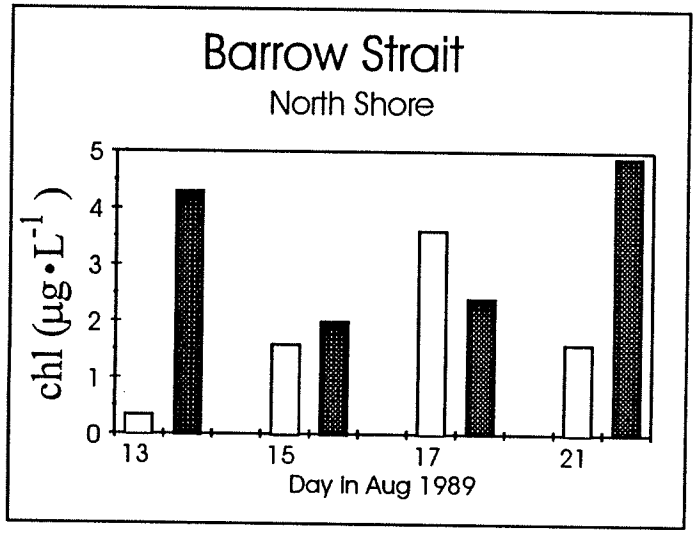
Density profiles for Barrow Strait (Bergman 1989) and Jones Sound just north of Barrow Strait (Platt et al. 1987) indicate the water column was stratified at each sampling period during August but destratified in September. At each of the two years in this study, Barrow Strait in August showed a more dynamic picture of the stratification-destratification cycle due to wind mixing. Each year the water column was stratified initially as indicated by low conductivity and chlorophyll values in surface water compared to deeper water (Fig. 5.10, Table 5.3) and then as a result of strong winds, the water column became well mixed and chlorophyll and conductivity became more homogeneous throughout the water column. In 1989, following mixing, the chlorophyll, SRSi and nutrient status data indicated a return to stratified conditions, whereas conductivity and NO_3 indicated unstratified conditions suggesting

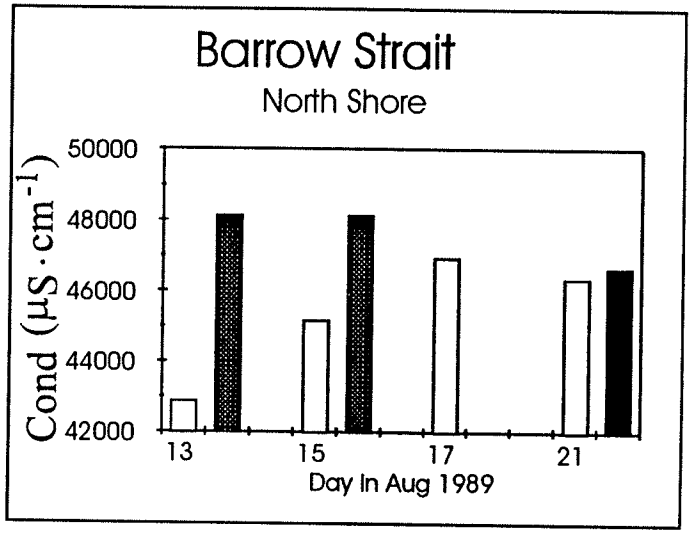
coastal or tidal currents may have imported different water masses. The implication of this frequent cycle of stratification-destratification suggested by these two short temporal snapshots in the same location, is that high levels of secondary production may be a direct function of the frequency with which stratification-destratification takes place. Such variability likely prevents either strong nutrient-deficiency or light limitation from keeping growth rates below optimum. More data on the frequency and duration of stratification would be necessary, however, to model seasonal photosynthesis accurately in this physically variable area. Stole-Hansen and Slagstad (1991) noted the importance of vertical mixing to biological processes in the Barents Sea. Sakshaug and Slagstad concluded chlorophyll in the mixed layer of the Barents Sea is a function of mixed depth which in turn is often a function of the stabilizing influence of meltwater from sea ice is furthermore. Harrison and Cota (1991) stressed that nutrients controlled by physical processes (vertical mixing) as opposed to nutrients controlled by biological processes (regeneration) are more important in controlling photosynthesis in the Arctic than Antarctic phytoplankton.

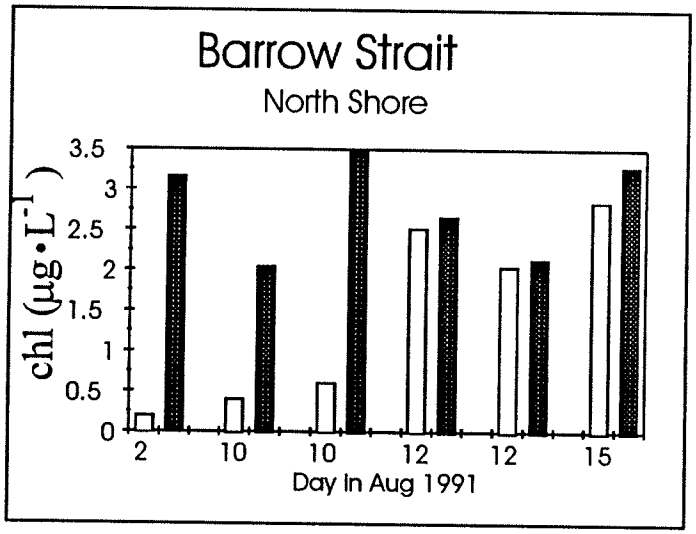
N-deficiency

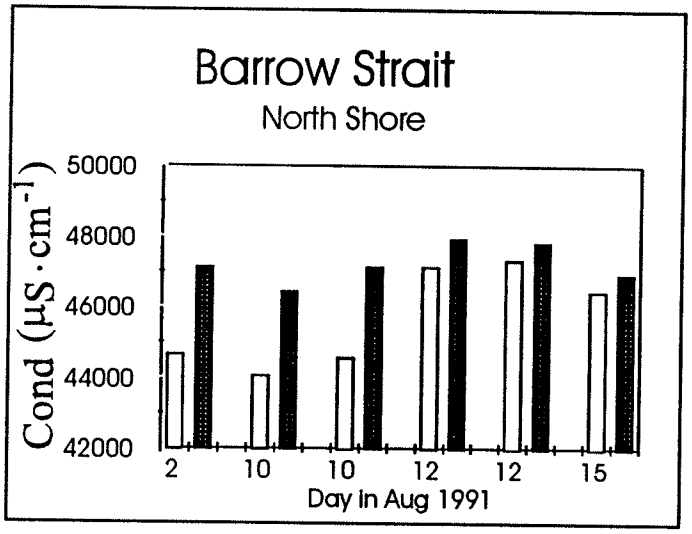
Nitrogen has traditionally been considered most often to limit phytoplankton growth in marine waters. Recently other nutrients such as P (Karl et al. 1995), Si (Sommer 1991; Nelson and Treguer 1992; Ragueneau et al. 1994), Fe (Martin et al. 1990), or factors such as light (Sakshaug et al. 1991; Mitchell et al. 1991), or

Figure 5.10. Temporal changes in chlorophyll *a* (chl) and conductivity (cond) with fluctuations in water column stratification in the Barrow Strait during August 1989 and 1991. White bars are 10 m samples in 1989 and 5 m samples in 1991. Black bars are 30 m samples in 1989 and 15 m samples in 1991.


