Chapter 6

Factors controlling pelagic algal abundance and composition in Lake Malawi/Nyasa

Stephanie J. Guildford and William D. Taylor
Department of Biology, University of Waterloo, Waterloo, ON, N2L 6A3, Canada

Harvey A. Bootsma
Lake Malawi/Nyasa Biodiversity Conservation Biodiversity Project
P.O. Box 311 Salima, Malawi

Len L. Hendzel
Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent
Winnipeg, MM, R3T 2N6, Canada

Robert E. Hecky
Environment Canada, National Water Research Institute
P.O. Box 5050, Burlington, Ontario, L7R 4A6, Canada

Lisa Barlow-Busch
Department of Biology, University of Waterloo, Waterloo, Ontario, N2L 6A3, Canada

Introduction

One of the main goals of the Lake Malawi/Nyasa Biodiversity Conservation Project (LMBCP) is to predict the effect of increased erosion and other catchment and atmospheric inputs on the water quality of Lake Malawi. A common symptom of degraded water quality is increasing occurrences of noxious algae. In North American lakes there have been many studies showing a strong correlation between increased input of critical plant nutrients, especially phosphorus, and abundance and frequency of occurrence of noxious algae (Schindler 1977, Makarewicz 1993). The increase in phosphorus is often related to increased erosion, as a result of development of land for agricultural use (Stone and Sanderson 1996, Stone et al. 1995). We have made measurements to determine the relationship between algae and nutrients in Lake Malawi in its present condition, and we conducted experiments to determine the effect of increased concentrations of the nutrients nitrogen (N) and phosphorus (P) on algal abundance and type of algae.

Degradation of water quality due to increased nutrient input is important for the following reasons. Toxin producing algal species such as *Microcystis*, *Anabaena, Aphanizomenon*, and *Cylindrospermopsis* are favoured in water with a high input of phosphorus. Increases in domestic and agricultural wastes and increases in algal abundance are accompanied by increases in bacteria, some of which, such as *Shigella* sp., *Escherichia coli* and *Salmonella* sp., are harmful to humans and animals. Disease causing protozoa, including *Giardia* sp. and *Cryptosporidium* sp. may also increase as water quality degrades. Algae are at the base of the food web that leads ultimately to fish and humans.

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The aquatic food web of Lake Malawi is currently in balance with fish production and good quality water as valuable products. If algal species change at the lower level of the aquatic food web, the upper levels in the food web could be affected.

In North American lakes, there exists a strong correlation between increases in the critical plant nutrient phosphorus, and increases in algae and changes in algal species. However, other nutrients, and other factors are also important in controlling algal abundance and species. This is especially true in lakes like Lake Malawi in its' present unpolluted state. Nitrogen is a second critical plant nutrient that is often cited in the control of algal growth (Hecky and Kilham 1988). Grazing by protozoa and zooplankton can keep even fast growing algal populations at low concentrations in some cases (Taylor 1984). Another factor important in the control of algal growth is light. In large, clear lakes such as Malawi, when the depth of mixing is very large, e.g. > 100 m, a significant portion of the algal community is likely to be at sub optimal light for growth for at least part of the day (Guildford et al.1998). In this study we assessed the conditions and processes controlling algal in 3 ways. 1) Defining the physical and chemical environment that the algae are experiencing in the lake. 2) Studying the nutritional status of the algae as soon as they are removed from the lake. 3) Conducting experiments where nutrient supply and grazing pressure were manipulated over incubations ranging from 12 to 48 hours.

In this chapter we present our current results from studying the factors controlling algal abundance and species composition in Lake Malawi. We begin by examining the spatial and temporal variability, with respect to some biological variables, for the lake as a whole. This is done in order to determine how representative our measurements are. We sampled one station intensively during three periods in 1997. We then present our data from our intensively monitored station, followed by the results of our experiments conducted to determine the effects of increased nutrients on algal abundance and species composition. We conclude by predicting the likely effect of increased erosion on the algal abundance and species composition in Lake Malawi, based on our current understanding.

Methods

Study area and study design **-** Lake Malawi is the southernmost of the African rift valley lakes, located between 9.5^{o} and 14.5^{o} S (Figure 6.1). The lake is 580 km long and 75 km at its widest. The mean depth is 292 m and the maximum depth is 785 m. A more detailed physical description can be found in Bootsma and Hecky (1993). During this study we sampled Station 928 (Figure 6.1) intensively during the rainy, windy and dry seasons of 1997. This station was chosen because it was relatively close to the laboratory at Senga Bay, yet far enough from the mainland, that it was representative of the deep, pelagic area of the lake. We made physical, chemical and biological measurements to determine the nutritional status of the algae and to define the environment experienced by the algae during the three seasons. As well as monitoring Station 928, we conducted experiments on water taken from Station 928 to simulate enrichment with nutrients and changes in the food web. Each season we also analyzed water samples from along a transect starting at the mouth of the Linthipe River and ending at Station 928 (Figure 6.1). The purpose of this transect data was to determine the influence of the Linthipe River plume, on the algal community, as it flowed out into the lake. We expected that stations near the mouth of the Linthipe would be receiving more P than offshore stations and thus be representative of conditions that may occur more frequently in the lake as erosion increases (see Chapter 2, Kingdon et al.1998).

Field Sampling **-** Station 928 was sampled 4 times over approximately three-week periods in January (rainy), June (windy) and November (dry) 1997. The transect stations 929 through 934 were sampled once each of the 3 seasons. Water samples were collected using 5 L Niskin bottles from depths expected to be representative of the upper and lower part of the epilimnion. This depth was usually 5 and 20 m or 10 and 30 m. Water was passed through a 200 μm nytex screen, to remove larger zooplankton, and stored in acid cleaned, polyethylene containers in light-proof, insulated boxes until being analyzed. Zooplankton samples were also taken with twin nets from approximately 2 m from the bottom to the surface. Zooplankton were preserved to have a final concentration of 10% fomalin. Profiles for temperature, conductivity, in situ fluorescence, pH, and oxygen were taken at each station usually from the surface to within 2 m of the bottom, using a Seabird CTD profiler. Light attenuation

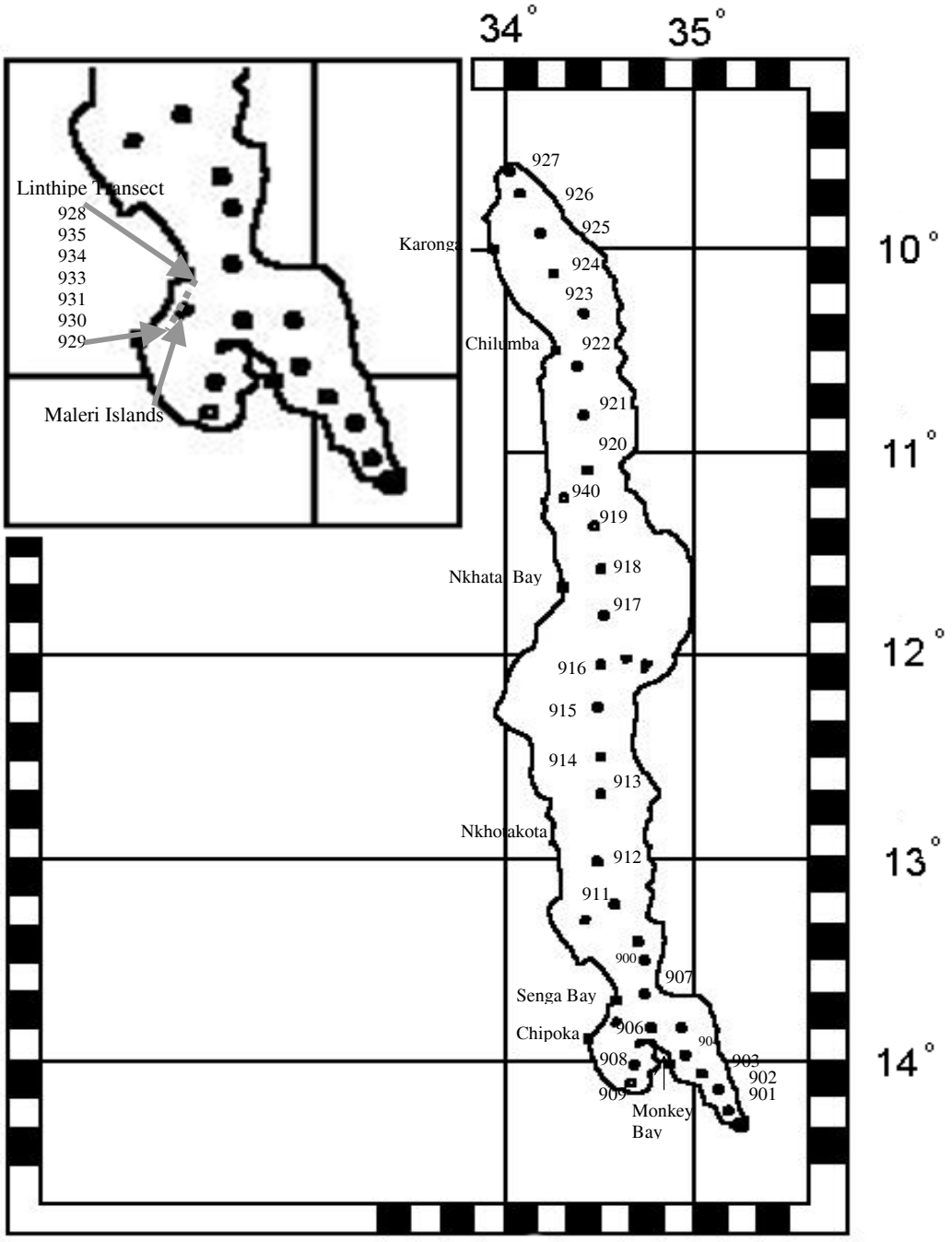


Figure 6.1. Map of Lake Malawi showing stations and inset showing Linthipe transect and Maleri Islands.

was measured with a Li-Cor LI-185 underwater quantum sensor (flat plate, cosine corrected collector). A mercury thermometer was used to measure surface temperature. Secchi disk depth was measured at each station using a black and white 30 cm disk.

Laboratory Procedures **-** Water samples were subdivided for plankton identification and counting, nutrient status measurements and photosynthetic measurements. For phytoplankton and protozoa identification and counting we preserved 100 mL of lake water with Lugol's iodine (final concentration 1%). For autotrophic picoplankton counting we preserved 20 mL with paraformaldehyde (final concentration 0.2%), for bacteria we preserved 20 mL with formalin (final concentration 4%). All preserved samples were stored at 4o C in the dark.

Measurements to determine the nutritional status of algae consisted of four seston composition ratios and three metabolic indicators. The seston ratios were carbon:nitrogen (C:N), carbon:phosphorus (C:P), nitrogen:phosphorus (N:P), and carbon:chlorophyll *a* (C:chl). The amounts of the critical plant nutrients N and P, and the plant pigment, chlorophyll *a*, change in relation to C in algae that are deficient in nutrients (Healey 1975). The metabolic nutrient status indicators were nitrogen debt (N debt), phosphorus debt (P debt), and phosphorus uptake constants. Algae growing at low growth rates because they are deficient in either N or P will take up more of that nutrient per unit chlorophyll *a* than algae not deficient in that nutrient (Healey and Hendzel 1980). Algae growing at low growth rates because they are deficient in P will have much higher phosphorus uptake constants, as determined with the radioactive tracer ^{33}P, than algae that are not P deficient. Particulate C, N and P samples were filtered through pre-ignited GF/F filters and were kept frozen until analyzed (Stainton et al.1977). 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 on triplicate sub-samples at the beginning and end of the incubation (Stainton et al. 1977). Samples were incubated in the dark at room temperature. Nitrogen debt was calculated as the nutrient removed over a 24-h period per unit of chlorophyll *a* (Healey 1977). Phosphorus debt was measured in a similar way to N debt except that potassium di-hydrogen phosphate was added (final concentration 5 μM). Soluble reactive P (SRP) was measured on triplicate sub-samples (Stainton et al. 1977). On one or two occasions each season water from Station 928 was subdivided into 3 size fractions, before being processed for nutritional status and rates of photosynthesis. The size fractions were < 2.0 μm, < 18 μm, and < 200 μm. Phosphate uptake by plankton was measured by placing 50 mL of lake water in a polyethylene beaker and adding about 10 MBq of carrier-free ^{33}P. Filtration of several 1-mL aliquots on 0.2, 0.8, and 18 μm filters over time was used to assess translocation of ^{33}P to various particulate fractions. Uptake constants for phosphate were calculated as the slope of a plot of the logarithm of the fraction of ^{33}P remaining in solution (passing through a 0.2 μm filter) versus time (Taylor and Lean 1991).

Photosynthesis was measured using the incubator method described by Fee et al. (1992). Water was incubated with ^{14}C labeled $NaHCO_3$ for approximately 3 hours in a water filled incubator at in situ temperatures. For each sample, 2 dark and 10 light bottles were incubated. During the incubation, photosynthetically active radiation (PAR) was measured at each bottle position using a Biospherical QSP-200 spherical quantum sensor (400-700 nm) (Biospherical Instruments Inc., San Diego, California). Carbon uptake was obtained by filtering the sample at the end of the incubation and fuming the filter over HCl before adding fluor and counting. Carbon uptake vs irradiance curves from the incubator were used to obtain the photosynthetic parameters P_{opt}, P^b_m, α, and $P_{opt}.C^{-1}$. P_{opt} is the unnormalized rate of photosynthesis at PAR optimal for photosynthesis, P^b_m is P_{opt} normalized to chlorophyll *a*, α is the slope of the C uptake vs irradiance curve as irradiance approaches zero, normalized to chlorophyll *a*, Popt.C^{-1} is Popt normalized to particulate carbon.

Nutrient and grazer manipulation experiments were conducted once each season. The same procedure was followed each time. Eighty L of water was collected from 20 m at Station 928, passed through a 200 μm mesh net and stored in acid cleaned 20 L polyethylene containers, in insulated boxes. In the laboratory, the 80 L was divided into eight, 10 L sub-sub-samples which received the following treatments. 1a and 1b: controls, no nutrients added. 2a and 2b: grazers > 50 μm removed, no nutrients added. 3a and 3b; lake water amended with N and P to give final concentrations of approximately 15 μM N and 5 μM P. 4a and 4b: grazers > 50 μm removed and lake water amended with N and P to give final concentrations of approximately 15 μM N and 5 μM P. The 8, polyethylene containers were incubated in a large water filled tank outside the laboratory exposed to natural light.

Sub-samples were taken for biomass, nutrient status and photosynthetic measurements at 0, 24 and 48 hours.

Results

Spatial and temporal variability of nutrient status measurements **-** We sampled intensively in the area of Senga Bay 3 times during the year, trying to target the rainy, windy and dry season. To establish whether we did in fact hit the targeted seasons and whether our data collected in this south central lake region was representative of the whole lake, we examined the whole lake data available for particulate C:N, C:P, N:P ratios and chlorophyll a. The data were divided into four groups (Figure 6.1). Group 1 is the southeast arm and includes stations 901 to 905. Group 2 is station 900 only, because there is so much data from this standard station. Group 3 is the south central area and includes station 928 our main station as well as station 906-910, 929-934, 936-938, 940. Group 4 is the north part of the lake and includes stations 911-927. The C:N, C:P, and N:P composition ratios plotted by month for the four regions indicate that the lake is relatively homogeneous spatially with respect to these indicators of phytoplankton nutrient status (Figure 6.2a, 6.2b, 6.3a). On the four occasions when the four regions were sampled at the same time, there is very little difference between the regions with respect to C:N, C:P and N:P ratios. There was more spatial variability in the chlorophyll *a* concentration (Figure 6.3b) with the northern stations generally lower than the other regions. Temporally, the C:N, C:P and N:P ratios look lower in the windy season (April through August) while the chlorophyll *a* concentrations look higher in the windy season but highly variable. The patterns found in these data are similar to the patterns that emerged in the historical particulate data summarized in Guildford et al. (1998), although the means for the historical data are higher.

Station 928: Description of nutrient chemistry, nutrient status and photosynthesis during the rainy, windy and dry season.

Variability with depth **-** We routinely sampled the upper (5 or 10 m) and lower (20 or 30 m) mixed layer at station 928. We did not see a consistent pattern with depth, so for this report we plotted both depths for each day for each season. Depth profile data from station 900 show that there was frequently a deep chlorophyll peak at approximately 30 m (H. A. Bootsma, personal communication).

Nutrients **-** There were clearly seasonal differences in the concentrations of ambient NH_4 and PO_4 at station 928. Ambient NH_4 concentrations were highest in November, the end of the dry season, when the rains were beginning (Figure 6.4a). Ambient PO_4 concentrations were highest in June, the deep mixing season (Figure 6.4b).

Phytoplankton biomass and size distribution **-** Total chlorophyll *a* at station 928, on average, was higher in June but day to day variability in January was greater than variability between seasons (Figure 6.5a). During all seasons sampled at station 928, 50 % of the total chlorophyll *a* was in the pico-plankton size range (< 2 μm), 30% was 2-18 μm, and 20% 18-200 μm (Figure 6.5b).

Phytoplankton nutrient status **-** In each of the three seasons, NH_4 uptake normalized to chlorophyll *a* indicated N deficiency (Figure 6.6a). Particulate C:N ratios in January indicated moderate to severe N deficiency and no to moderate deficiency in November (Figure 6.6b). C:N ratios are not available for station 928 in June, however C:N ratios at station 900 and other areas in the lake were in the range of no to moderate N deficiency (Figure 6.2). Rates of N fixation were measured at station 928 in November. Of the 7 times rates were determined only one date had detectable rates. These data are in Annex 1 of this chapter.