Barrow Strait
North Shore
chl (µg•L-1)
0
1
2
3
4
5
13
15
17
21
Day In Aug 1989


Barrow Strait
North Shore
Cond (µS·cm-1)
42000
44000
46000
48000
50000
13
15
17
21
Day In Aug 1989


Barrow Strait
North Shore
chl (µg•L-1)
0
0.5
1
1.5
2
2.5
3
3.5
2
10
10
12
12
15
Day In Aug 1991


Barrow Strait
North Shore
Cond (µS·cm-1)
42000
44000
46000
48000
50000
2
10
10
12
12
15
Day In Aug 1991

grazing (Frost 1991), and sinking (Waite et al. 1992) have become foci of investigations along with nitrogen. At high latitudes, temperature is considered an important factor controlling growth rates of phytoplankton when light or nutrients are not already controlling growth (Smith and Sakshaug 1990; Harrison and Cota 1990). Observed specific growth rates (0.76-1.03 doublings per day) from high latitudes (Smith and Sakshaug 1990) are within the limits predicted by Eppley's (1972) equation relating algal growth rates to temperature which was based on nutrient sufficient cultures. Growth rates from temperate and tropical waters are often as low due to nutrient-limitation but can also be much higher (up to 8.0 doublings per day) than any reported from polar waters (Furnas 1990).

Phytoplankton in the upper mixed layer of stratified water columns were moderately to severely N-deficient. This conclusion is based on the absence of measurable NO_3 in the upper mixed layer (Fig. 5.3), the high particulate C:N ratios (Fig. 5.6), and the N debt assay (Fig. 5.6). Phytoplankton below the mixed layer in stratified water columns and in well mixed water columns were not, on average, N-deficient although there are some samples that had high particulate C:N ratios and elevated N-debt values.

The absence of measurable NO_3 is often cited as an indication of N-deficiency. Although undetectable NO_3 concentration may be an indication that new production is low relative to regenerated production (Harrison et al. 1987), it does not always follow that phytoplankton growth rates are low as well as rates of new production because NH_4^+ can be used as a N source. Regeneration of NH_4^+, by a

combination of grazing and microbial processes, may maintain phytoplankton in non N-deficient condition with particulate C:N ratios that are similar to N-sufficient algae in culture. The use of the particulate C:N ratio alone is not conclusive evidence that growth rates are N-deficient. Elemental ratios of natural populations can be variable and unreliable due to the presence of detritus and the fact that different species have different optimum C:N ratios (Smith and Sakshaug 1990). However, the combination of high N debt, low ambient NO_3 and high C:N is strongly indicative of severe N-deficiency of phytoplankton in the upper mixed layer in the Barrow Strait. The TN:TP ratio of 19 is another indication of N-deficiency since this is similar to the loading ratios that precipitated N_2-fixing cyanobacterial blooms in Lake 227 of the Experimental Lakes Area (Healey and Hendzel 1980).

Si-deficiency

There is little strong evidence for Si-deficiency of phytoplankton growth rates. Ambient silicate concentrations appeared to be controlled by biological uptake as demonstrated by the gradient in concentrations in the upper mixed layer of stratified waters (Fig. 5.3) and at the surface silicate did become sufficiently low to possibly limit phytoplankton biomass (<5.0 μM) as suggested by Levasseur et al. (1990). Particulate C:Si ratios for two Antarctic diatoms (Sommer 1991) were 7.6 and 6.3 for Si-replete and 24.4 for Si-limited cells with a minimum cell quota. These were obtained from natural samples that had been sorted using nets. Particulate C:Si ratios of the natural assemblages from Barrow Strait averaged 5.0. Our data from Barrow

Strait would be an overestimate because non-diatom C would tend to inflate the ratio. The uncorrected ratio certainly indicates that Si-deficiency is very unlikely.

Coastal centric diatoms in the Antarctic had C:Si ratios around 29 (Shimoto and Ishii 1995) while oceanic pennate diatoms measured in the same study had C:Si ratios closer to 3. On the basis of these ratios compared to published culture values, one would expect the oceanic diatoms to be Si-sufficient while the coastal diatoms would be classified as Si-deficient. However, surface Si concentrations were much higher in the coastal area than the oceanic so the difference in C:Si was attributed to species differences rather than any indication of Si-deficiency. In fact, it was suggested that the heavily silicified oceanic species were Si-limited at some time because of their high Si demand. However, low half-saturation values for Si uptake (1.1 to 4.6 μM) for *Nitzschia curta*, i.e. *Nitzschia*, a dominant oceanic diatom from the Antarctic, were recorded by Nelson and Treguer (1992) indicating that ambient Si concentrations (20 to 50 μM) were rarely low enough to limit growth rates. Smith et al. (1995), in their study of the Northeast Polyna in the Greenland Sea, also found no change in C:Si ratios over a range of samples where they observed a wide range in the C:N and C:chl ratios and concluded Si was not likely deficient.

Collectively the information for Si nutrition indicates that phytoplankton was not Si-deficient in the Barrow Strait samples. The gradient observed in the upper mixed layer of ambient Si (Fig. 5.3) indicated that Si was being drawn down by phytoplankton to low concentrations (average of 3 μM) in the 5 and 10 m samples. These are concentrations below half-saturation concentrations reported for Si uptake

or growth (Nelson and Treguer 1992; Sommer 1991). The Si demand assays and the C:Si ratios (Fig. 5.8) did not exhibit any pattern with depth or stratification unlike the C:N and N debt assays which were strongly correlated with depth within stratified samples. The low ambient Si concentrations, although not growth limiting, may, however, be expected to influence community species composition and succession (Sommer 1991).

Light-deficiency

Light as influenced by daylength, angle of incidence and cloudiness, controls photosynthesis in Arctic waters on a seasonal basis (Smith and Sakshaug 1990). During the ice free season, however, the main factors will be cloudiness and vertical mixing depth. In the upper mixed layer of the stratified water column of the Barrow Strait, there is more than enough light to saturate photosynthesis in August (Table 5.4) based on measured light extinctions and cloudless irradiance. Using the representative data in Table 5.4, the amount of light calculated to saturate photosynthesis (I_k), based on simulated *in situ* incubations, was always met or exceeded at 10 m. However, even although the amount of light required to saturate photosynthesis (I_k-30) in the 30 m samples was significantly less than that required to saturate photosynthesis in the 10 m sample (I_k-10) (Fig. 5.9, Table 5.4), this lower light requirement was still much higher than the light available at a depth of 30 m and the ratio of I-30 to I_k-30 (Table 5.4a) was much less than 1.0 which would indicate light limitation under average conditions.

Whereas the above discussion is appropriate to stratified conditions in a water column mixed to ca. 80 m, it is more appropriate to describe the light environment in terms of an average amount that phytoplankton may be exposed to over a unit of time. Mean water column light intensities for a series of hypothetical mixing depths (Table 5.4) are given. Some of the low I_k values obtained from incubating the 30 m samples are low enough that the mean water column light intensity in a water column mixed as deep as 80 m would saturate photosynthesis. However, when the shallow stratification is broken down in the Barrow Strait, it is likely that the water column mixes to depths greater than 80 m and it is expected that when the water column is not stratified that the mean water column light intensity is not high enough to saturate photosynthesis (Table 5.4). Frequent cloud cover would intensify light limitation under these circumstances.

Ratios of C:chl provide indirect evidence of low light exposure. In the 15 and 30 m samples from stratified water columns in the Barrow Strait (depth of the thermocline is usually 10 m), the C:chl ratio is significantly lower than in samples from the upper mixed layer (5 and 10 m) (Fig. 5.6, Table 5.3). In culture and in nature, C:chl varies with light in light-limited cultures, with NO_3^- or NH_4^+ in N-limited cultures (Healey and Hendzel 1979a; Laws and Bannister 1980; Healey 1985), and with depth in the water column (Dortch et al. 1985; Smith et al. 1995). In the Barrow Strait samples, C:chl in the stratified water column probably changes as a result of N and light conditions, both of which fluctuated.