PO_4 uptake normalized to chlorophyll *a* indicated the presence of P deficient phytoplankton in all three seasons (Figure 6.7a). Particulate C:P ratios in January indicated moderate to severe P deficiency and moderate in November (Figure 6.7b). Particulate N:P indicated no P deficiency for all but one set of samples in January (Figure 6.8a). ^{33}P uptake constants at station 928 (Figure 6.8b) were very low, indicative of a large supply of P relative to demand. The uptake constants for P in November indicated

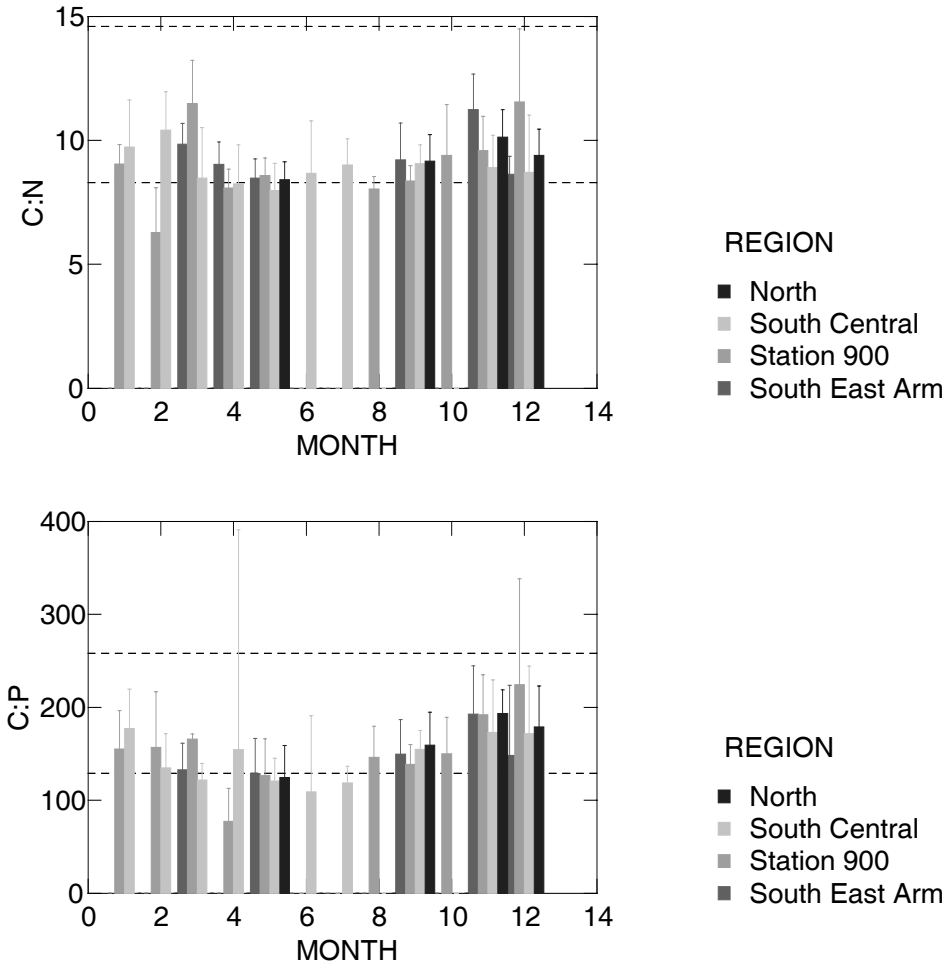


Figure 6.2a. The molar ratio of particulate carbon to particulate nitrogen (C:N). Bar graphs represent the monthly mean and standard deviation of samples taken from the upper mixed layer for the years 1997 and 1998. Values above the top horizontal line indicate severe N deficiency and values between the two horizontal lines moderate N deficiency.

Figure 6.2b. As above but for particulate carbon to particulate phosphorus (C:P). Horizontal lines indicate P deficiency.

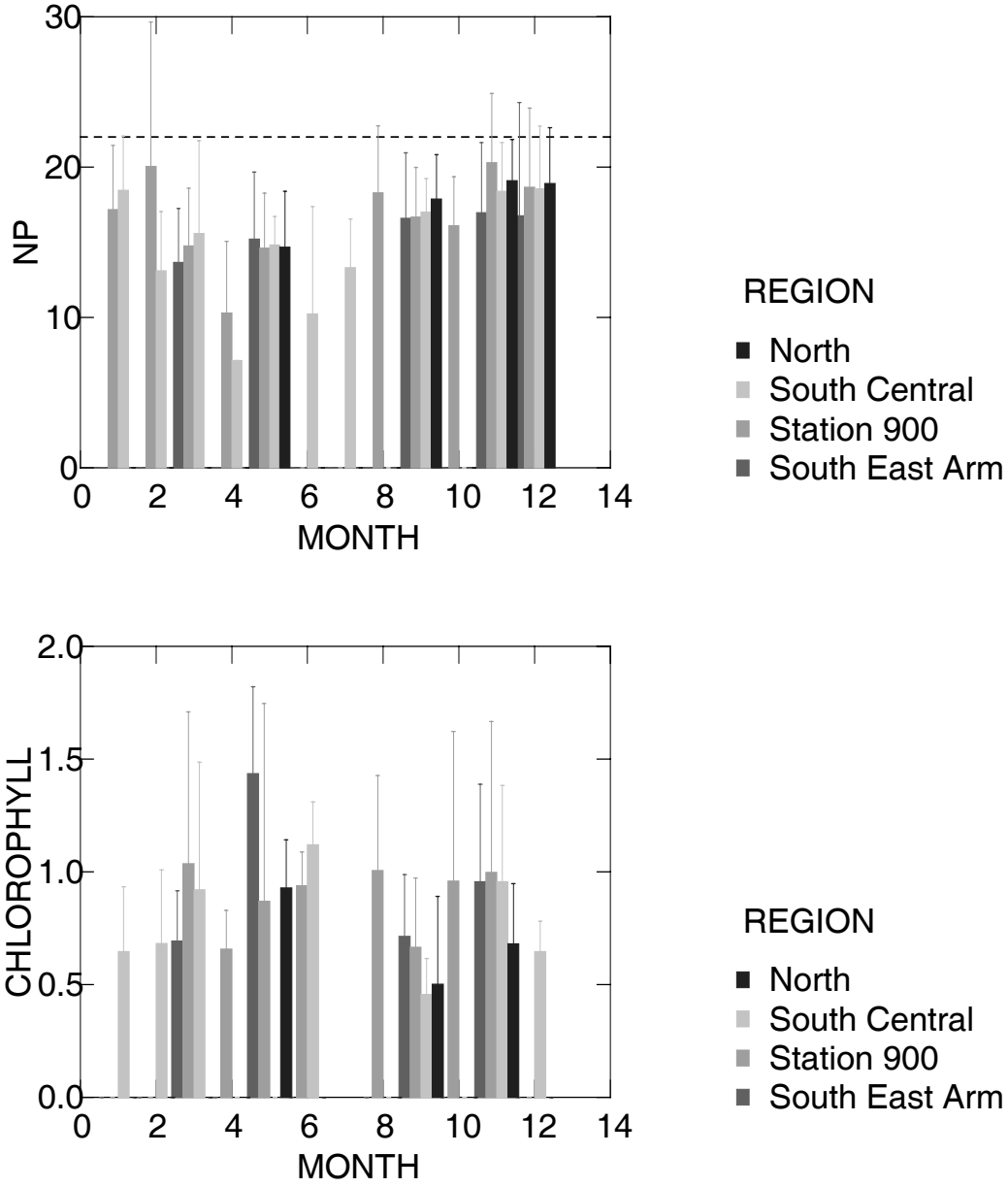
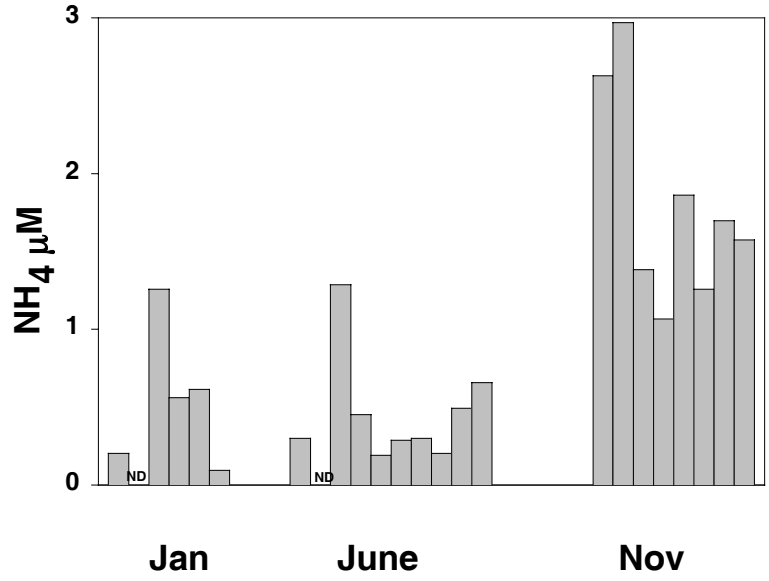


Figure 6.3a. The molar ratio of particulate nitrogen to particulate phosphorus (N:P). Bar graphs represent the monthly mean and standard deviation of samples taken from the upper mixed layer for the years 1997 and 1998. Values above the horizontal line indicate P deficiency.
Figure 6.3b. Chlorophyll *a* concentration ($\mu g.L^{-1}$). Bar graphs represent the monthly mean and standard deviation of samples taken from the upper mixed layer for the years 1997 and 1998.



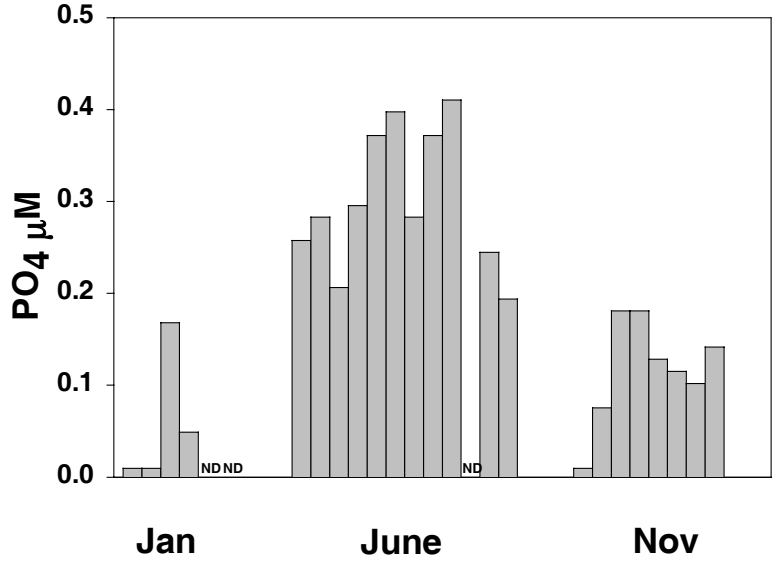


Figure 6.4a. Ambient NH_4 concentrations in individual samples from the upper mixed layer of Station 928. ND = not detectable.
Figure 6.4b. As Figure 6.4 but for PO_4.

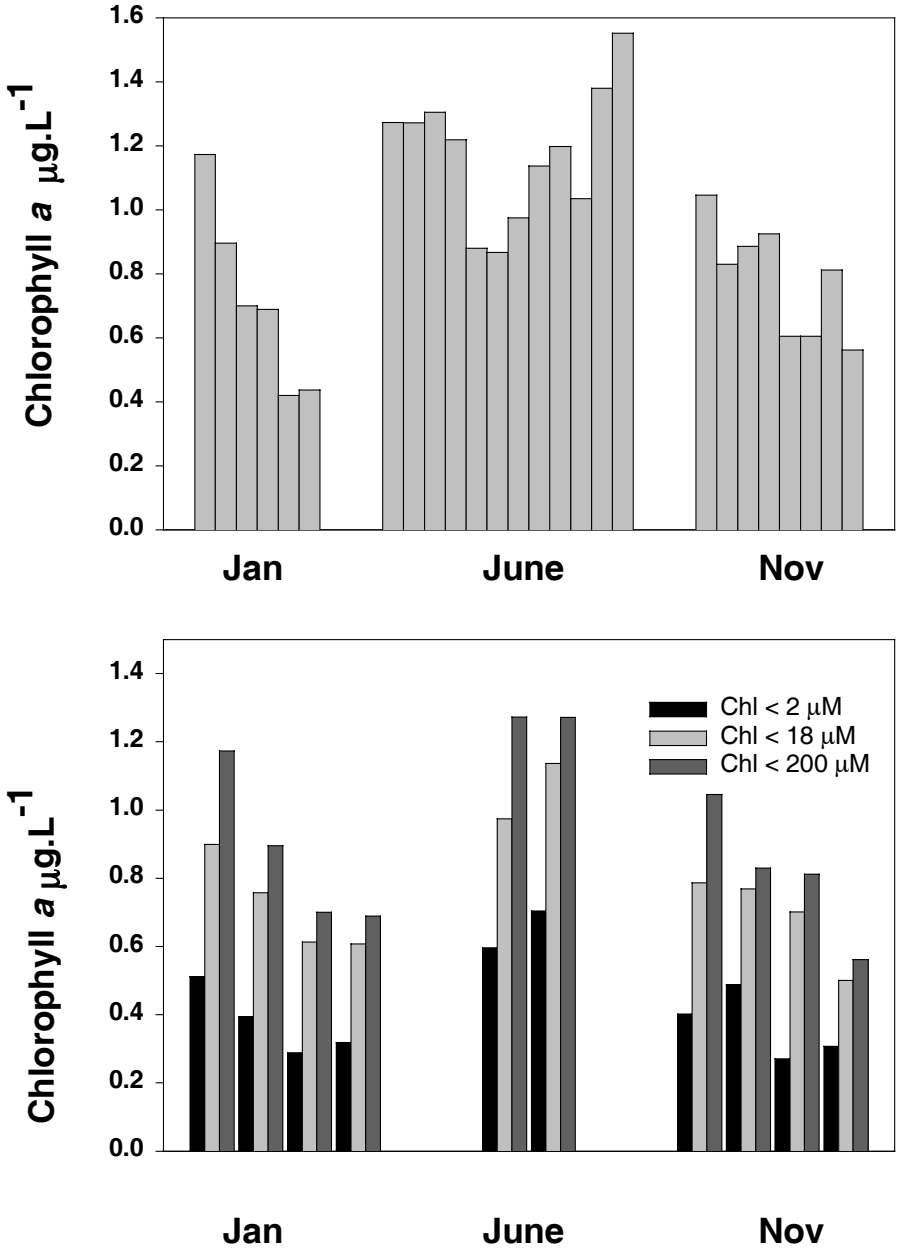


Figure 6.5a. Chlorophyll *a* concentrations in individual samples from the upper mixed layer of Station 928.
Figure 6.5b. Chlorophyll *a* concentrations for size fractioned samples from Station 928.

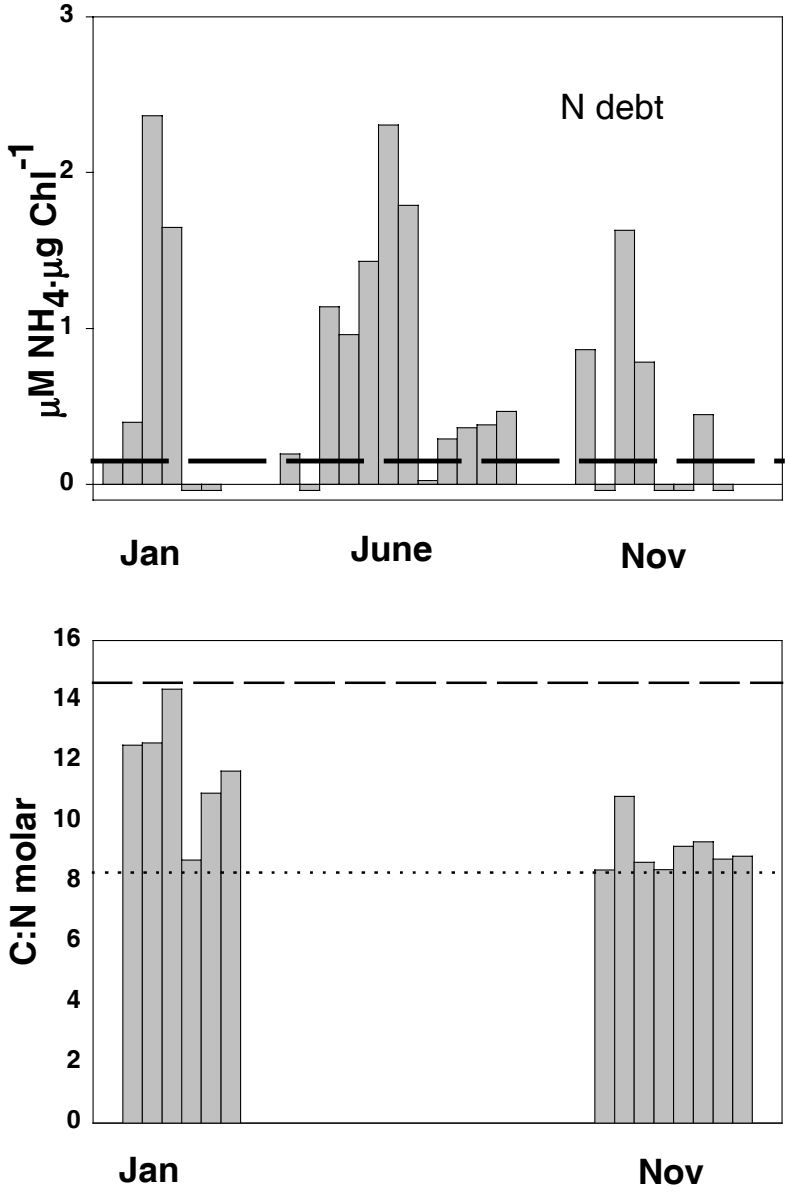


Figure 6.6a. Nitrogen debt for individual water samples from the upper mixed layer at Station 928. Values above the horizontal dashed line indicate N deficiency.
Figure 6.6b. The molar ratio of particulate carbon to particulate nitrogen (C:N) for individual water samples from the upper mixed layer of Station 928. Values above the top horizontal line indicate severe N deficiency and values between the two horizontal lines indicate moderate N deficiency.

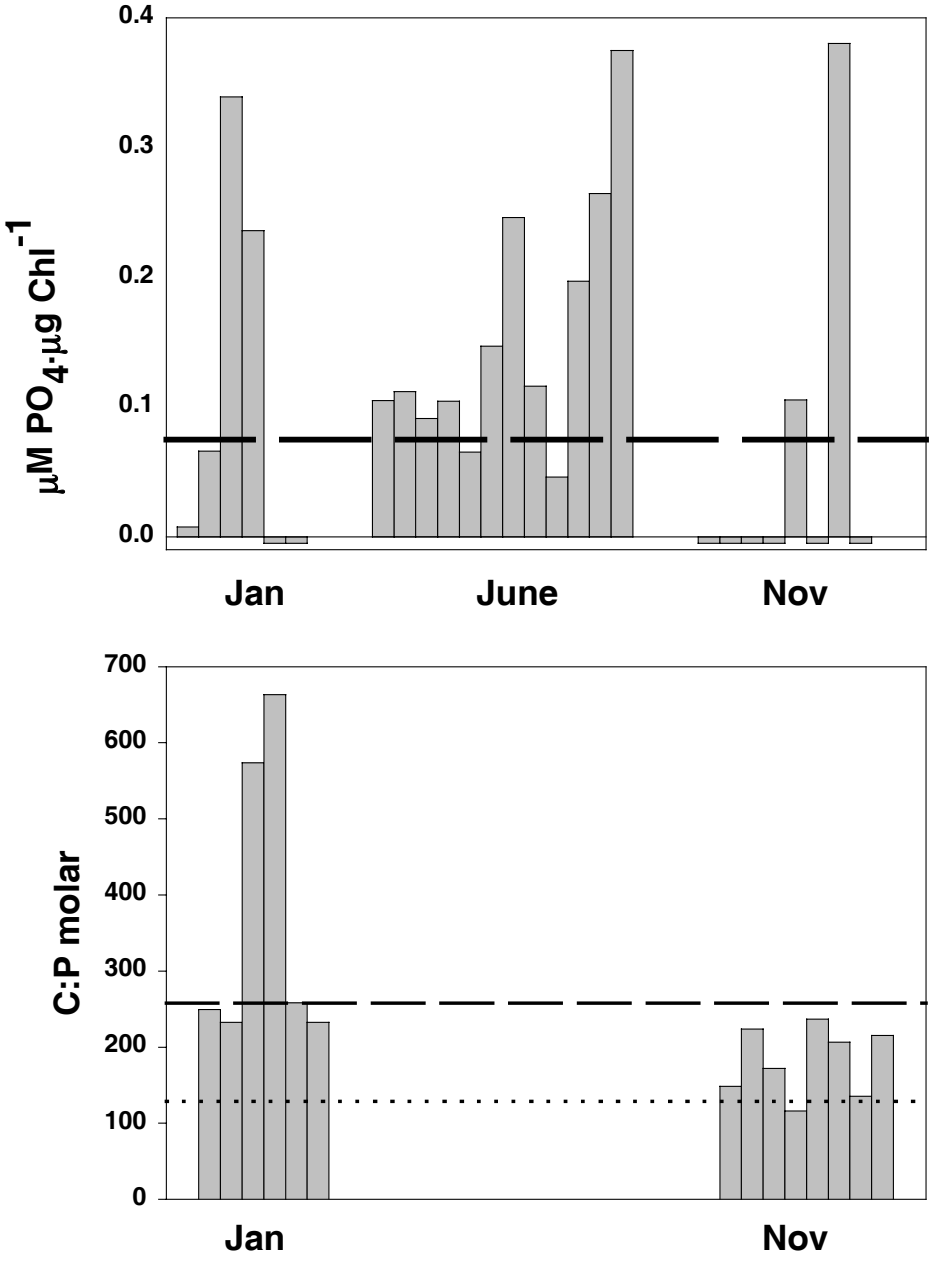


Figure 6.7a. Phosphorus debt for individual water samples from the upper mixed layer at Station 928. Values above the horizontal dashed line indicate P deficiency.
Figure 6.7b. The molar ratio of particulate carbon to particulate phosphorus (C:P) for individual water samples from the upper mixed layer of Station 928. Values above the top horizontal line indicate severe P deficiency and values between the two horizontal lines indicate moderate P deficiency.

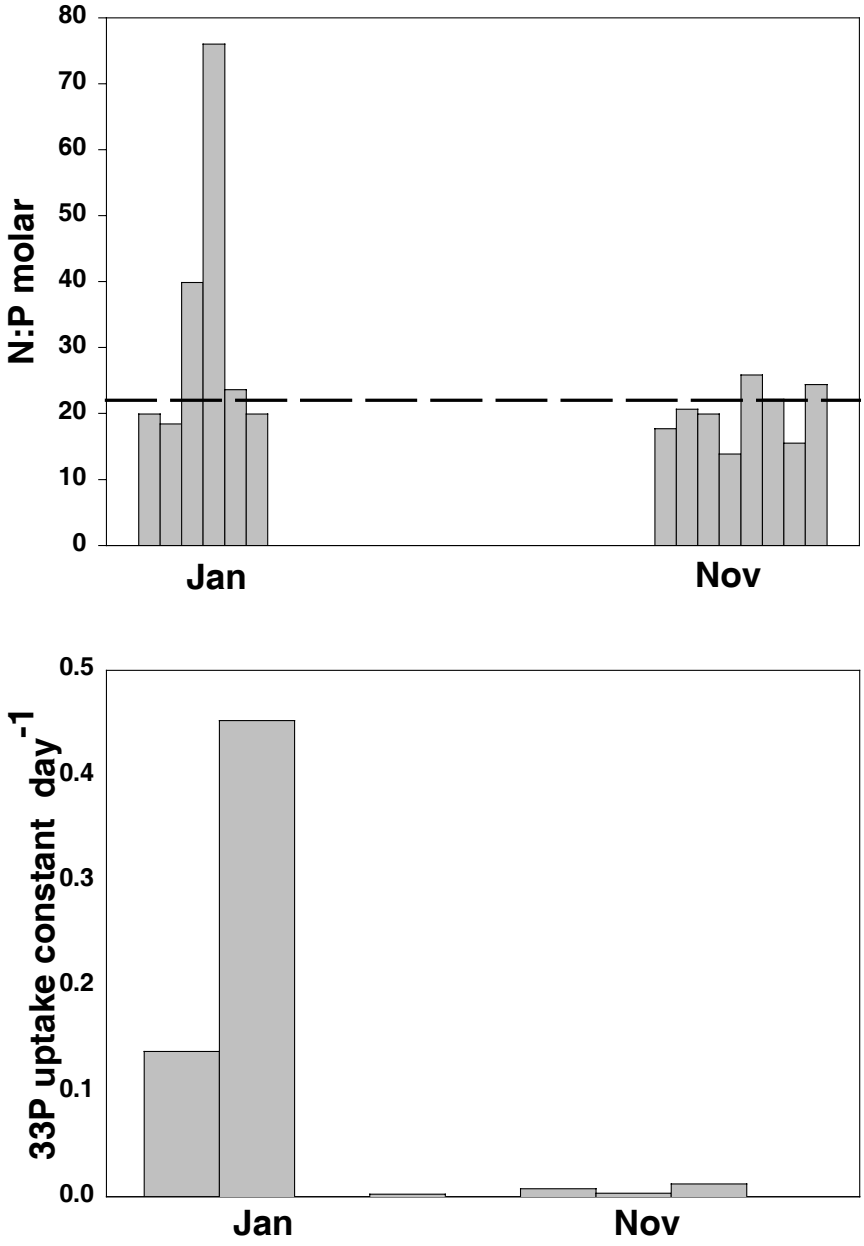


Figure 6.8a. The molar ratio of particulate nitrogen to particulate phosphorus (N:P) for individual water samples from the upper mixed layer of Station 928. Values above the horizontal line indicate P deficiency.
Figure 6.8b. ^{33}P uptake constants for individual water samples from the upper mixed layer of Station 928.

even less P demand than January. Rates of alkaline phosphatase, another indicator of phosphorus deficiency, were measured in January (not given) and November (Annex 1, this chapter). Both times the rates were low to undetectable. Particulate carbon normalized to chlorophyll *a*, used as an indicator of general nutrient deficiency (Figure 6.9) was in the range indicating nutrient deficiency but on average higher in January than November.

Photosynthesis **-** The rates of carbon uptake (Figure 6.10a), were highly variable from day to day at station 928 but on average similar in the three seasons at about 1.75 mg $C.m^{-3}.h^{-1}$. Normalized to chlorophyll *a* (Figure 6.10b) rates were less variable. α was clearly lowest in November and highest in January (Figure 6.11a). Carbon uptake normalized to chlorophyll *a* at optimum light ($Popt.C^{-1}$) was variable (Figure 6.11b).

Size fraction data from station 928 **-** Over half the total chlorophyll *a* is < 2 μm (Figure 6.5b). This is consistent at different depths and in different seasons. In the P and N debt incubations, the smaller size fractions often took up more NH_4 and PO_4 per unit of chlorophyll *a* than the whole water sample (Figure 6.12a, 6.12b). Size fractioned ^{33}P uptake experiments conducted in January at station 928 and at other stations indicated that the smaller size fractions were responsible for more than 80% of the ^{33}P uptake (Figure 6.13). C:N, C:P, N:P and C:Chlorophyll *a* ratios were sometimes different in the different size fractions (Figures 6.14a, 6.14b, 6.15a, 6.15b). Rates of ^{14}C uptake at optimum light normalized to chlorophyll *a* or to particulate carbon were always less in the small size fractions than the whole water (Figure 16a, 16b). Rates of ^{14}C uptake at low light (Figure 6.17) were in most cases higher in the < 2 μm size fraction compared to whole water rates.

Grazer removal and N and P enrichment experiments **-** In each season the addition of nutrients N and P to lake water resulted in either an increase in chlorophyll *a* relative to the controls or the maintaining of original chlorophyll *a* while the controls decreased (Figure 6.18). Removal of grazers > 50 μm had no effect on chlorophyll concentration over time in January but had a positive effect in June and a negative effect in November. In each season, the incubation of water for 48 hours, without the addition of nutrients N and P resulted in an increase in P and/or N deficiency as indicated by P and N debt (Figure 6.19, 6.20). In January, ^{33}P uptake constants increased from 0.5 per day to 262 per day after 48 hours without the addition of N and P (Figure 6.21). In November, the initial ^{33}P turnover time was very low, 0.005 per day, but again an increase was observed, this time to 0.25 per day (Figure 6.22). Particulate composition ratios usually did not increase in the controls but they often decreased in the enriched samples (Figure 6.22, 6.23, 6.24, 6.25). Rates of photosynthesis normalized to chlorophyll *a* did not appear to be stimulated by the addition of nutrients in January or June (Figure 6.26) but were in the November incubations (Figure 6.26). Rates of photosynthesis at low light appeared to decrease over the course of the experiments, regardless of nutrient or grazer manipulation (Figure 6.27).

Transect from the Linthipe River mouth to offshore Station 928 **-** Chlorophyll *a* concentrations were higher at the mouth of the Linthipe River than at the offshore stations in January, the rainy season, and in November, the end of the dry season (Figure 6.28a). In November there was a gradual decrease in chlorophyll *a* concentration with distance form the river mouth. There was no gradient observed in the ambient NH_4 concentration (Figure 6.28b), but ambient PO_4 was higher near the river month in January and November (Figure 6.29a) There were no patterns with distance from the river mouth with respect to N and P debt (Figure 6.29b, 6.30a) . The N and P debt data showed seasonality. ^{33}P uptake constants were measured along the plume in January and in November and in each transect there was no pattern with distance form the river mouth (Figure 6.30b). ^{33}P uptake constants were much higher in January ranging from 0.30 to 0.36 per day in January especially compared to November (0.002 to 0.018 per day) (Figure 6.30b). Particulate ratios C:P and N:P tended to increase with distance from the river mouth in January and November (Figure 6.31a, 6.31b), but C:N did not (Figure 6.32a). There was no pattern with ^{14}C uptake in January and June, however in November, ^{14}C uptake normalized to chlorophyll and to particulate C was clearly higher at the river mouth than the offshore stations (Figure 6.32b).

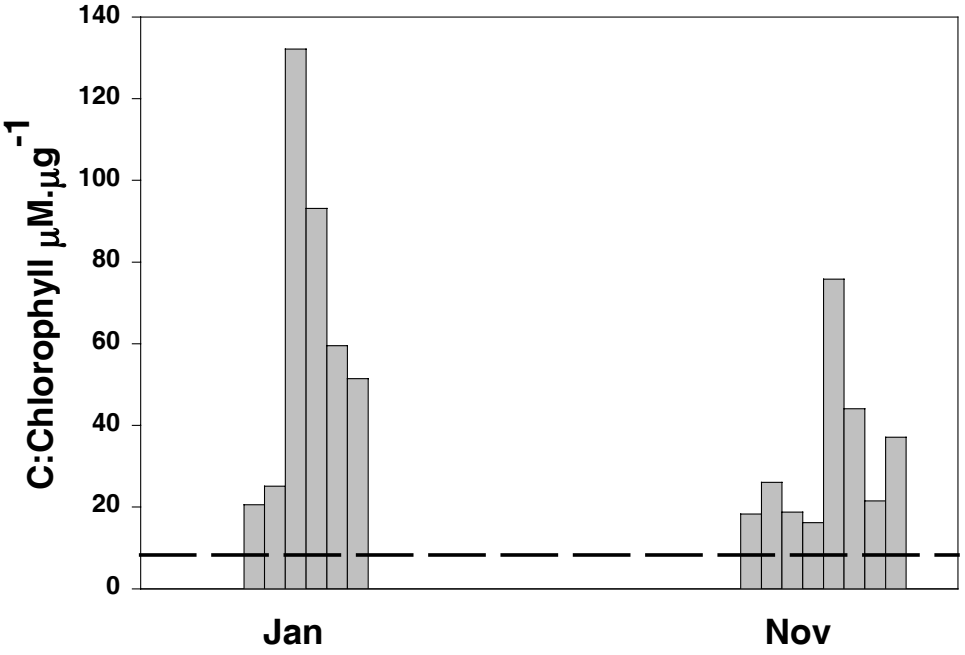


Figure 6.9. The ratio of particulate carbon to chlorophyll *a* for individual water samples from the upper mixed layer of Station 928. Values above the horizontal line are indicative of general nutrient deficiency.

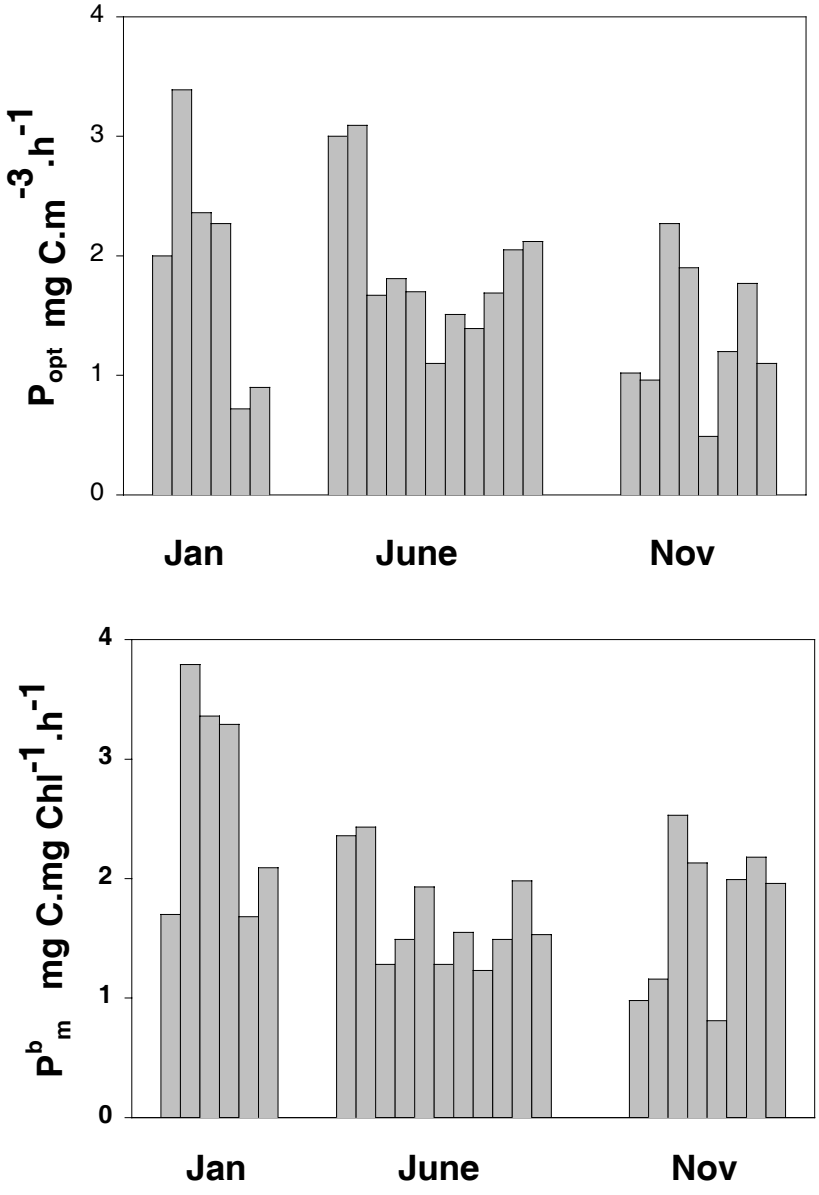


Figure 6.10a. The maximum rate of carbon uptake from photosynthesis-irradiance curves (P_{opt}). Bars represent individual water samples from the upper mixed layer at Station 928.
Figure 6.10b. The same as Figure 6.10a except rates are normalized to chlorophyll *a*.