Helbling et al. (1995) correlated chlorophyll and areal photosynthesis in the Antarctic with depth of the upper mixed layer. During years with mixed depths <40 m chlorophyll, concentration and areal photosynthesis was significantly greater than when the mixed layer was >40 m. Using mean values for incident irradiance, and I_k, the differences were explained in terms of light. Gowen et al. (1995) correlated nutrient concentration and chlorophyll with the subsurface light climate in the northwestern Irish Sea and Sakshaug et al. (1991) used a mathematical model to describe the development of phytoplankton blooms as a function of the depth of the wind-mixed layer, spectral distribution of light, passage of atmospheric low-pressure systems, size of the initial phytoplankton stock and loss rates. Realistic mixed layers and frequency of high wind events produced output where macronutrients were rarely exhausted.

In lakes, irradiance in the upper mixed layer may be less than that required to saturate photosynthesis but high light extinction due to suspended sediments (Hecky and Guildford 1984) or high chlorophyll concentration (Agusti et al. 1990) rather than depth of the mixed layer were the controlling factors.

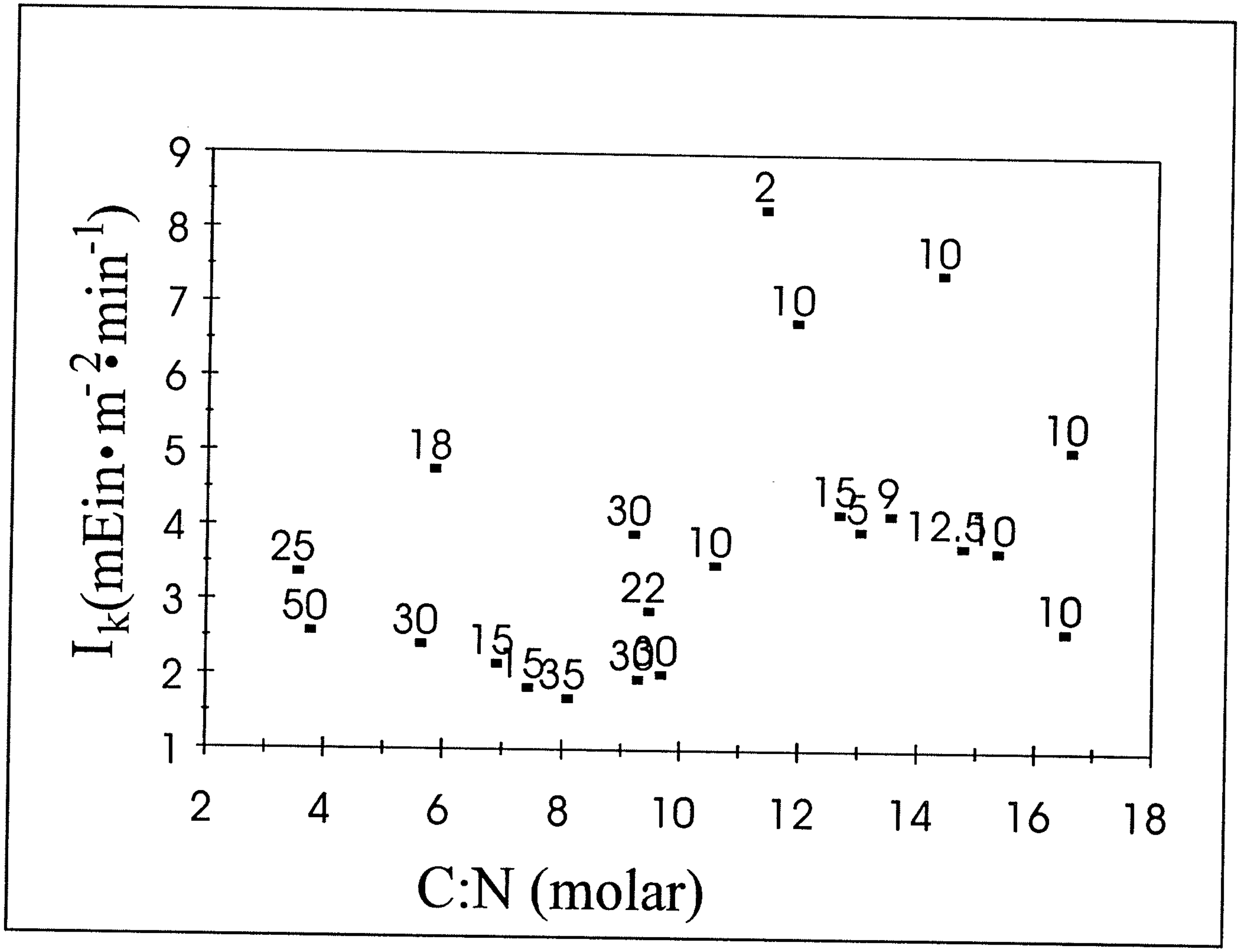
Light- and N-Deficiency

The Barrow Strait data show clear examples of N-deficiency in the upper mixed layer of stratified water columns (N debt, C:N and NO_3 concentrations) (Figs. 5.3, 5.6). In the deeper waters of stratified water columns (i.e. below the mixed layer) and in non-stratified waters, there is evidence for light limitation [low C:chl

ratios (Fig. 5.6) and I/I_k <1.0 (Table 5.4)]. Another way of looking at the data is to plot C:N, an indicator of N status, against I_k, the light level required to saturate photosynthesis (Fig. 5.11) used here as an indicator of light status. Figure 5.11 includes data of Platt et al. (1987) and Irwin et al. (1985) from Jones Sound and Lancaster Sound during August and September 1983. When N is not deficient, as indicated by C:N ratios less than 10, values for I_k are usually low <4.0 mEin·m^{-2}·min^{-1} and when N is deficient, I_k is usually higher (Fig. 5.11). Based on theoretical grounds, it would be expected that the lower I_k under non-N-deficient conditions was a function of acclimation in the form of α^B increasing at low light. That is, the efficiency of chlorophyll is greater at lower light levels than at higher levels because at low light the cells are less nutrient stressed than at high light. The scatter in both the α^B and P^B_m data is too large to see any pattern with nutrient-deficiency, however I_k, the ratio of P^B_m to α^B, does exhibit a fairly clear pattern when plotted against N-deficiency (Fig. 5.11).

Samples showing N-deficiency and higher I_k are generally from the top 10 m of the water column. N debt was also closely correlated to I_k (Fig. 5.12) and C:chl, an indicator of nutrient and light status, demonstrated a similar pattern (Fig. 5.13). High C:chl ratios are indicative of nutrient stress and low C:chl ratios are indicative of light stress. The combined data sets indicate that most of the nutrient stressed samples are from the 5 and 10 m depths and the most nutrient stressed are from

Figure 5.11. The relationship between the particulate C:N molar ratio and I_k. Numbers indicate the depth of the sample in m. Data include 1989 values from this study and values from the same vicinity (Jones Sound and Lancaster Sound) from Platt et al. 1987 and Irwin et al. 1985.



I_k(mEin•m^{-2}•min^{-1})
C:N (molar)
9
8
7
6
5
4
3
2
1
2
4
6
8
10
12
14
16
18
2
10
10
10
18
30
10
15
5
9
12.5
10
25
50
30
22
15
15
35
30
30
10

stratified water column. The low C:chl ratios, indicative of light stress, are found in the deeper samples and/or unstratified water columns (Fig. 5.13).