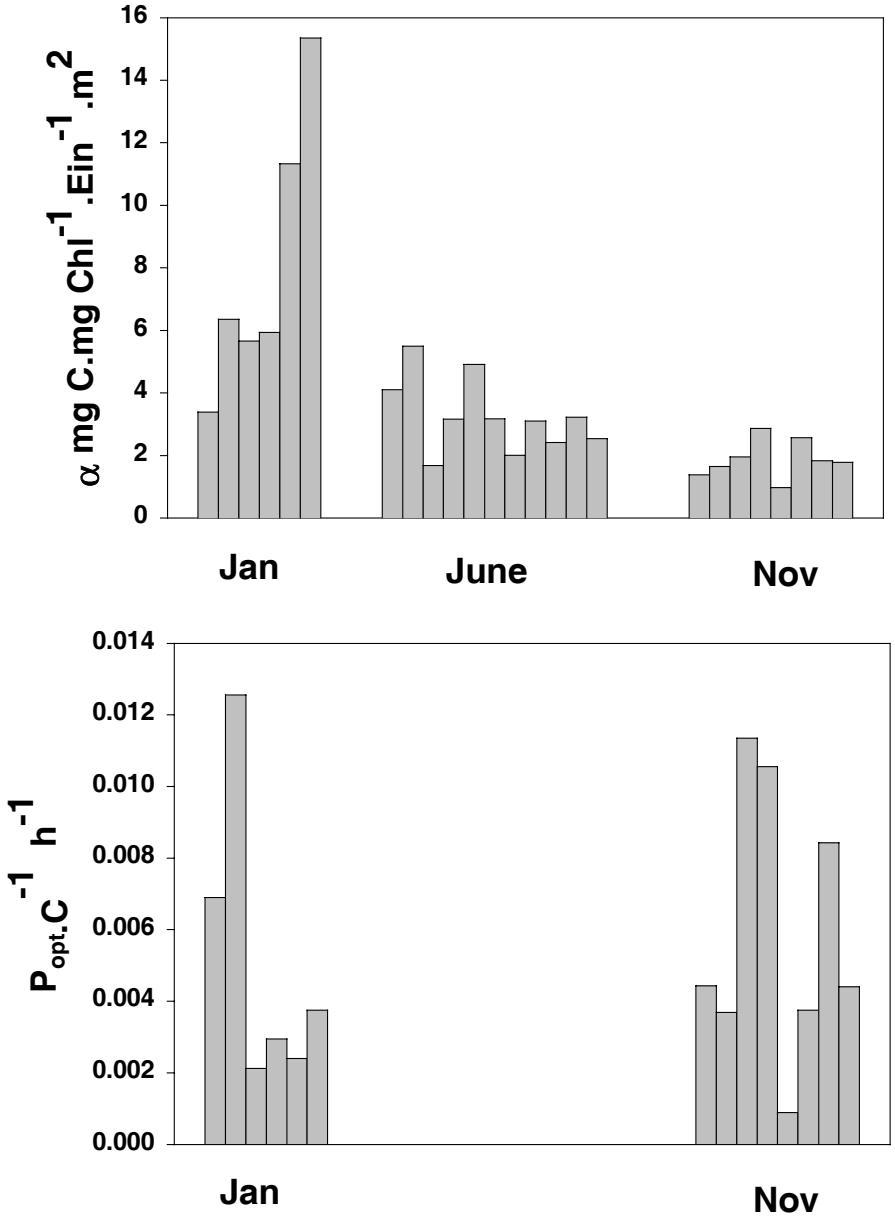


Figure 6.11a. The slope of carbon uptake at the lowest irradiances (α) from the photosynthesis-irradiance curve. Bars represent individual water samples from the upper mixed layer at Station 928.
Figure 6.11b. Carbon uptake at optimum irradiance normalized to particulate carbon ($P_{opt}.C^{-1}$). Bars represent individual water samples from the upper mixed layer at Station 928.

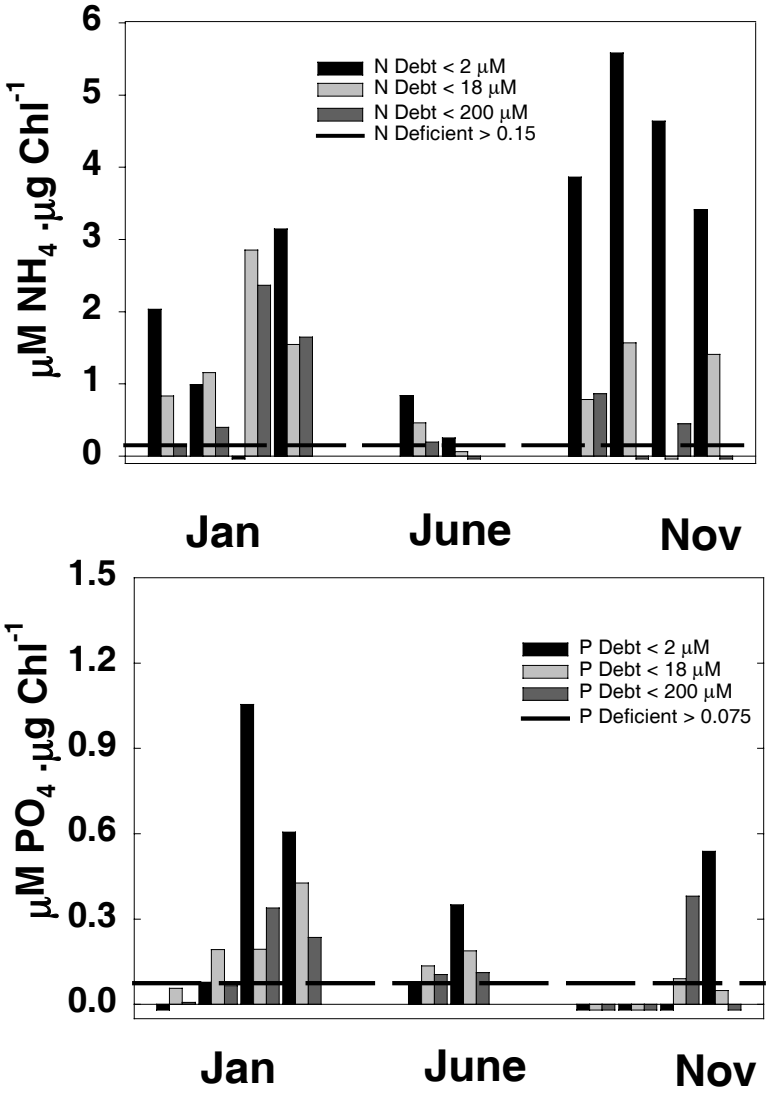


Figure **12a**. Nitrogen debt for size fractioned water samples from the upper mixed layer of Station 928. Values above the horizontal line indicate N deficiency.
Figure **12b**. Phosphorus debt for size fractioned water samples from the upper mixed layer of Station 928. Values above the horizontal line indicate P deficiency.

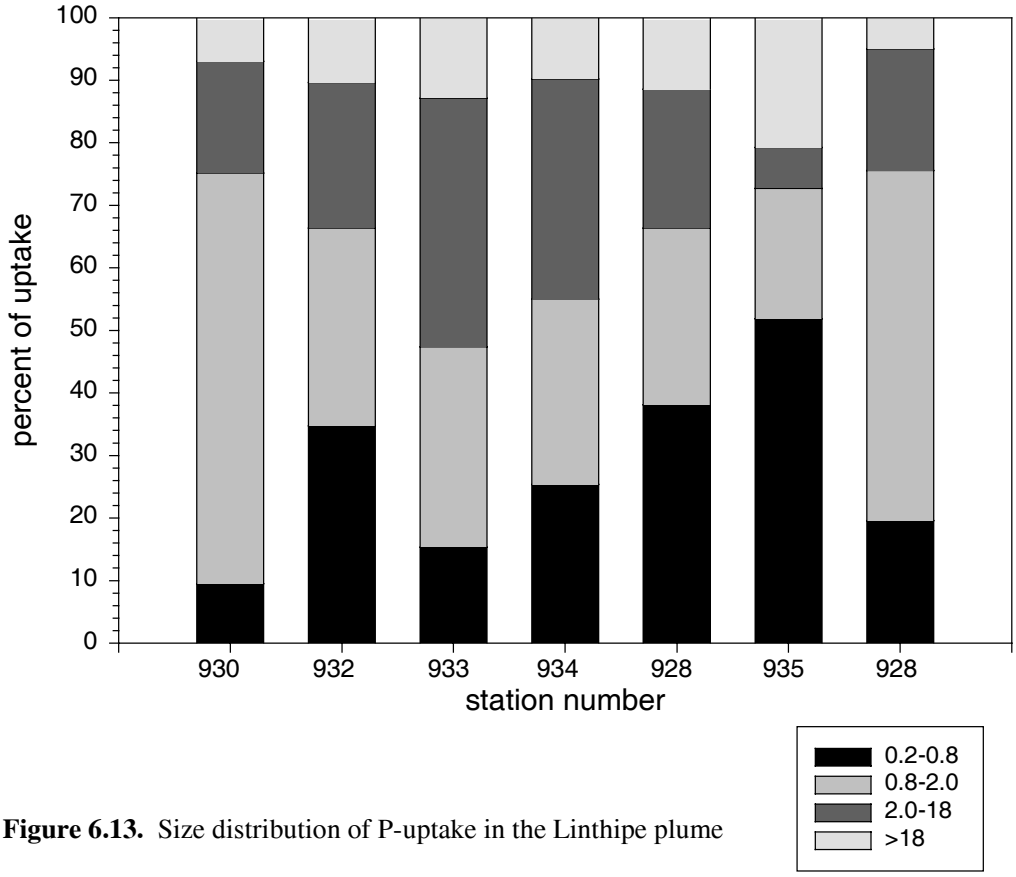


Figure 6.13. Size distribution of P-uptake in the Linthipe plume

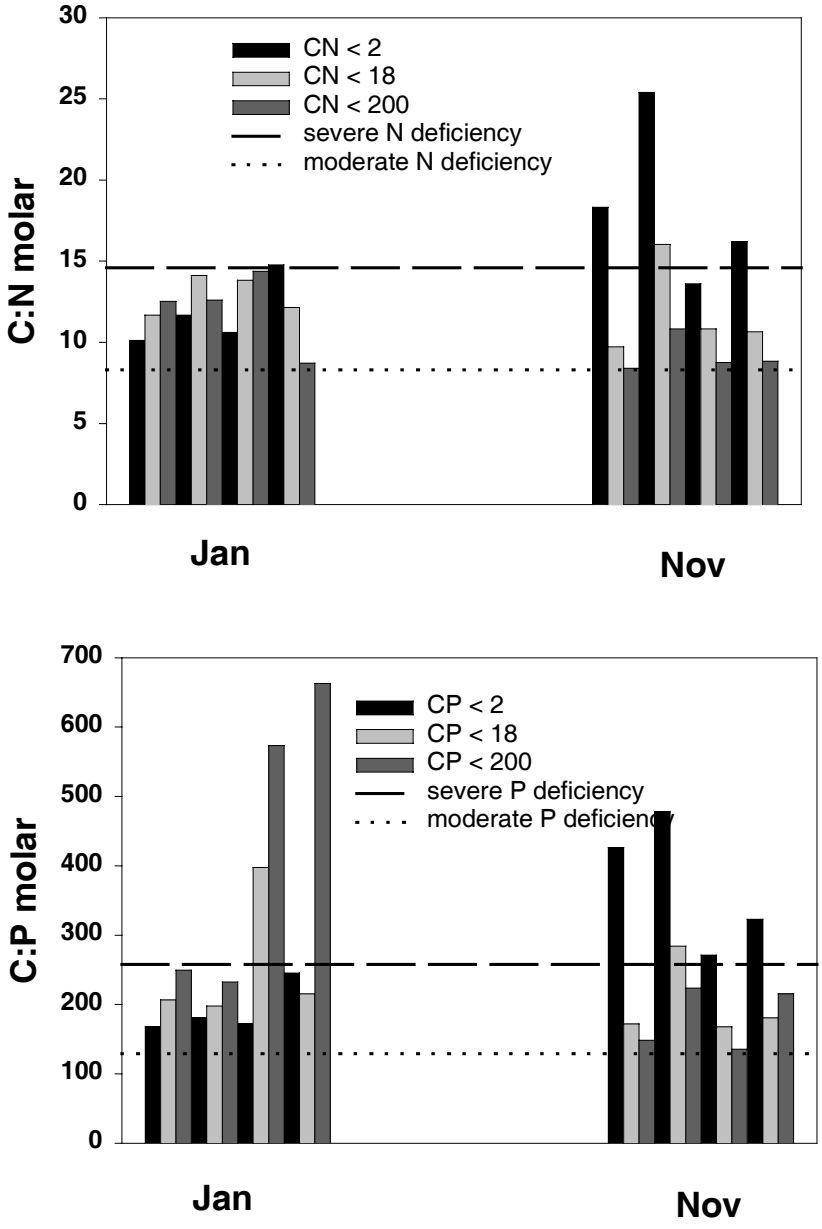


Figure 6.14a. The molar ratio of particulate carbon to particulate nitrogen (C:N) for size fractioned water samples from the upper mixed layer of Station 928. Values above the top horizontal line indicate severe N deficiency and values between the two horizontal lines indicate moderate N deficiency.
Figure 6.14b. As above but for particulate carbon to particulate phosphorus(C:P). Horizontal lines indicate P deficiency.

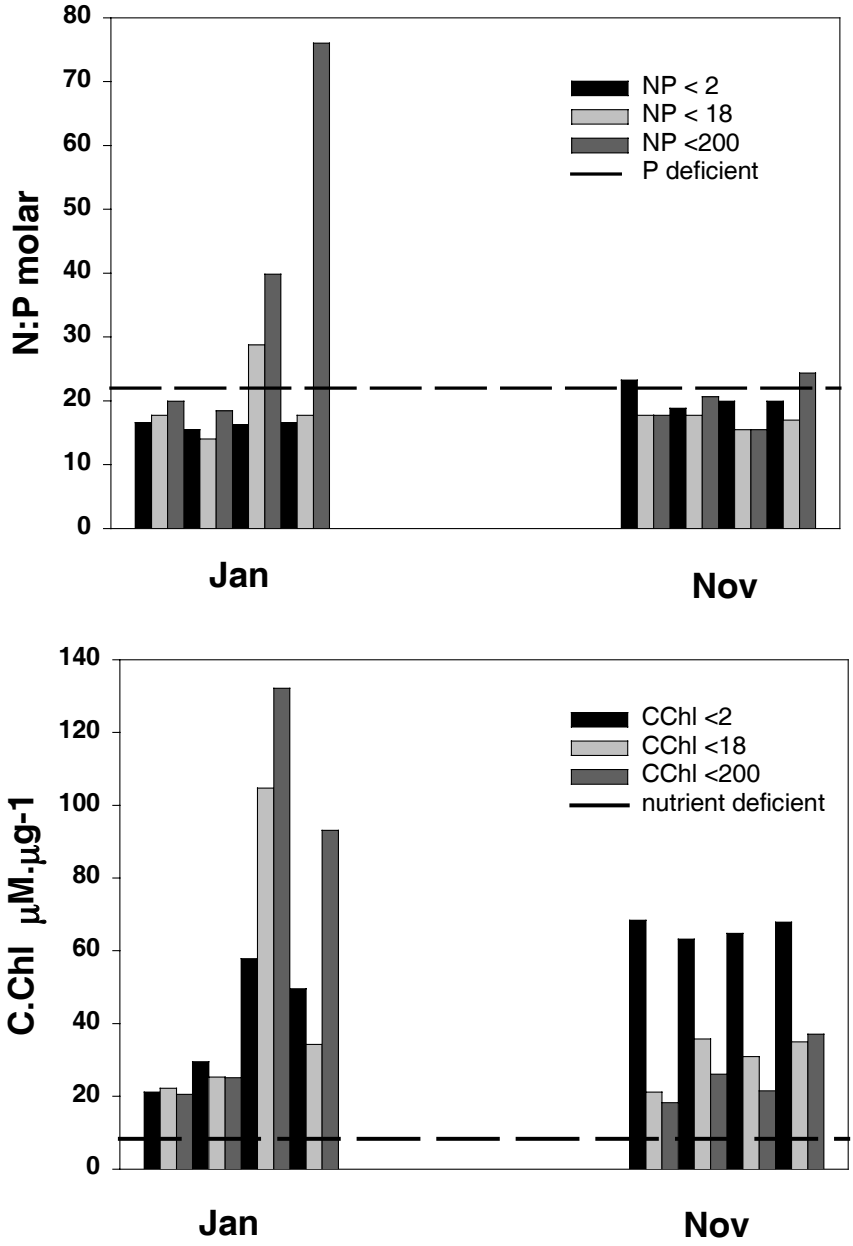


Figure 6.15a. The molar ratio of particulate nitrogen to particulate phosphorus (N:P) for size fractioned water samples from the upper mixed layer of Station 928. Values above the horizontal dashed line indicate P deficiency.
Figure 6.15b. The ratio of particulate carbon to particulate chlorophyll *a* (C:Chl) for size fractioned water samples from Station 928. Values above the horizontal dashed line indicate general nutrient deficiency.