The tradeoff between light and nutrient-deficiency is frequently observed in a variety of natural systems. Hecky and Guildford (1984) observed light-deficiency in a northern reservoir due to erosion increasing suspended sediment. When mean water column light intensity was greater than I_k in the reservoir, light-deficiency was replaced by P-deficiency. Pennock and Sharp (1994), in the Delaware Estuary, observed light-deficiency in spring due to high turbidity which was followed by first P and then N deficiency.

The higher the I_k, the more likely is higher light intensity and the more likely is a phytoplankton assemblage which is nutrient stressed. Rey (1991) compared mean I_k values for the Canadian Arctic (4.68 mEin·m^{-2}·min^{-1}) (from Harrison and Platt 1986) with Barents Sea Arctic (2.82 mEin·m^{-2}·min^{-1}). The lower I_k in the Barents Sea data set may be the result of deeper mixing depths on average. The average I_k in the data from this study was similar to Harrison and Platt, ≈4 mEin·m^{-2}·min^{-1}. These results may suggest that the Barents Sea is more light and less nutrient-deficient than in the Canadian Arctic where more physical protection because of persistent ice cover prevents deep mixing.

Alkaline Phosphatase Activity

Nutrient status and light data together yield a convincing picture of N-deficiency during stratified periods and light-deficiency during unstratified periods.

Figure 5.12. The relationship between I_k and N debt in Barrow Strait during August 1989. Numbers indicate sample depth. Abbreviations as in Figs. 5.6 and 5.9.

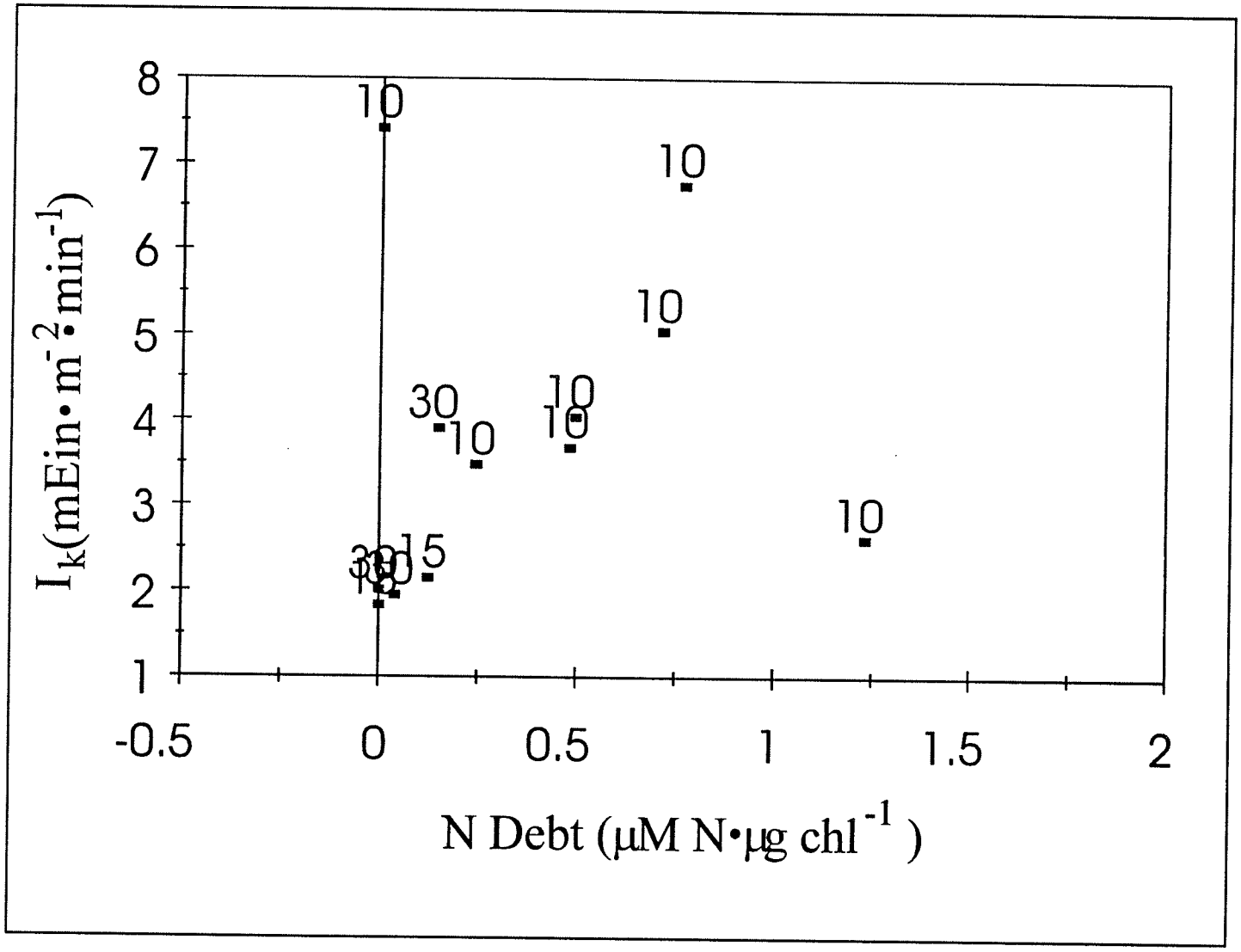
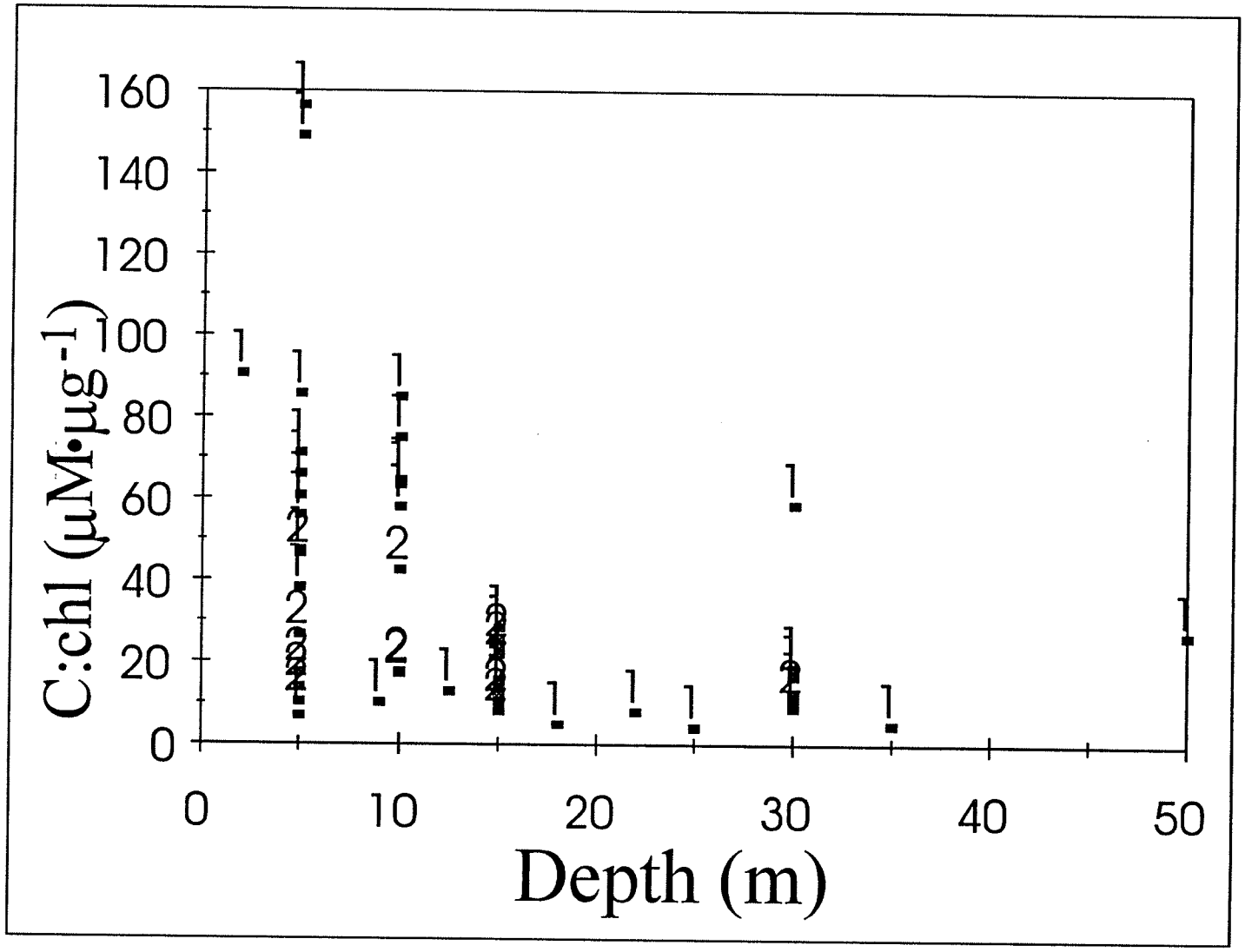