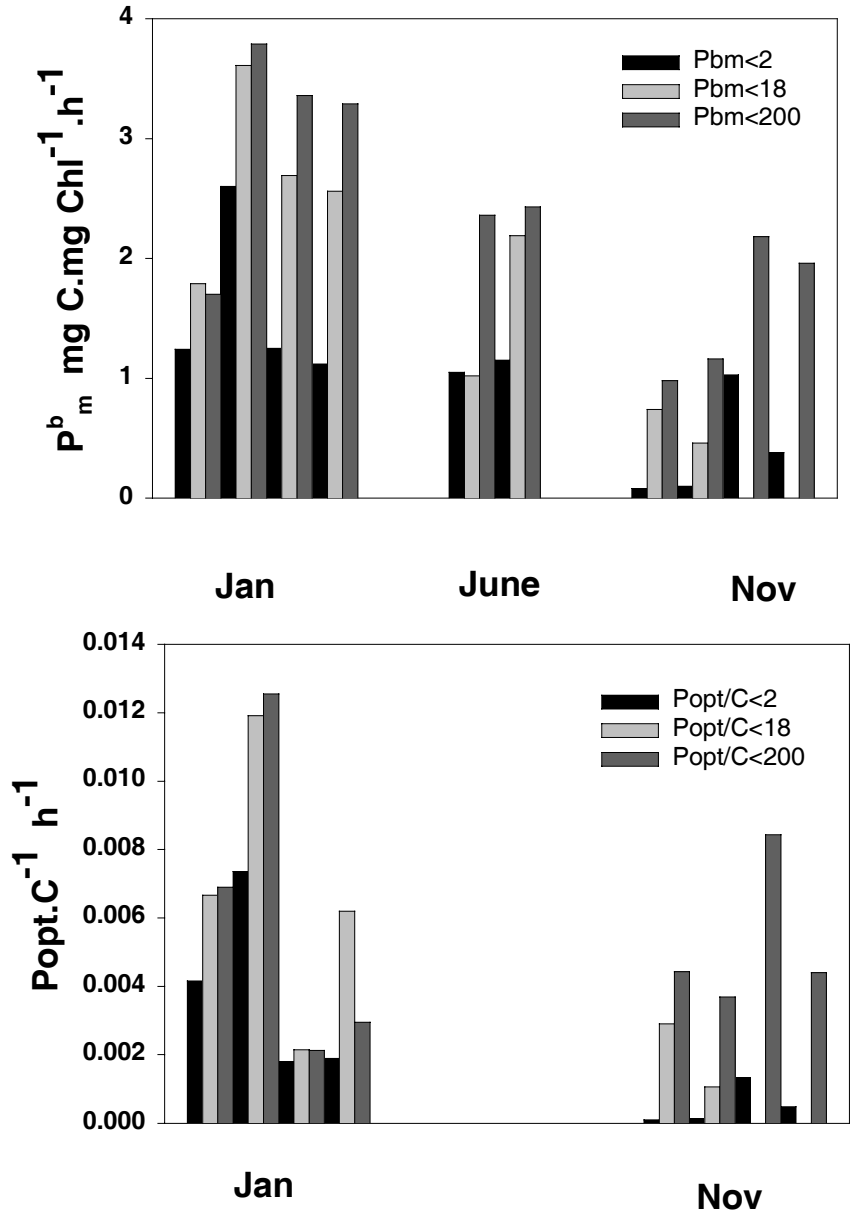


Figure 6.16a. The maximum rate of carbon uptake from photosynthesis-irradiance curves normalized to chlorophyll *a* (P^b_m). Bars represent size fractioned water samples from the upper mixed layer ar Station 928.
Figure 6.16b. The same as Figure 6.16a except that rates are normalized to particulate carbon.

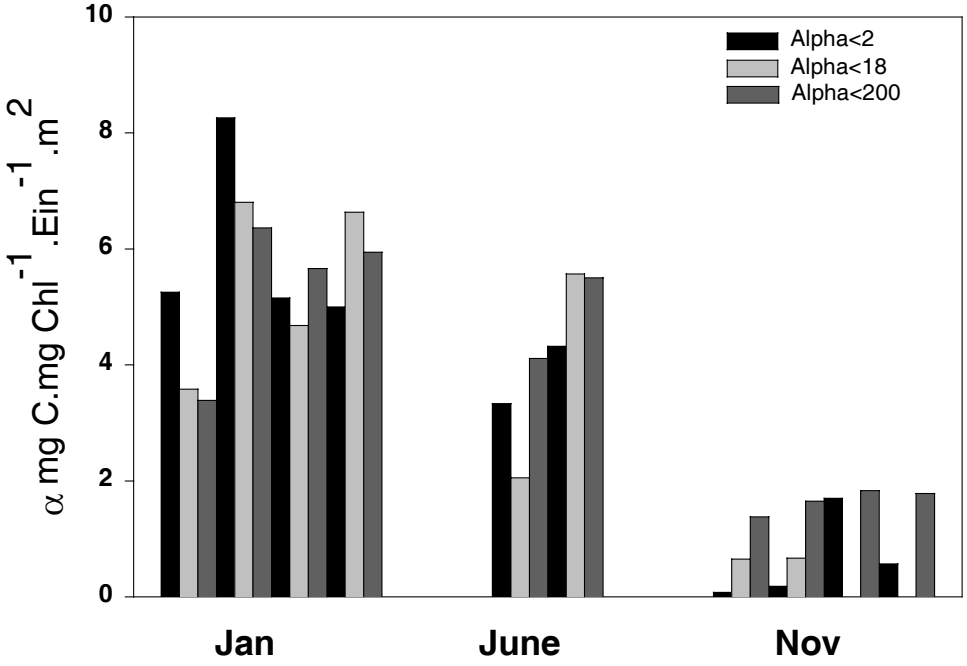


Figure 6.17. The slope of carbon uptake at the lowest irradiances (α) from the photosynthesis-irradiance curve normalized to chlorophyll *a*. Bars represent size fractioned water samples from the upper mixed layer at Station 928.

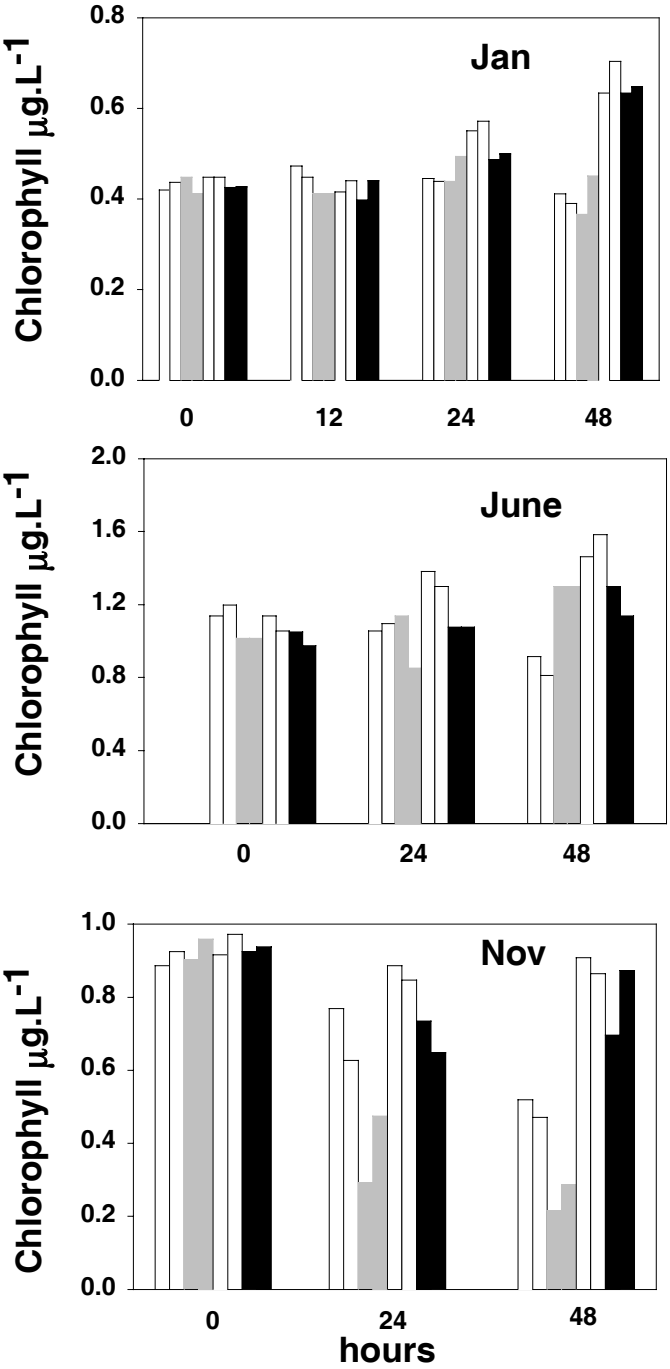


Figure 6.18. Chlorophyll *a* concentrations over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 μm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 μm removed.

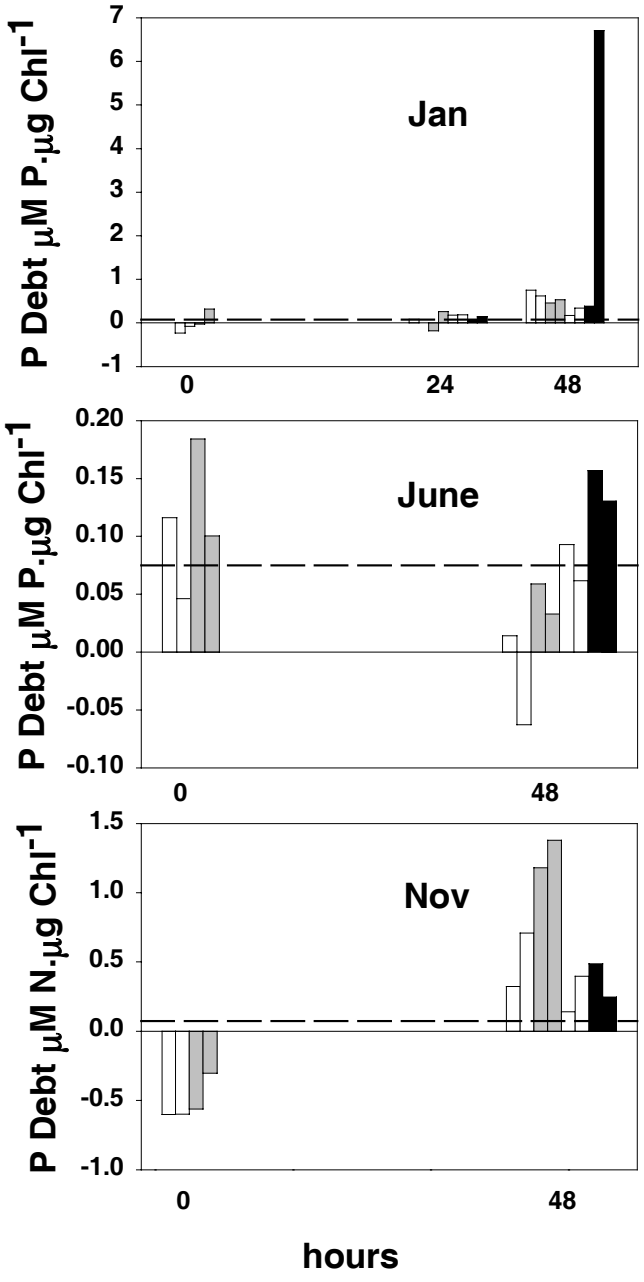


Figure 6.19. Phosphorus debt over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 µm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 µm removed. Values above the horizontal dashed line indicate P deficiency. Note the different scales.

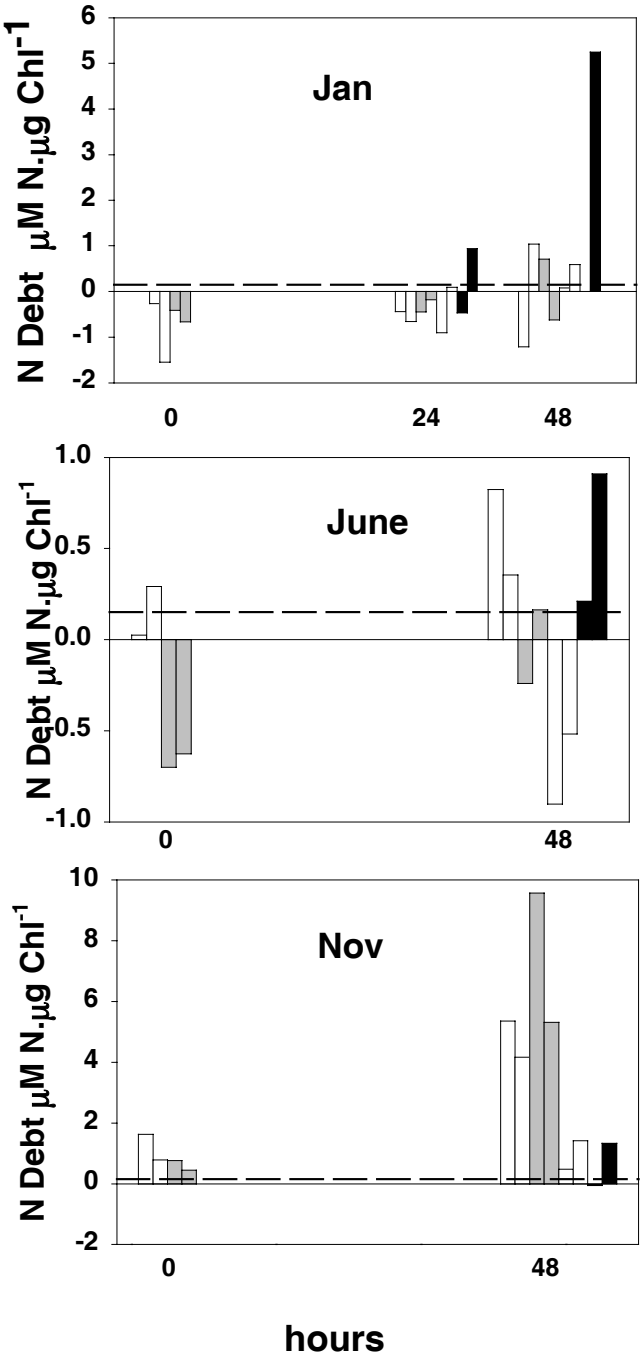


Figure 6.20. Nitrogen debt over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 µm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 µm removed. Values above the horizontal dashed line indicate N deficiency. Note the different scales.

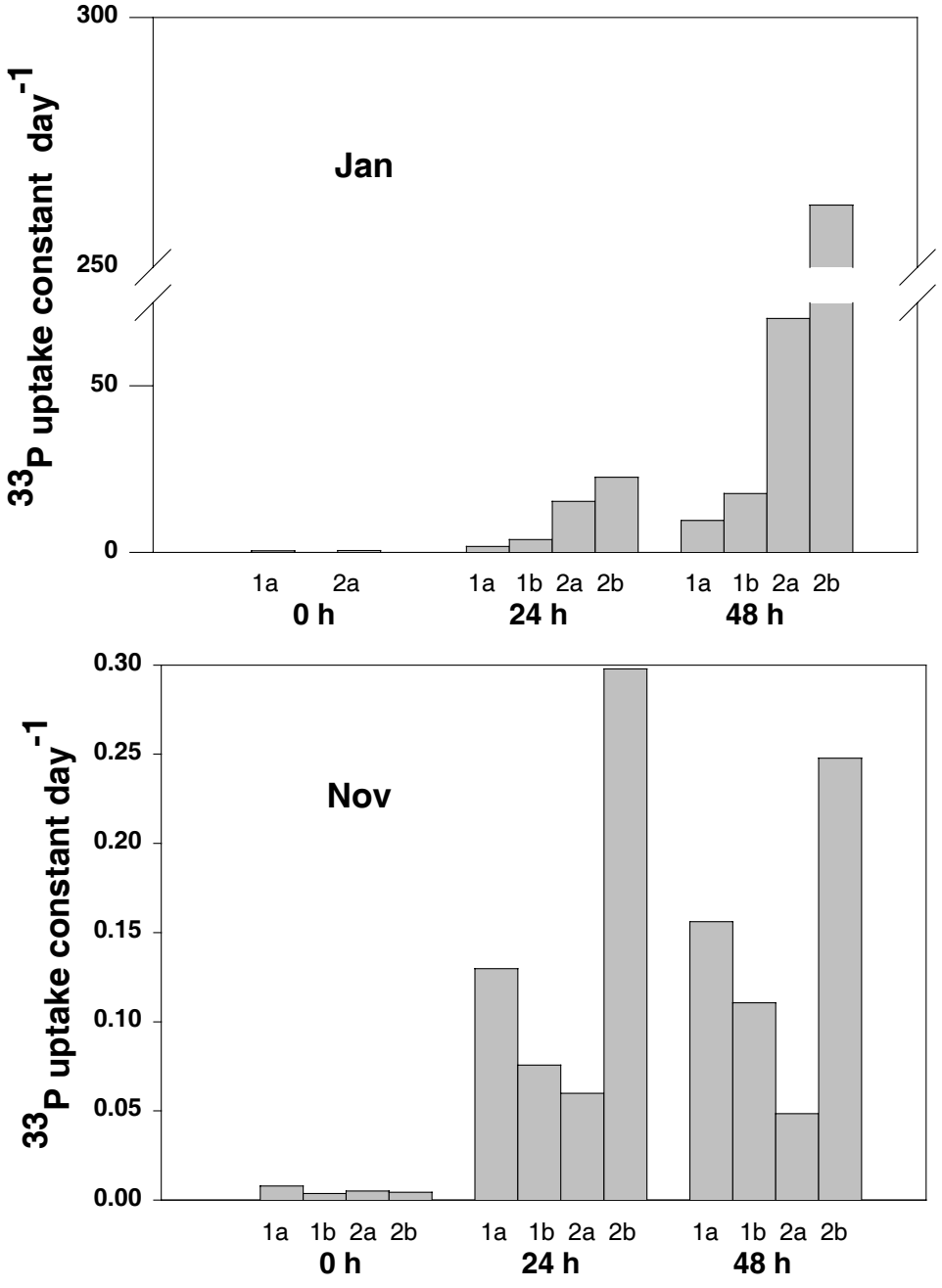


Figure 6.21. ^{33}P uptake constants over the course of the grazer removal, nutrient enrichment experiments. 1a and 1b are controls, 2a and 2b are containers with grazers > 50µm removed.