8
7
6
5
4
3
2
1
-0.5
0
0.5
1
1.5
2
I_k(mEin•m^{-2}•min^{-1})
N Debt (µM N•µg chl^{-1})
10
10
10
30
10
10
10
10
15

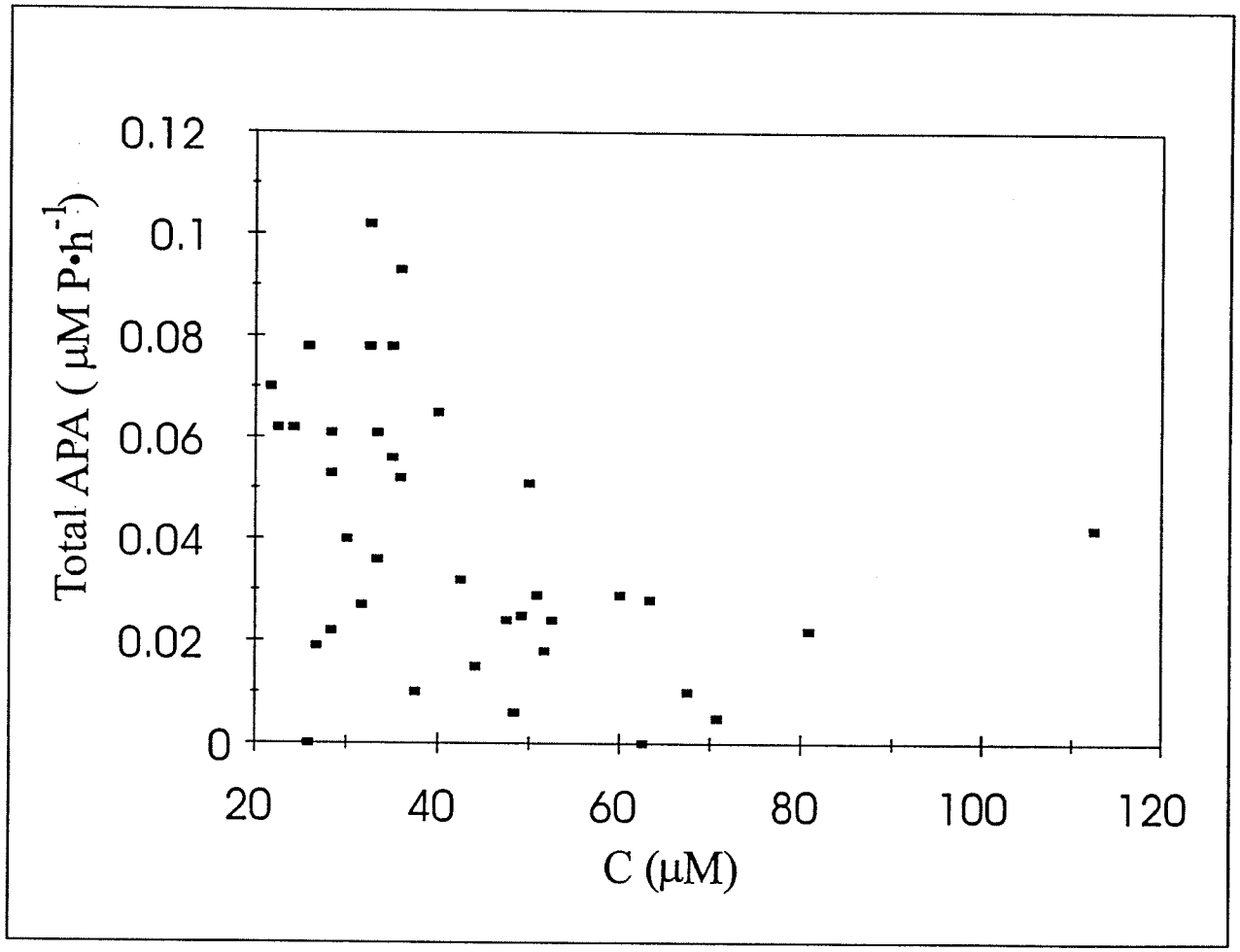
Figure 5.13. Carbon:chl at different depths. Data include 1989 and 1991 values from this study and values from Jones Sound and Lancaster Sound (Platt et al. 1987; Irwin et al. 1985). Samples from stratified water columns are denoted by the number 1, and 2 denotes unstratified. Abbreviations as in Fig. 5.5.


C:chl (µM•µg-1)
160
140
120
100
80
60
40
20
0
0
10
20
30
40
50
Depth (m)

Except for the alkaline phosphatase activity, there is no evidence for P-deficiency. SRP concentrations are high and exhibit no vertical structure in stratified water columns; C:P ratios and P debt measurements all imply no P-deficiency. APA is a commonly used measure of the presence and degree of P-deficiency in freshwater (Pick 1986; Guildford et al. 1994) and is occasionally used in the ocean (Perry 1972; Davies and Smith 1988; Guildford 1993). The rates of APA measured in the Barrow Strait are comparable to those of a moderately P-deficient lake on the Canadian Shield during the summer stratified season. It does not seem likely that the APA activity in the Barrow Strait samples is the product of P starved algae. It is also not likely that the SRP measured is somehow unavailable to the phytoplankton. It is well known that APA is produced by bacteria as well as phytoplankton, but it is not expected that bacteria in the Barrow Strait samples are any more likely to be P-deficient than the phytoplankton. It is much more likely that the bacteria are substrate-limited (Thingstad and Martissen 1991). Organic carbon is more likely to limit bacterial growth in the Arctic Ocean where there are low terrestrial inputs and low aquatic production on an annual basis. It is possible that the levels of APA observed are the product of bacterial phosphatases used to break down organic matter to obtain organic carbon for growth. In this study, highest total rates of APA occurred at lowest suspended C concentrations (Fig. 5.14). Harrison noted in two studies (Harrison et al. 1982; Harrison 1983) that rates of regeneration of SRP in Arctic samples were anomalously high compared to temperate and tropical SRP

regeneration rates. Cleavage of phosphate ester bonds may be necessary to allow effective metabolism of organic carbon sources in C starvation situations.

Figure 5.14. Total alkaline phosphatase activity (APA) plotted against particulate C for samples from the Barrow Strait during August 1989 and 1991.


0.12
0.1
0.08
0.06
0.04
0.02
0
Total APA (μM P•h-1)
20
40
60
80
100
120
C (μM)

Chapter 6

Summary and Conclusions

1. Gradient of lake size

Phytoplankton in large, stratified lakes (20 to 82,300 km^2) on the Canadian Shield in northwestern Ontario were on average less phosphorus deficient than smaller stratified lakes (<20 km^2) in the same area. Nutrient status measurements and photosynthesis at optimum light normalized to particulate carbon indicated phytoplankton had higher relative growth rates in the large lakes compared to the small lakes (Table 6.1). Larger lakes had deeper mixing depths on average than the smaller lakes (Table 6.1) and this resulted in lower mean water column light intensities in the larger lakes. Although lower, these mean water column light intensities were still high enough that light limitation did not replace P-limitation in the larger lakes. Nor did the deeper mixing depths and higher eddy diffusivity coefficients in the larger lakes appear to result in a significantly increased supply of P from below the thermocline (Fee et al. 1994). It is suggested that in lakes with deep mixed layers that nutrients are cycled more efficiently because they spend a longer time within the mixed layer. In contrast, nutrients are more quickly lost by sedimentation from the shallow very stable mixed layers of the smaller lakes.

2. Aquacultural gradient

Salmon pens and mussel strings located in a large bay on the south coast of Nova Scotia provided a gradient in point source anthropogenic nutrients. On the basis of physical, chemical and chlorophyll measurements, it was difficult to see any pattern distinguishing the sites located near aquaculture activity from those over

Table 6.1. Summary data form the study locations. TN:TP = total nitrogen:total phosphorus atomic ratio; Deficiency: N = nitrogen, P = phosphorus, Si = silicon; $P_{opt} \cdot C^{-1}$ = light-saturated rate of photosynthesis normalized to particulate carbon ($\mu M\ C \cdot h^{-1}\ \mu M \cdot C^{-1}$).

Location	TN:TP	Stratified	Deficiency	$P_{opt} \cdot C^{-1}$
Arctic	19	yes	N; no P or Si	0.004
Arctic	19	no	no N, P or Si; possibly light	0.016
Shelf	26	no	no N, P, or Si	0.030
Slope	36	no	no N, P; possibly Si	0.011
Sargasso Sea	50	both	N and P, no Si	0.011
Canadian Shield				
large lakes	68[1]	yes Z_{mix}>8m	P and N	0.014
small lakes	86	yes Z_{mix}<8m	P and N	0.01

[1] not including Lake Superior

1.6 km way from the aquaculture sites. Nutrient status measurements indicated that phytoplankton at the sites remote from the aquaculture activity were N-deficient while the phytoplankton at the aquaculture sites were less N-deficient and had higher rates of Si uptake.

3. Stratified and unstratified Arctic coastal water

Straits and Sounds in the Canadian Arctic Archipelago are physically dynamic environments due to currents, tides and ice. Melting water from Arctic sea ice creates a density gradient and the broken pans of sea ice promote stability in the upper water column. Phytoplankton nutrient status measurements indicated that phytoplankton were strongly N-deficient in shallow mixed layers but more likely light-deficient in unstratified water.

4. Coastal to Sargasso Sea gradient in the North Atlantic

This transect provided a gradient in physical energy, vertical mixing, total nutrient supply and ratio of TN:TP. Nutrient status measurements indicated that phytoplankton were not nutrient-limited in the coastal upwelling Shelf location and were probably growing at high relative growth rates. At the Shelf Break, N and P were not deficient but Si may have been a factor for diatom growth. In the Sargasso Sea, N and P were both low and nutrient status measurements indicated severe P-deficiency as well as N-deficiency. The TN:TP ratio was much higher in the mid-

ocean gyre than on the Shelf, and this high ratio is likely the reason P-deficiency occurs in the Sargasso Sea.

5. Freshwater to marine gradient

When the marine and freshwater data sets are combined, some clear patterns emerge. The elemental ratios of the nutrient pool and the degree of stratification determine the phytoplankton nutrient status. In the high Arctic where the lowest TN:TP ratio (Table 6.1) was found, severe N-deficiency was measured (as indicated by high particulate C:N and high N debt assay results) when the water column was stratified. Under stratified conditions the nutrient status indicators and carbon turnover (Table 6.1) implied low relative growth rates. When the Arctic water column was not stratified no strong indicators of nutrient-deficiency were observed and carbon turnover rates were higher when samples were incubated at optimum light (Table 6.1).

Strong stratification was not observed on the Shelf during April and no indication of N, P or Si-deficiency was observed. Carbon turnover rates were consistently the highest measured in the entire study (Table 6.1). These results imply high relative growth rates in the Shelf water which is not surprising since this area supports a very productive fishery.

Strongly stratified conditions did not develop during the time on the Slope station and N or P-deficiency was not observed. Carbon turnover rates were low even at optimum light (Table 6.1) in Slope water. A nutrient status indicator for Si,

the C:Si ratio was higher in the Slope water than any other marine locations in the study. Si-deficient diatoms may have been the reason carbon turnover was low in Slope water.

In the Sargasso Sea, the TN:TP ratio was 50, much higher than the coastal or slope water (Table 6.1) and when stratification occurred, nutrient status measurements indicated severe P as well as N-deficiency. Carbon turnover was lower than the Shelf water.

In a group of stratified lakes on the Canadian Shield in northwestern Ontario, the TN:TP ratios were much higher than any of the marine sites (Table 6.1). All the lakes in the study were severely P-deficient. Smaller stratified lakes with mixing depths on average under 8 m were the most strongly P-deficient and had low carbon turnover rates (Table 6.1). Larger lakes with mixed depths greater than 8 m were also P-deficient but not as severely P-deficient as the smaller lakes and the carbon turnover rates were on average higher in the large lakes than the small lakes. The lakes were on average more nutrient-deficient and had lower carbon turnover rates than the unstratified, non nutrient-deficient marine stations (Table 6.1), but were similar to the stratified, nutrient-deficient marine locations examined (Table 6.1).

General Conclusions

When physical, chemical and nutrient status measurements were made across the wide range of conditions provided in lakes and oceans some common patterns emerged. Stable, stratified physical conditions were necessary for nutrient-deficiency

to develop. Whether N or P that became deficient under stratified conditions was predictable from the TN:TP ratio. At low TN:TP, such as in the Arctic study, N was severely deficient in stratified water. At higher TN:TP, such as in the Sargasso Sea and in lakes on the Canadian Shield, P-deficiency occurred under stratified conditions. The nutrient status measurements tested in steady state culture were useful for understanding the processes controlling phytoplankton growth in nature.

The nutrient status measurements applied in this research are simple and robust. They can and should be utilized to evaluate the factors that control phytoplankton growth in waters around the world, but these methods will be especially useful to the scientific evaluation of water quality in developing countries. They can help to define the nature of nuisance and toxic algal growth problems which increasingly occur in lakes and coastal areas globally. They can also help to define the necessary conditions for improving or maintaining trophic efficiencies in these aquatic ecosystems by identifying the nutrient imbalances which limit phytoplankton growth or quality of the phytoplankton ration for consumers.

No single physical, chemical or nutrient status measurement will be adequate to evaluate the processes controlling phytoplankton growth because growth conditions are multifactorial and dynamic. It is important to recognize temporal and spatial scales relevant to growth and design sampling schemes appropriately. A suite of nutrient status measurements should be employed and redundancy is encouraged because individual measurements may have specific methodological limitations or unappreciated interpretations. In this study the alkaline phosphatase method in the

Sargasso Sea gave evidence of moderate to extreme P limitation and was detectible in coastal environments when stoichiometric ratios indicated P sufficiency. These results may either call into question the applicability of the assay in marine environments OR that the enzyme is playing some as yet undetermined role in the cycling of nutrients. Further research is necessary on this topic.