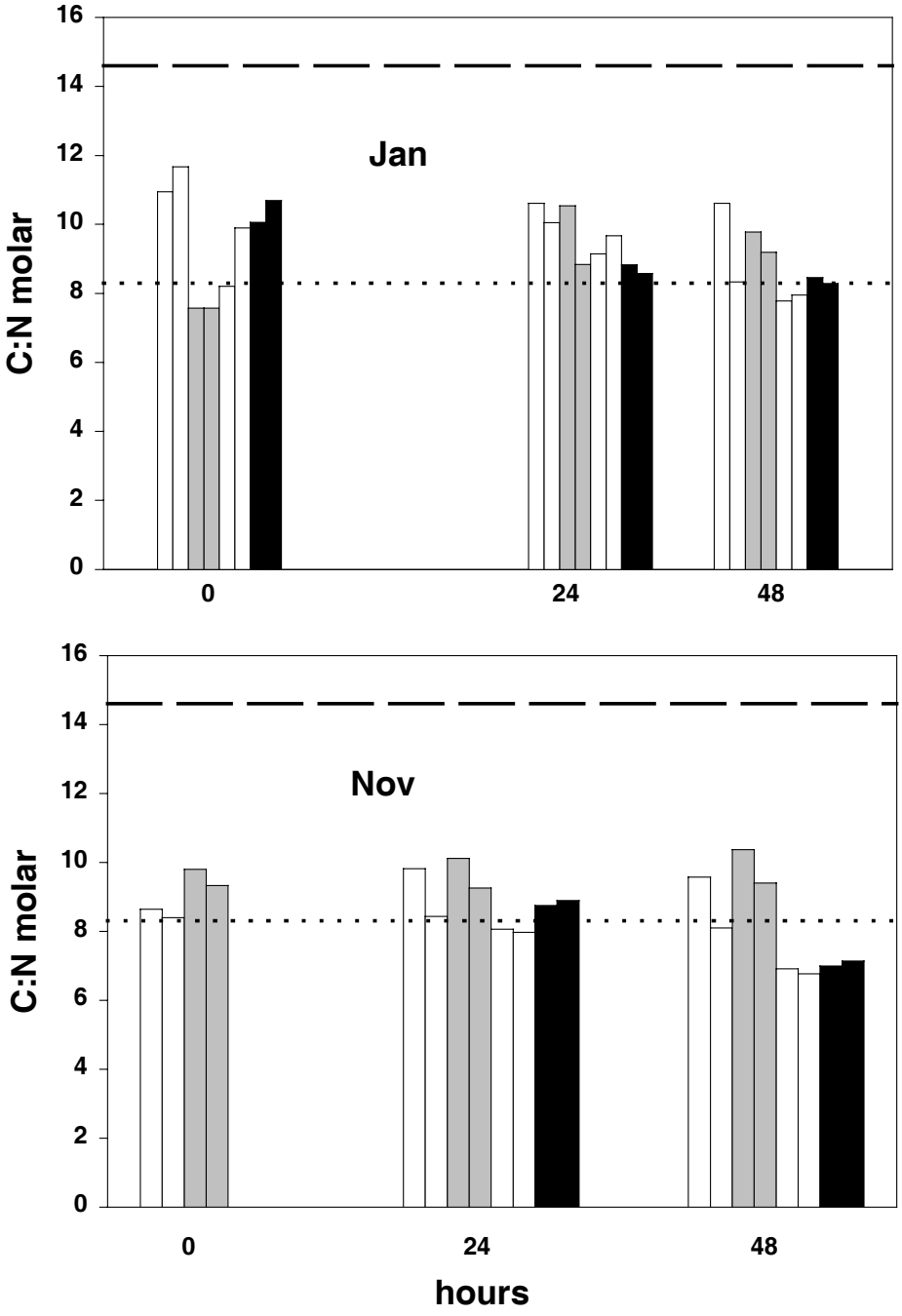


Figure 6.22. C:N ratio over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 μm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 μm removed. Values above the horizontal dashed line indicate severe N deficiency. Values between the horizontal lines, moderate.

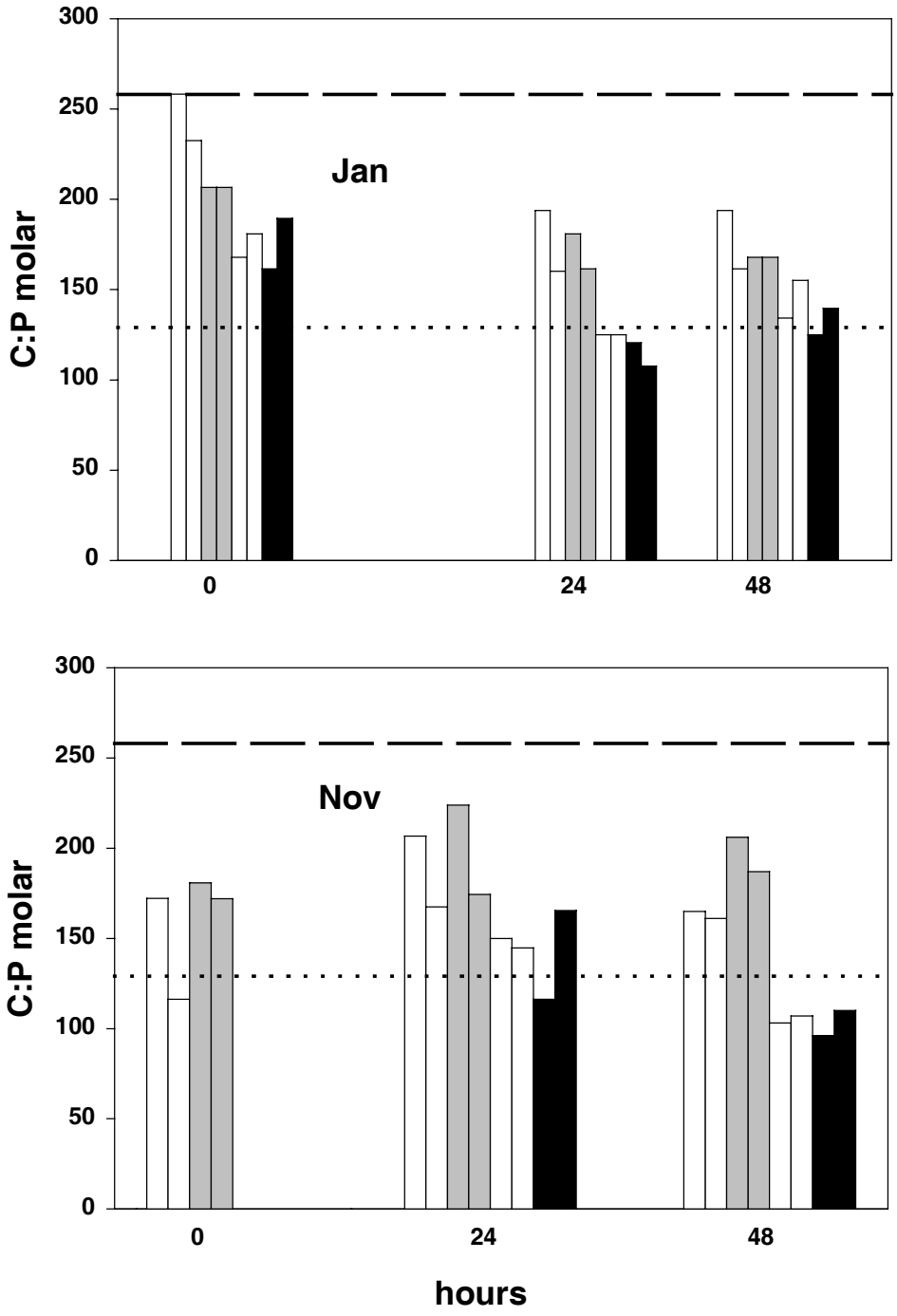


Figure 6.23. C:P ratio over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 μm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 μm removed. Values above the horizontal dashed line indicate severe P deficiency. Values between the horizontal lines, moderate.

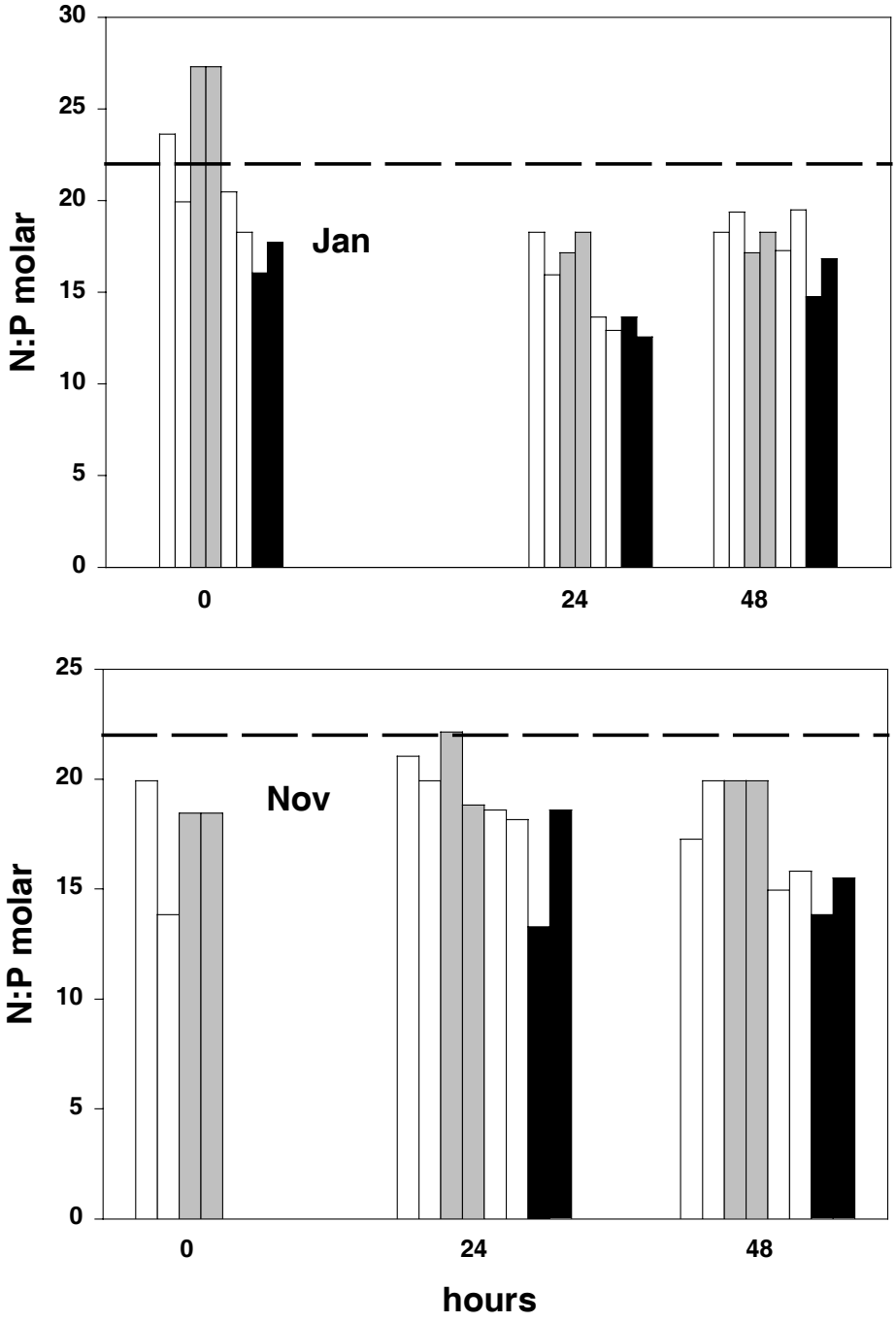


Figure 6.24. N:P ratio over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 μm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 μm removed. Values above the horizontal dashed line indicate P deficiency.

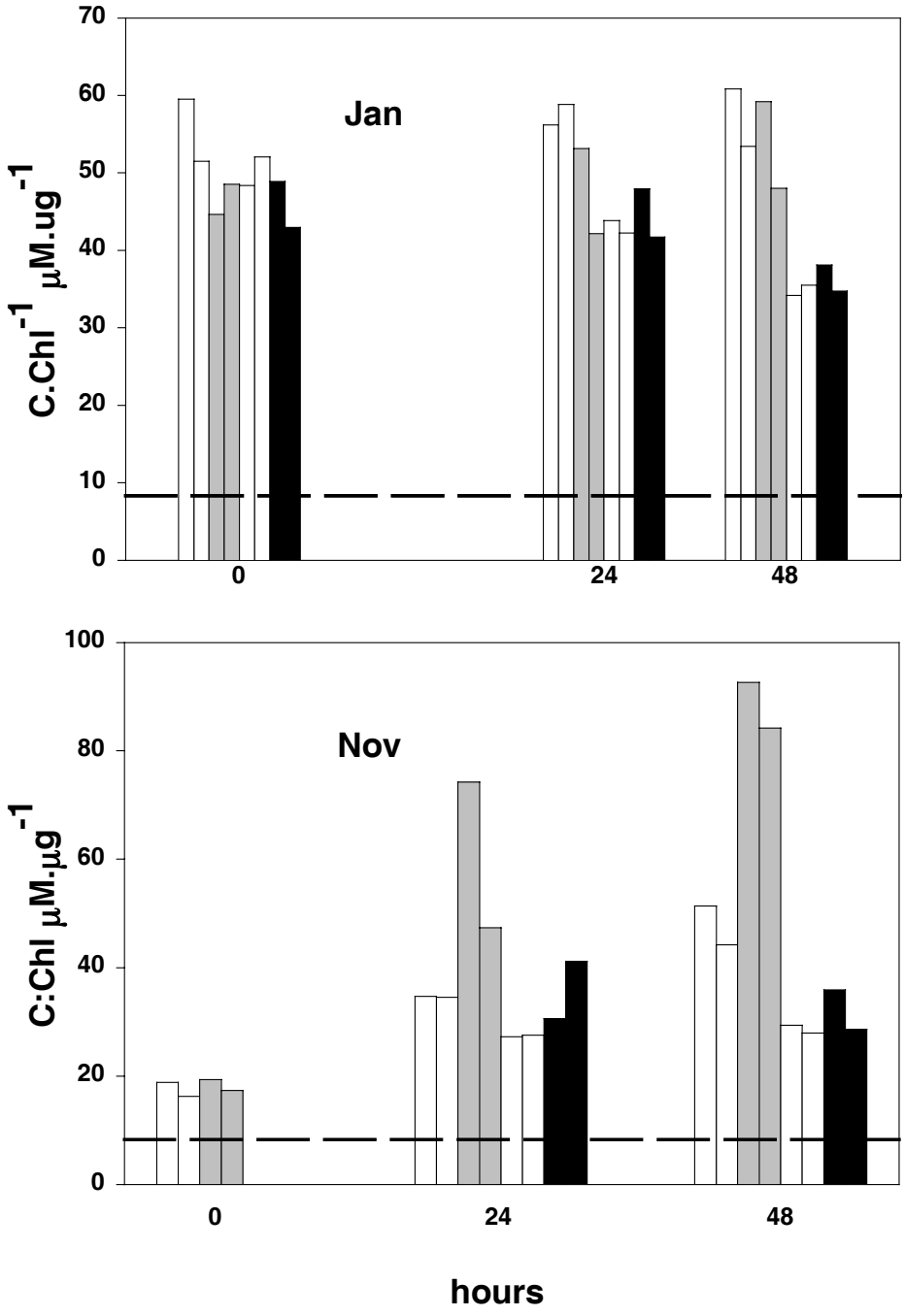


Figure 6.25. Particulate carbon: chlorophyll *a* ratio over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 µm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 µm removed. Values above the horizontal dashed line indicate nutrient deficiency.

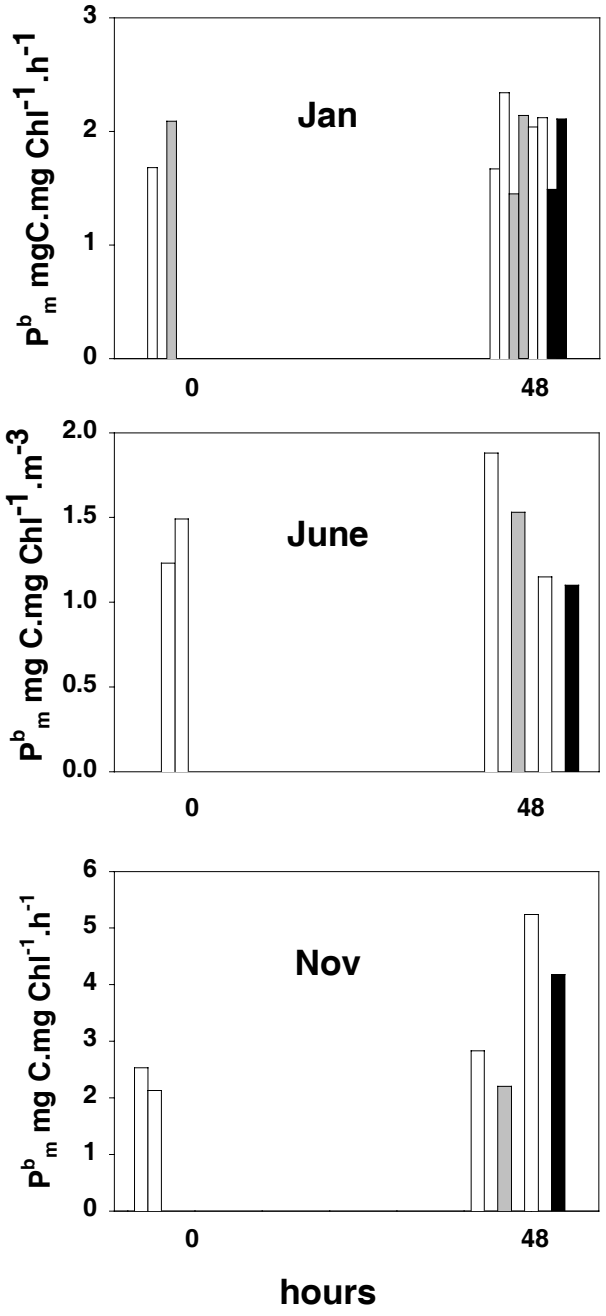


Figure 6.26. P^b_m over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 μm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 μm removed.