New, sensitive probes for nutrient deficiency are being developed and should be welcomed after appropriate testing and evaluation in defined environments. However, the same concern about maintaining redundancy will apply to new methods. The methods applied in this research have demonstrable utility and will continue to provide valuable and cost effective information alongside newer methods. The simplicity and utility of the current methods will certainly insure their application for the foreseeable future in the study and modelling of phytoplankton growth.

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Appendix 1. Chemical data from the upper mixed layer collected along the Shelf, Slope, Sargasso Sea transect from April 4-19, 1991. -1 = below detection.

1 Date
2 Z = depth (m)
3 L = location, Y = Shelf, S = Sargasso, G = Slope, R = Shelf
4 Lat = latitude
5 Long = longitude
6 NO_3 = nitrate measured at the Freshwater Institute (µmole)
7 NO_3 = nitrate measured at the Bedford Institute of Oceanography (µmole)
8 Susp N = suspended nitrogen measured at the Freshwater Institute (µmole)
9 Susp N = suspended nitrogen measured at the Bedford Institute of Oceanography (µmole)
10 TDN = total dissolved nitrogen measured at the Freshwater Institute (µmole)
11 SRP = soluble reactive phosphate measured at the Freshwater Institute (µmole)
12 PO_4 = phosphate measured at the Bedford Institute of Oceanography (µmole)
13 Susp P = suspended phosphorus measured at the Freshwater Institute (µmole)
14 TDP = total dissolved phosphate measured at the Freshwater Institute (µmole)
15 DOC = dissolved organic carbon measured at the Freshwater Institute (µmole)
16 Susp C = suspended carbon measured at the Freshwater Institute (µmole)
17 Susp C = suspended carbon measured at the Bedford Institute of Oceanography (µmole)
18 Chl a = chlorophyll a measured at the Freshwater Institute ($\mu g \cdot L^{-1}$)
19 Chl a = chlorophyll a measured at the Bedford Institute of Oceanography ($\mu g \cdot L^{-1}$)
20 Phae = phaeophytin measured at the Bedford Institute of Oceanography ($\mu g \cdot L^{-1}$)
21 SRSi = soluble reactive silicon measured at the Freshwater Institute (µmole)
22 SRSi = soluble reactive silicon measured at the Bedford Institute of Oceanography (µmole)
23 Susp Si = suspended silicon measured at the Freshwater Institute (µmole)

Table 1. Chemical data from the upper mixed layer collected along the Shelf, Slope Sargasso Sea transect from April 4-19, 1991.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Date	Z	L	Lat	Long	NO_3	NO_3	Susp N	Susp N	TDN	SRP	PO_4	Susp P	TDP	DOC	Susp C	Susp C	CHLA	CHLA	PHAE	SRSI	SRSI	Susp Si
					FWI	BIO	FWI	BIO	FWI	FWI	BIO	FWI	FWI	FWI	FWI	BIO	FWI	BIO	BIO	FWI	BIO	FWI
4/4/91	20	Y	4321	6510	1.21	0.78	3.9	6.1	30.0	0.52	0.58	0.32	0.94	80	27.5	34.7	5.64	5.38	0.16	1.679	0.44	5.61
4/4/91	40	Y	4321	6510	2.50	2.36	2.9	5.6	30.0	0.52	0.69	0.19	1.00	170	23.3	23.2	4.76	3.97	0.13	1.929	0.8	5.46
5/4/91	10	Y	4320	6510		0.17		5.5			0.46					42.2		6.35	0.13		0.21	
5/4/91	20	Y	4320	6510		1.52		5.1			0.59					31.0		5.83	0.1		0.33	
5/4/91	30	Y	4320	6510		5.62		1.6			0.78							0.5	0.11		5.72	
6/4/91	10	Y	4320	6510	0.21	0.01	3.7		27.1	0.39	0.55	0.32	0.84	120	30.0		3.32	5.83	0.1	1.143	0.16	2.32
6/4/91	1	Y	4320	6510	0.14	0.01	3.8	3.4	27.9	0.39	0.43	0.35	1.13	180	29.2	30.5	3.07	4.22	0.11	1.179	0.04	3.21
6/4/91	10	Y	4320	6510	0.14	0.02	4.2	3.5	29.3	0.39	0.45	0.35	1.00	130	31.7	31.8	4.54	4.86	0.05	1.536	0.03	3.75
6/4/91	30	Y	4320	6510	2.43	2.51	2.9	2.8	32.1	0.52	0.6	0.32	1.03	80	21.7	24.3	2.99	3.52	0.12	2.714	1.27	2.64
7/4/91	1	Y	4316	6514	0.14	0.28	3.4		27.9	0.32	0.45	0.39	0.81	70	35.0		2.99	5.95	0.17	1.321	0.77	3.57
7/4/91	5	Y	4316	6514	0.14	0.64	4.5		26.4	0.32	0.48	0.42	0.97	60	45.0		3.4	6.23	0.15	1.464	1.12	4.11
7/4/91	1	Y	4316	6514		0.6		4.6			0.42					32.7		4.46	0.16		0.88	
7/4/91	10	Y	4316	6514		1.94		3.7			0.48					27.0		3.82	0.15		1.94	
7/4/91	40	Y	4316	6514		3.29		2.5			0.58					18.8		2.72	0.17		2.69	
9/4/91	1	S	3601	6330	0.21	0	0.7	0.6	26.4	-1	0.09	0.06	0.45	100	10.8	6.3	0.10	0.13	0.03	1.214	0.43	0.68
9/4/91	20	S	3601	6330	0.21	0	0.9	0.6	27.9	-1	0.05	0.10	0.45	60	12.5	6.5	0.06	0.12	0.04	0.857	0.38	0.43
9/4/91	40	S	3601	6330	0.14	0	0.9	0.6	27.9	-1	0.05	0.10	0.48	40	10.0	7.8	0.17	0.16	0.05	0.857	0.23	0.50
10/4/91	30	S	3610	6311	0.14	0	0.8		29.3	-1	0.03	0.06	0.68	30	8.3		0.10	0.13	0.05	0.929	0.35	0.79
10/4/91	70	S	3610	6311	0.14	0.03	0.8		26.4	-1	0.06	0.10	0.42	30	7.5		0.31	0.35	0.08	0.679	0.18	0.96
10/4/91	60	S	3610	6311		0.18		0.9			0.07					6.8		0.5	0.14		0.58	