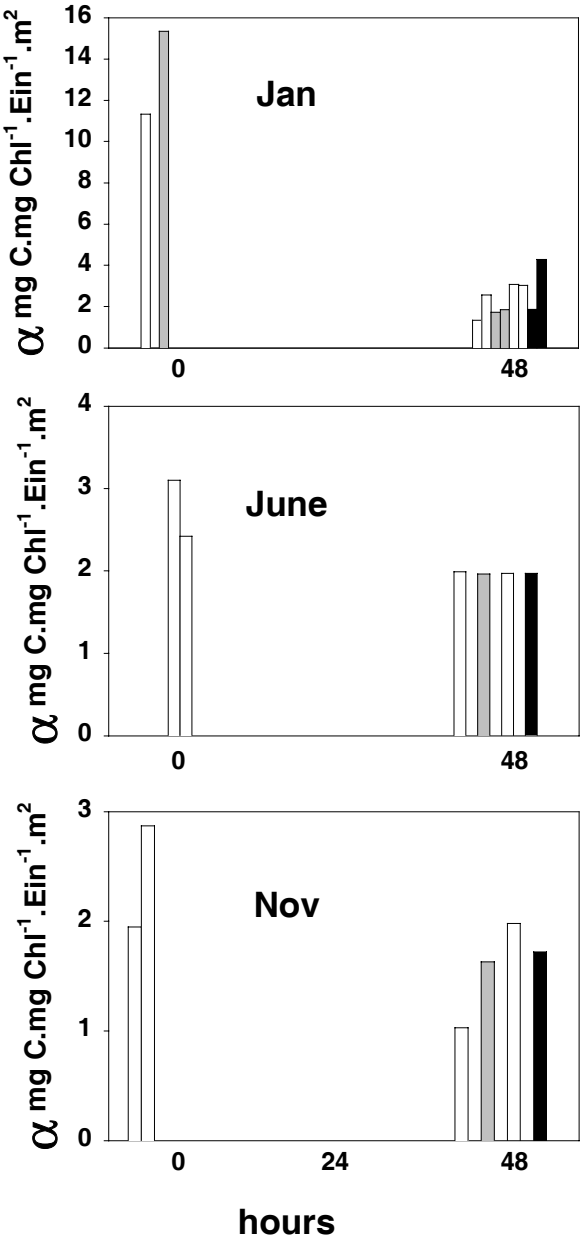


Figure 6.27. α over the course of the grazer removal, nutrient enrichment experiments. The white bars on the left represent controls, the grey bars represent containers with grazers > 50 μm removed and no nutrients added, the white bars on the right represent containers ammended with N and P, the black bars represent containers ammended with N and P and grazers > 50 μm removed.

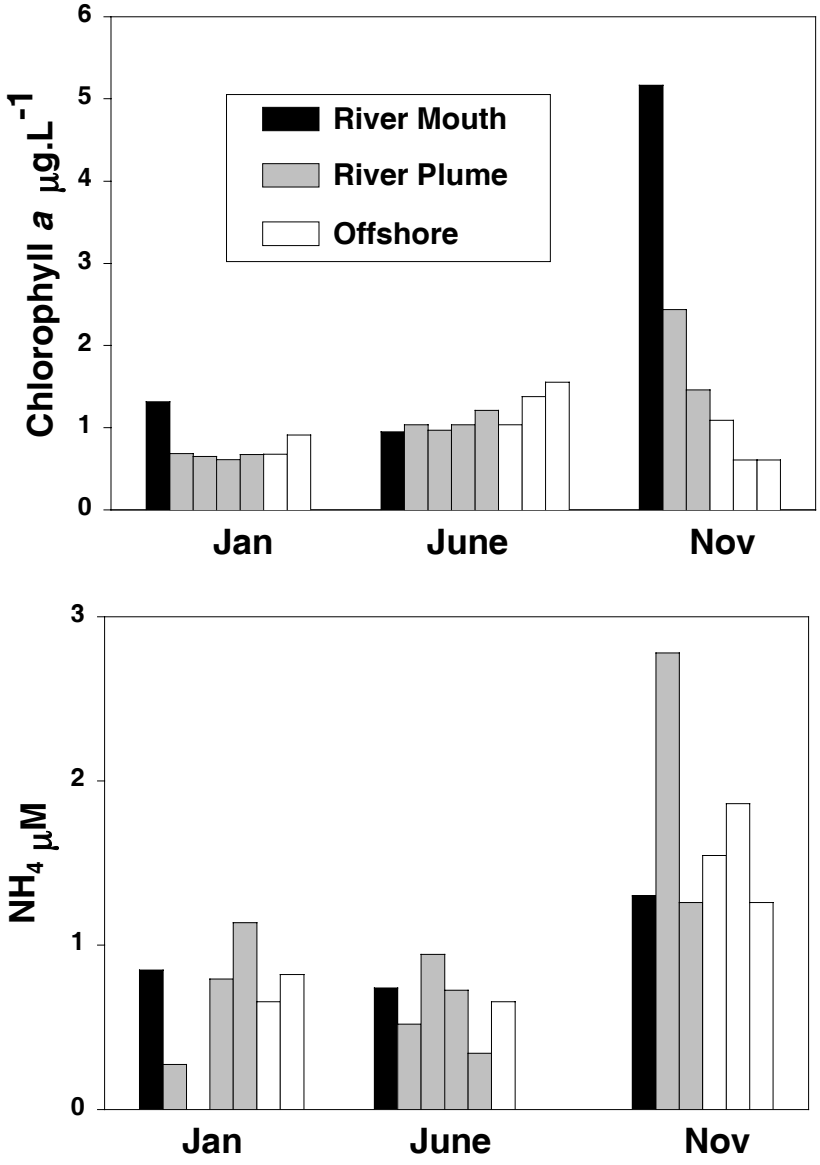


Figure 6.28a. Chlorophyll *a* concentrations in individual samples from the upper mixed layer at stations along the transect from the mouth of the Linthipe River to Station 928.
Figure 6.28b. As Figure 6.28a but for NH_4.

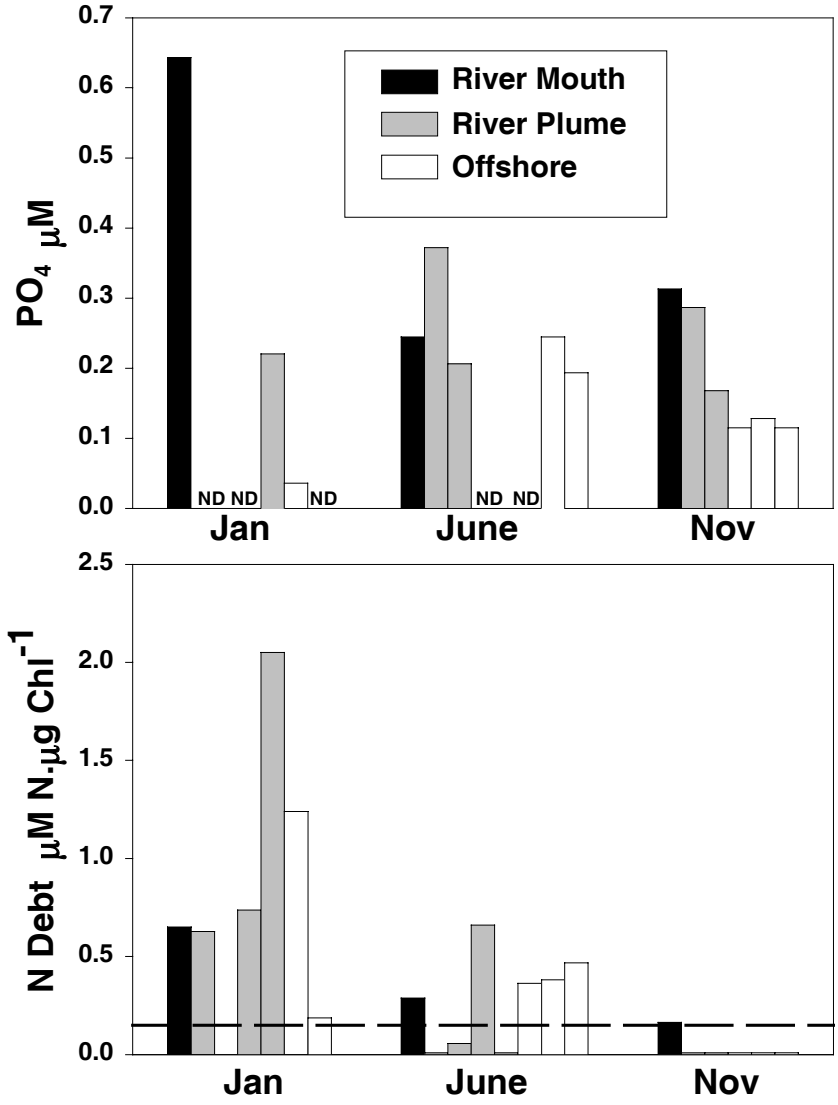


Figure 6.29a. Ambient PO_4 concentrations in individual samples from the upper mixed layer at stations along the transect from the mouth of the Linthipe River to Station 928. ND means not detectable.
Figure 6.29b. As Figure 6.29a but for N debt. Values above the horizontal line indicate N deficiency.

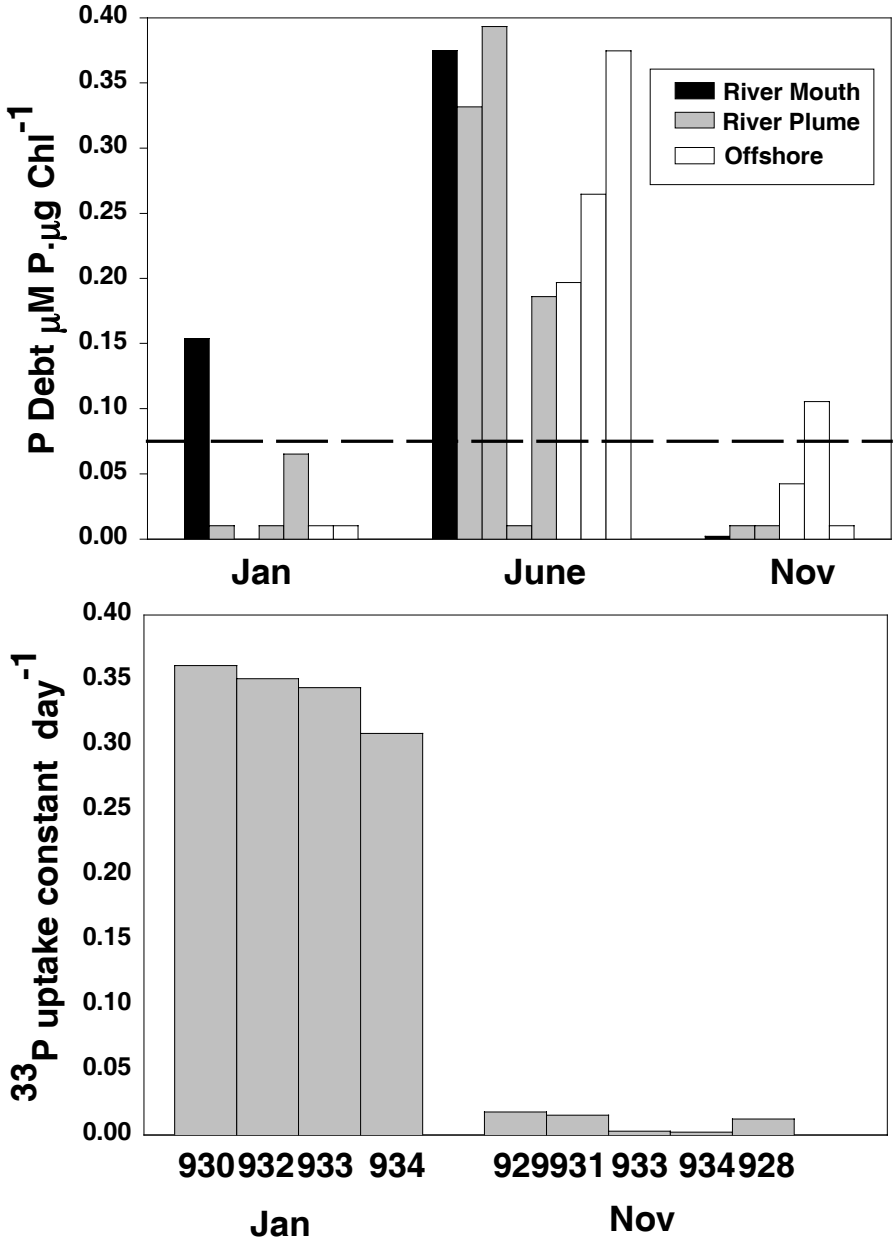


Figure 6.30a. P debt in individual samples from the upper mixed layer at stations along the transect from the mouth of the Linthipe River to Station 928. Values above the horizontal line indicate P deficiency.
Figure 6.30b. As for Figure 30a but for ^{33}P uptake constants. Station numbers are given below each bar.

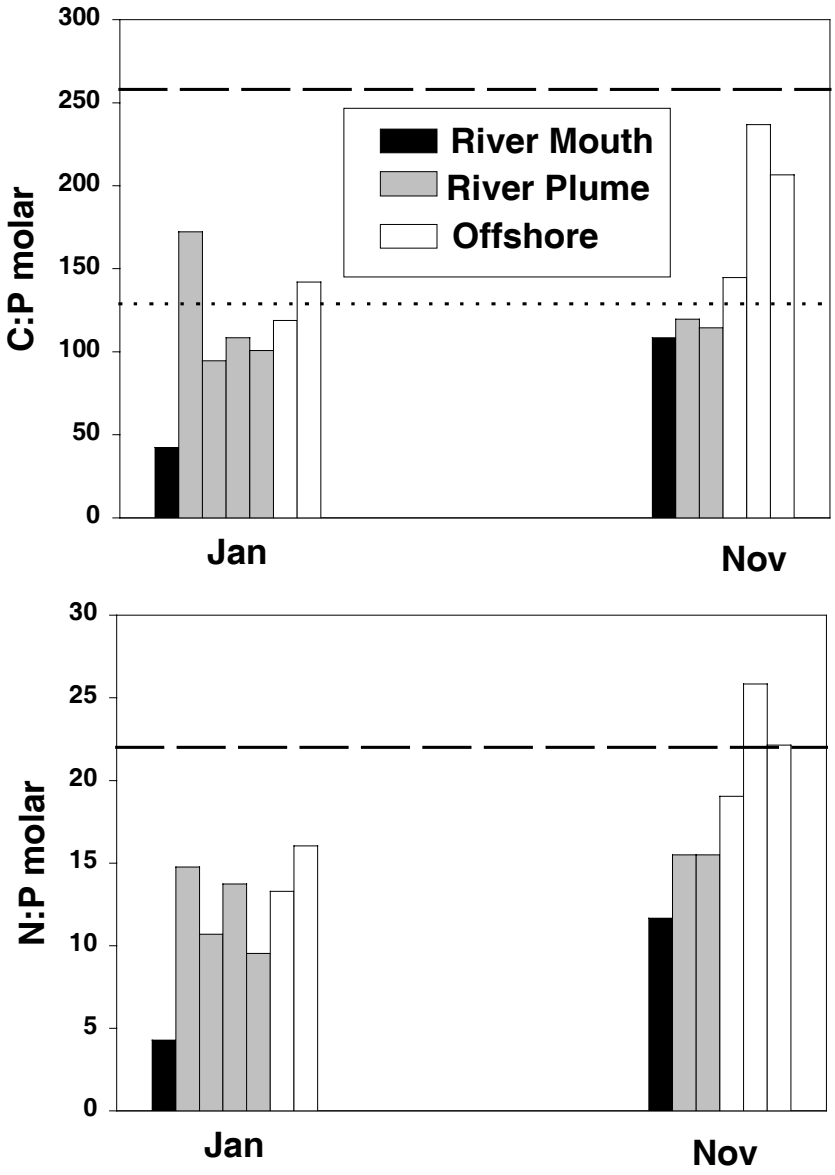


Figure 6.31a. The molar ratio of particulate carbon to phosphorus (C:P) in individual samples from the upper mixed layer at stations along the transect from the mouth of the Linthipe River to Station 928. Values above the top horizontal line indicates severe P deficiency and values between the two horizontal lines indicate moderate P deficiency.
Figure 6.31b. As Figure 6.31a but for particulate N:P. Values above the horizontal line indicate P deficiency.

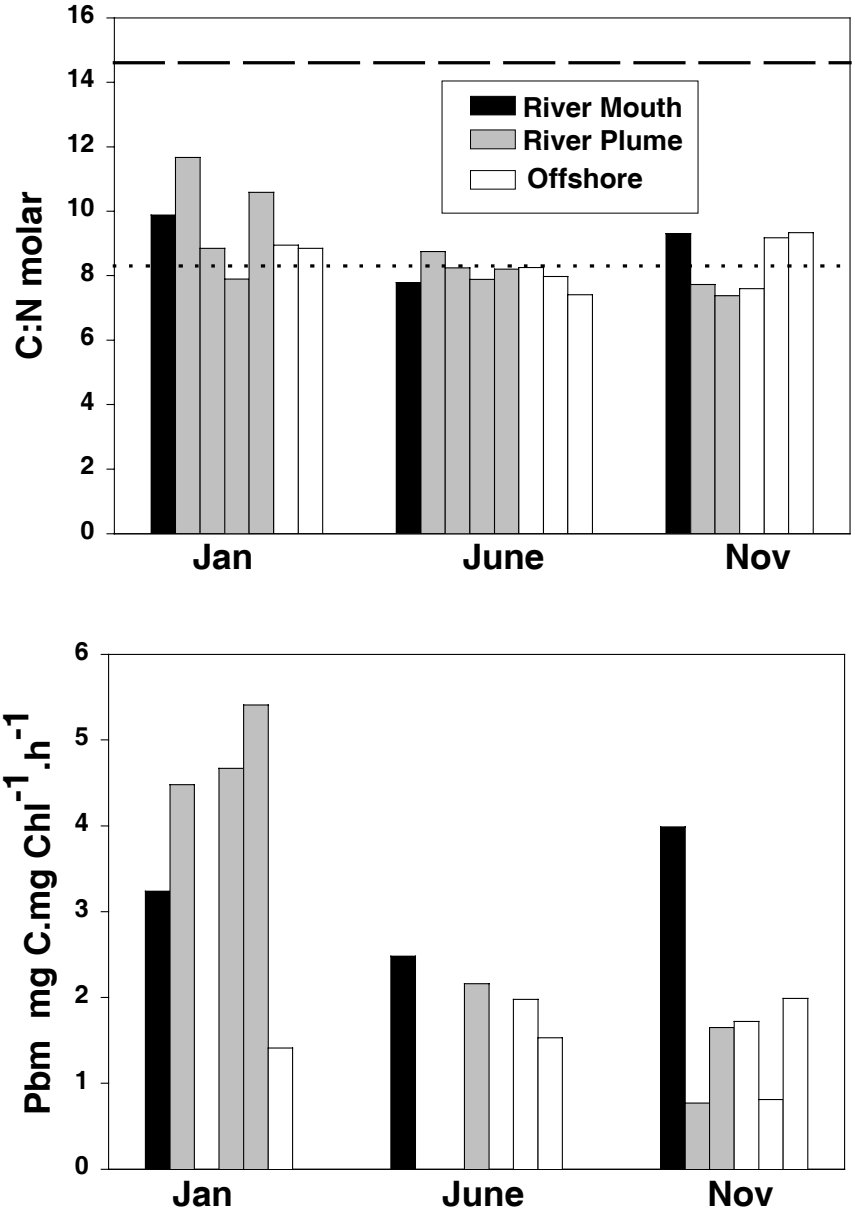


Figure 6.32a. The molar ratio of particulate carbon to nitrogen (C:N) in individual samples from the upper mixed layer at stations along the transect from the mouth of the Linthipe River to Station 928. Values above the top horizontal line indicates severe N deficiency and values between the two horizontal lines indicate moderate N deficiency.
Figure 6.32b. As Figure 32a but for carbon uptake at optimum irradiance normalized to chlorophyll *a*.