Date	Z	L	Lat	Long	NO_3	NO_3	Susp N	Susp N	TDN	SRP	PO_4	Susp P	TDP	DOC	Susp C	Susp C	CHLA	CHLA	PHAE	SRSI	SRSI	Susp Si
					FWI	BIO	FWI	BIO	FWI	FWI	BIO	FWI	FWI	FWI	FWI	BIO	FWI	BIO	BIO	FWI	BIO	FWI
10/4/91	80	S	3610	6311		0.1		0.8			0.08					8.2		0.32	0.13		0.44	
11/4/91	30	S	3609	6245	0.14	0	0.7		26.4	-1	0.08	0.10	0.42	20	7.5		0.05	0.13	0.06	0.929	0.65	1.00
11/4/91	50	S	3609	6245	0.29	0.21	0.8		26.4	-1	0.07	0.10	0.42	20	9.2		0.1	0.21	0.09	0.964	0.72	2.68
11/4/91	80	S	3609	6245	0.93	1.2	0.6		27.9	-1	0.09	0.10	0.52	20	7.5		0.13	0.12	0.07	1.071	0.82	0.82
11/4/91	10	S	3609	6245		0		0.6			0.12					4.8		0.13	0.06		0.51	
11/4/91	30	S	3609	6245		0		2.0			0.1					6.3		0.12	0.06		0.48	
11/4/91	50	S	3609	6245		1.1		1.3			0.12					5.8		0.23	0.12		0.78	
12/4/91	1	S	3547	6237		0		0.8			0.06					9.6		0.38	0.14		0.23	
12/4/91	30	S	3547	6237	0.14		1.2		26.4	-1		0.10	0.45	20	19.2		0.46	0.39	0.12	0.857	0.48	2.50
12/4/91	60	S	3547	6237	0.21		1.0		40.0	-1		0.13	0.52	20	10.0		0.53	0.53	0.17	0.929	0.48	0.86
12/4/91	70	S	3547	6237		0.05		1.0			0.05					10.1		0.5	0.23		0.48	
12/4/91	80	S	3547	6237	0.29		0.9		34.3	-1		0.13	0.52	20	10.0		0.47	0.48	0.16	0.929	0.48	0.57
12/4/91	90	S	3547	6237		0.36		0.8			0.06					7.6		0.42	0.2		0.55	
13/4/91	10	S	3618	6259		0		1.0			0.06					12.7		0.29	0.09		0.19	
13/4/91	50	S	3618	6259		0		0.9			0.08					8.2		0.22	0.09		0.17	
13/4/91	70	S	3618	6259		0.02		0.9			0.06					9.5		0.21	0.08		0.18	
14/4/91	10	S	3843	6342	0.14	0.03	0.7	0.6	33.6	-1	0.05	0.13	0.65	20	9.2	7.0	0.17	0.26	0.09	0.857	0.51	0.89
14/4/91	50	S	3843	6342	0.36	0.63	0.9	0.9	34.3	-1	0.08	0.13	0.71	20	8.3	8.0	0.54	0.5	0.15	1.143	0.7	0.68
14/4/91	75	S	3843	6342	0.57	1.05	0.6	0.6	32.9	-1	0.07	0.13	0.61	40	7.5	6.6	0.4	0.37	0.14	1.036	0.89	0.39
14/4/91	1	S	3843	6342		0.26		0.9			0.09					7.8		0.51	0.13		1.07	
14/4/91	50	S	3843	6342		3.08		0.4			0.12					4.8		0.13	0.08		1.54	
14/4/91	75	S	3843	6342		2.25		0.1			0.16					2.2		0.08	0.04		1.3	

Date	Z	L	Lat	Long	NO_3	NO_3	Susp N	Susp N	TDN	SRP	PO_4	Susp P	TDP	DOC	Susp C	Susp C	CHLA	CHLA	PHAE	SRSI	SRSI	Susp Si
					FWI	BIO	FWI	BIO	FWI	FWI	BIO	FWI	FWI	FWI	FWI	BIO	FWI	BIO	BIO	FWI	BIO	FWI
15/4/91	1	G	4015	6435		1.47		2.4			0					19.8		1.26	0.15		1.75	
15/4/91	20	G	4015	6435	1.29	1.68	2.6	1.9	31.4	0.16	0	0.23	0.81	50	20.0	19.3	1.07	1.24	0.15	2.036	1.76	0.46
15/4/91	40	G	4015	6435	2.21	2.38	2.3	1.8	32.9	0.16	0.01	0.19	0.87	30	15.0	14.4	0.77	0.84	0.14	2.143	1.8	0.50
16/4/91	10	G	4022	6445	2.14	2.86	1.6	1.7	31.4	0.16	0.3	0.16	0.87	70	11.7	13.3	0.51	0.77	0.16	2.143	1.88	0.43
16/4/91	30	G	4022	6445	2.93	3.31	1.4	1.1	32.9	0.16	0.31	0.16	0.68	50	11.7	11.8	0.44	0.55	0.13	2.214	1.95	0.39
16/4/91	50	G	4022	6445	3.14	3.48	1.6	1.3	33.6	0.23	0.32	0.16	0.71	40	10.0	12.8	0.57	0.54	0.13	2.321	1.99	0.21
17/4/91	1	G	4194	6428		3.49					0.47							0.85	0.14		2.08	
17/4/91	10	G	4194	6428	1.50	3.5	1.5		30.0	0.16	0.49	0.16	0.77	30	12.5		0.48	0.82	0.15	1.893	2.11	0.79
17/4/91	20	G	4194	6428		3.54					0.48							0.79	0.16		2.12	
17/4/91	30	G	4194	6428	1.57	3.62	1.4		30.0	0.16	0.48	0.16	0.71	20	10.0		0.58	0.77	0.16	1.929	2.19	0.61
17/4/91	40	G	4194	6428		3.62					0.48							0.74	0.2		2.21	
17/4/91	1	G	4194	6428		3.58		2.0			0.51					18.7		0.91	0.17		1.94	
17/4/91	20	G	4194	6428		3.59		1.9			0.52					19.3		0.83	0.19		1.91	
17/4/91	40	G	4194	6428		3.63		1.5			0.52					15.5		0.76	0.19		1.93	
18/4/91	1	R	4319	6513		0.71		2.4			0.44					20.4		1.2	0.1		1.04	
18/4/91	5	R	4319	6513	0.43		2.4		29.3	0.39		0.23	0.84	70	15.8		0.82			1	1	1.17
18/4/91	10	R	4319	6513		0.66		2.1			0.43					18.2		1.09	0.12		1	
18/4/91	20	R	4319	6513	0.43	0.72	2.4	2.1	28.6	0.39	0.44	0.26	0.84	40	17.5	19.3	1.23	1.14	0.1	1.036	0.97	1.64
18/4/91	60	R	4319	6513	6.14		1.2		33.6	0.77		0.16	1.19	30	10.0		1.06			5.607		2.57
19/4/91	1	R	4320	6510	1.07		3.3		28.6	0.52		0.26	0.87	30	20.8		1.32			3.821		2.00
19/4/91	25	R	4320	6510	2.21		1.7		29.3	0.55		0.26	1.00	30	11.7		1.36			2.321		2.39
19/4/91	35	R	4320	6510	5.43		0.9		32.1	0.71		0.16	1.16	20	6.7		1.13			4.25		2.67

Table 2. Linear regressions between similar variables measured at the Freshwater Institute (FWI) and at the Bedford Institute of Oceanography (BIO). The model used is: variable (FWI) = variable (BIO) + constant chlorophyll (μg/L), susp C suspended carbon (μg), susp N = suspended nitrogen (μmole), NO_3 = nitrate (μmole), SRSi = soluble reactive silicon (μmole). Regressions were done when the analyses were done on water taken from similar depths.

Variable	R	n	Coefficient	Constant
Chlorophyll	0.85	30	0.716	0.127
Susp C	0.93	17	0.785	42
Susp N	0.73	17	0.608	0.761
NO_3	0.82	27	0.689	0.146
SRSi	0.57	31	0.633	0.821

Table 3. Comparison of variables measured at both the Freshwater Institute and the Bedford Institute of Oceanography. Abbreviations and units as in Table 2. Statistics were done on all samples from within the mixed layer.

Variable	n	Mean	Min	Max
Chl (FWI)	35	1.3	0.05	5.64
Chl (BIO)	59	1.47	0.08	6.35
Susp C (FWI)	35	190	80	540
Susp C (BIO)	43	183	26	506
Susp N (FWI)	35	1.86	0.57	4.5
Susp N (BIO)	43	1.92	0.14	6.1
NO_3 (FWI)	35	1.18	0.14	6.14
NO3 (BIO)	56	1.36	0	5.6
SRSi (FWI)	35	1.68	0.68	5.61
SRSi (BIO)	60	1.06	0.03	5.72