Discussion

Is Station 928 representative of the lake? **-** We conclude from the comparison of particulate C:N, C:P and N:P ratios from the upper mixed layer around the lake, that algal nutrient status measurements at Station 928 are representative of the upper mixed layer of the lake spatially and temporally. We also conclude that based on these data that although there is considerable day to day variability, the upper mixed layer is remarkably uniform in time and space in terms of biomass and nutrient content of the particulate matter.

Are pelagic algae in Lake Malawi N or P limited? - Despite low chlorophyll *a* concentration, Lake Malawi phytoplankton is only moderately and intermittently nutrient deficient. Our regular monitoring of phytoplankton nutrient status at Station 928 indicated that either, or both, N and P may be potentially growth limiting. Although indications of N and P deficiency were frequently observed, there was never a long sustained period of deficiency of a specific nutrient during the times we sampled. This is quite different from the data collected in North American Great Lakes, where phosphorus is consistently and strongly deficient in the stratified summer months (Guildford et al. 1996 and 1998). We concluded from the size fractionation experiments that one reason that algae rarely appear strongly nutrient deficient is that grazers in the 2 to 200 μm size range (and often in the 2 to 18 μm size range) supply the nutrients N and P through grazing and regeneration. We concluded this because of the strong degree of nutrient deficiency that developed in flasks after 12 hours, once grazers had been removed by filtration. In whole water samples, grazers maintain a low, but continuous supply of nutrients and simultaneously limit biomass by grazing. This grazing pressure selects algae that can grow rapidly at low nutrient concentrations without becoming nutrient deficient.

Are other factors important in controlling algal growth in Lake Malawi? **-** Lack of strong N or P deficiency implies a lack of a strong demand for N and P. This lack of strong, consistent demand could occur for several reasons. Firstly, the in situ algal community may be adapted to the nutrient conditions of the lake. That is, the community may be dominated by species with optimum growth rates and N and P uptake rates achieved at the low nutrient concentrations naturally occurring in Lake Malawi. We observed responses to N and P enrichment only after a lag time of 2 days, indicating the algal community present at the beginning of the experiment was not physiologically ready to take up the high concentrations of nutrients provided and immediately grow. It is likely that the algae that responded to the nutrient enrichment were present in the initial sample in small numbers. Small cells, with low optimum uptake concentrations would not be able to respond quickly to high concentrations of nutrients. Often large cells are better adapted than small cells to take up nutrients at higher concentrations. Small cells, < 2 μm, usually constituted 40–50 % of the phytoplankton community (Figure 6.5).

Secondly, algae receiving less than optimum light for growth would also lack strong N or P deficiency. During the windy season, the water column mixes to over 100 m. Such deep mixing would limit the average light exposure of a circulating algal cell to less than that needed for optimum growth (Guildford et al 1998). Indicators of N and P deficiency, C:N and C:P ratios from the whole lake data base (Figure 6.2a and 6.2b) are on average lower during the windy season, indicating a lower demand for N and P either as result of light deficiency or an increase in the supply of N and P. It is likely that both phenomenon are occurring as deep mixing will entrain nutrients from below the epilimnion as well as result in lower mean water column light intensity. Our data provide evidence that the algal community was light deficient at times, however as was observed with the nutrient deficiency indicators we did not observe strong, consistent indications of light deficiency. The rates of photosynthesis at low light levels (α) were high in January (Figure 6.11a), indicating a community adapted to low light. α values were much less in June and especially November, indicating communities adapted to higher light levels than January. The size fractionation experiments indicated that in general, the < 2 μm size fraction was more efficient photosynthetically at low light (Figure 6.17). It was expected that if light were limiting algal growth in situ, we would see a response by the algae in the containers incubated in tanks outside the lab, where light levels were higher than in situ. We observed development of strong N and or P debt in all the control containers in all months, indicating growth was occurring in the presence of grazing, and nutrients were being consumed. We

observed an increase in the C:Chlorophyll *a* ratio in the November enrichment experiment, concomitant with a decrease in α, both indicators of adaptaion to increased light. The development of nutrient deficiency and an increase in the C:Chlorophyll *a* ratio over the course of the 2 day experiment may be interpreted as an indication that the initial population was light deficient .

Thirdly, it is possible that iron or some other trace element critical for plant growth is controlling algal growth. Iron deficiency has been invoked as the factor controlling growth of phytoplankton in parts of Pacific and Antarctic oceans (Martin et al. 1991), and is currently being investigated in some North American Great Lakes (Twiss 1998). We have recently conducted further enrichment experiments, not included in this report, where we tested the effect of Fe. Initial results suggest that Fe as well as N and P can stimulate chlorophyll production.

Prediction of the effect of increased P loading from the watershed - We conclude from the monitoring at station 928, and experiments conducted on water from station 928, that the algal community in pelagic waters of Lake Malawi is potentially N and P deficient. However, most of the time the algae are experiencing balanced growth with biomass limited by grazing and adequate nutrients supplied by regeneration. It is a community adapted to a low, but relatively steady supply of nutrients supplied through the mechanisms of regeneration by grazers and continuous introduction of nutrients from below the epilimnion by upwelling (see Hamblin et al. chapter 5). We conclude from the nutrient enrichment experiments that the algal community present in the lake was not immediately stimulated by an increase in nutrients because of its adaptation to continuously low nutrient supply. However after 24 to 48 hours in a container, some species which may have been present in low numbers initially, and which could make use of the higher concentrations, began to grow. Increased nutrients will result in higher chlorophyll *a* concentrations and dominance by different species. These species may well be larger cells or chain forming species that are larger and not readily grazed. These enrichment experiments illustrate what may occur if nutrients increase in the lake. Further evidence for an increase in chlorophyll *a* with increased nutrient input can be seen in the transect data. In January and November, when the Linthipe River was flowing we found evidence that the high loading rate of P relative to N from the river (see Kingdon et al. chapter 2) was affecting the algal community. We observed higher chlorophyll *a* concentrations at the river mouth compared to offshore (Figure 6.28) and lower C:P and N:P particulate ratios (Figure 6.31a, 6.31b). High rates of P loading relative to N, have been shown to favour increases in nitrogen fixing cyanobacteria (Hendzel et al. 1994). Hendzel (Annex 1, this chapter) observed that although absolute rates of N fixation were low, water sampled closer to shore in Lake Malawi, had higher rates of nitrogen fixation than water collected from farther offshore. It is very likely that increased P input to the lake, due to increased erosion, will disrupt the balanced algal growth at least in the near shore areas of the lake and favour the development of nitrogen fixing, filamentous cyanobacteria such as *Anabaena*. *Anabaena* blooms were observed in the southern portion of the lake in March and April of 1997 and 1998 (Chapter 7, Hecky et al.).

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Chapter 6 (Annex 1)

Nitrogen Fixation

Introduction

Algal biomass or productivity are often stated as being controlled by the relative availability of nitrogen and phosphorus in aquatic ecosystems. Healey and Hendzel (1980) and Schindler (1977) described how most phytoplankton in freshwater lakes primarily will be phosphorus limited, while a number of other studies have shown nitrogen to be both a primary as well as a secondary limiting nutrient (Goldman, 1981; Axler et al, 1984; Setaro and Melack, 1984). The chemical stoiciometry of lake particulate matter has been used as a tool to identify a number of African lakes as being either nitrogen or phosphorus limited. Based on the particulate composition ratios of carbon, nitrogen, and phosphorus, Hecky et al. (1993) suggest that Lake Malawi can be characterized as severely phosphorus limited which would be the case if nitrogen deficiency was being satisfied by nitrogen fixation (Hendzel et al, 1994). Patterson and Kachinjika (1995) citing seasonal phytoplankton data and relative cyanobacteria heterocyst abundance, suggest that nitrogen fixation is a significant mechanism to ameliorate periods of temporary nitrogen deficiency in the lake. This supports the hypothesis by Bootsma and Hecky (1993) that biological nitrogen fixation is the most important input source of nitrogen to the lake. Denitrification, effective sedimentation of particulate matter and selective replacement of phosphorus into the mixed layer by vertical mixing have been suggested to cause TN:TP ratios in the range where biological nitrogen fixation counters the n-deficit of the mixed layer. Nitrogen fixation in Lake Malawi will occur in both the pelagic as well as the benthic algal community. However the relative significance of inputs of nitrogen from either of these sources to Lake Malawi is still mostly unknown. Of importance to which community in Lake Malawi is fixing the most nitrogen may be the efficiencies offered to nutrient recycling in lakes with deep, energetic mixed layers leading to possible reduction of nutrient deficiencies in pelagic waters. This has been shown to be the case for other deep lakes (Guildford et al., 1994).

A preliminary summary based on data collected during November 1996 and 1997 will outline the relative apparent contribution of benthic and pelagic nitrogen fixation to the lake. Protocols used for this study were similar to those previously used for measuring nitrogen fixation on Lake Victoria (Mugidde and Hendzel, unpublished data) and north temperate lakes (Hendzel et al, 1994; Flett et al, 1976).

Methods

Nitrogen fixation estimated from nitrogenase activity was measured using the acetylene reduction method described by Hendzel et al, 1994. Incubations were either conducted in-situ for approximately 2 hours (Maleri Islands samples) or incubator incubations for 4 hours (all other samples) at either ambient light levels or in a light gradient at a high and low light intensity (150 and 7.5μEin.$\cdot m^{-2} \cdot sec^{-1}$, respectively), all at in-situ temperatures. All measurements were conducted in duplicate or triplicate and were corrected to account for background ethylene contamination of the substrate. Following incubation all samples were collected into Vacutainers and were transported back to Winnipeg to be analyzed by FID gas chromatography. Particulate carbon (PC), particulate nitrogen (PN), and particulate phosphorus (PP) were filtered onto GF/C filters pre-ignited at 500^0C and were desiccated until analyzed. Chlorophyll a samples were collected on GF/C filters, desiccated, extracted in methanol and determined fluorometrically. All chemical analysis followed the methods of Stainton et al, 1977. Particulate alkaline phosphatase activity and phosphorus and nitrogen debts measurements were measured according to the methods of Healey and Hendzel, 1980.

Sampling Sites

November 1996 - Benthic nitrogen fixation associated with the bottom sand substrate was measured on sediment core samples from 2, 5, and 10 meters depth. Cores were incubated in-situ at a location situated on the west shore of the Maleri Islands (Figure 6.1). In addition nitrogen fixation was measured on a pelagic sample collected from each depth and incubated in-situ at 1 meter depth at ambient light levels. Water samples from these sites were returned to the lab for phosphorus and nitrogen debt measurements. Pelagic nitrogen fixation was also measured at three deep water stations during a whole lake limnological cruise. Measurements were made on samples from 5 meters at Stations 915 and 907 and at 1, 20, 35, 60 and 80 meters at station 913 (Figure 6.1).

November-December 1997 - Offshore and nearshore pelagic nitrogen fixation was measured at three stations located directly offshore from the research station at Senga Bay. These were: station 928 at 3.2 km, 928a at 2.0 km and 928b 1.0 km) from shore. Maximum station depths were >120, 80, and 2-3 meters, respectively. An integrated water sample was collected at each station, 0-30 meters at stations 928 and 928a, and 0-2 meters at 928b. Surface water temperature and secchi depth was measured at all stations while a CTD profile from surface to bottom was measured at the two deeper stations, with a 0-10 meter light profile taken at the deepest station. All nitrogen fixation experiments were done in triplicate for each station and at two light intensities, 150 and 7.5µEin.$\cdot m^{-2} \cdot sec^{-1}$ All incubations were approximately 4 hours in duration and conducted in a flat bed incubator back at the laboratory. In addition, phytoplankton alkaline phosphatase activity was measured fluorometrically on the same three water samples. This was done on a trial basis to see if the anticipated low rates were in fact measurable and also to determine if the methodology could be applied to an oligotrophic lake located in the tropics. On each experimental date particulate samples were collected for suspended phosphorus, suspended carbon and nitrogen and chlorophyll *a*.

Results

In November 1996 nitrogen fixation measured on that component of the littoral algal community associated with sand substrates (episammon) and adjacent overlying water decreased with increasing water depth over that range of 2-10 meters. Highest rates were measured on samples from the 2 meter site, decreasing with depth at the 5 and 10 meter sites (Figure 6.33). Even though sand samples were collected within close proximity to each other, it was apparent from the data that spatial variability can be significant. Water overlying the sediments supported nitrogen fixation rates which were as high as those measured on the sand substrate samples. Repeated measurements of nitrogen fixation rates at two day intervals over the course of two weeks during November-December 1997 at the three off-shore station (928, 928a, and 928b) out from Senga Bay were the highest for all stations on November 30 (Figure 6.34) decreasing rapidly over the next few days to rates that were either very low or below detection. Highest nitrogen fixation rates were measured on samples from the most in-shore station (928b) while rates from the two deeper stations were found to be lower in comparison and very similar to each other. In all cases, high light (150 vs 75 µEin. $\cdot m^{-2} \cdot sec^{-1}$) (Figure 6.34. Plate a and b) was observed to stimulate nitrogen fixation in samples from the near-shore site whereas there was no apparent affect on samples from both of the deep, off-shore sites. In contrast, pelagic samples collected from the upper part of the mixed layer at stations 915, 913 and 907 and from one deeper profile at station 913 in the northern part of the lake during a whole lake limnological cruise in November 1996 had nitrogen fixation rates (Figure 6.35) which were very low when compared to these near-shore measurements from the south basin of the lake. Measured surface and profile nitrogen fixation rates were only between 0.001-0.003 µM N·L·h at these pelagic stations. These were approximately an order of magnitude lower than those measures at the Maleri Islands and off-shore from Senga Bay (Figure 6.33 and 6.34).

Assessment of algal nutrient status indicated little or no nitrogen or phosphorus deficiency in those same water samples that were used to measure nitrogen fixation. Nitrogen and phosphorus debt were only detected in the 10 meter sample at the Maleri Islands (Table 6.1) whereas there was no measurable phosphorus debt at 5 and 2 meters. Similarly, phosphorus debt in the surface water sample at station 915 and in profile at station 913 (Table 6.1) was negligible and while nitrogen debt was

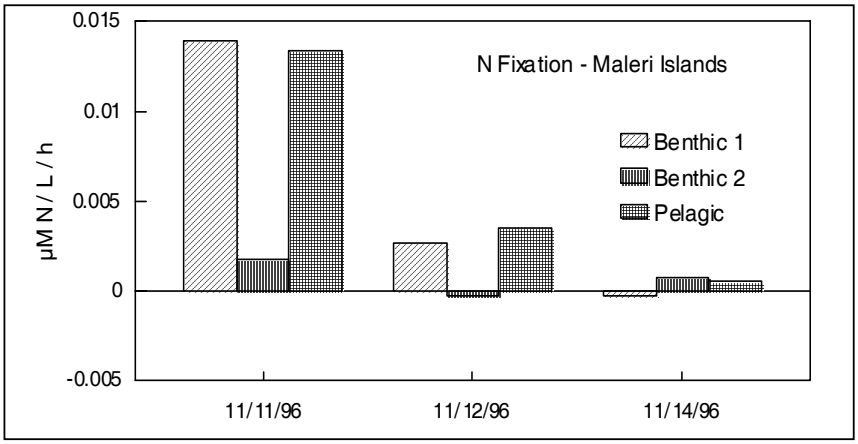

Figure 6.33. Benthic nitrogen fixation rates at the Maleri Islands

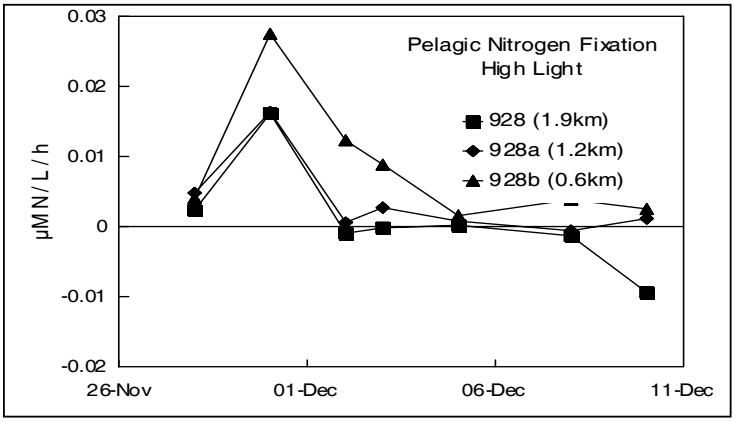

Fig. 6.34a. Pelagic nitrogen fixation at high light.

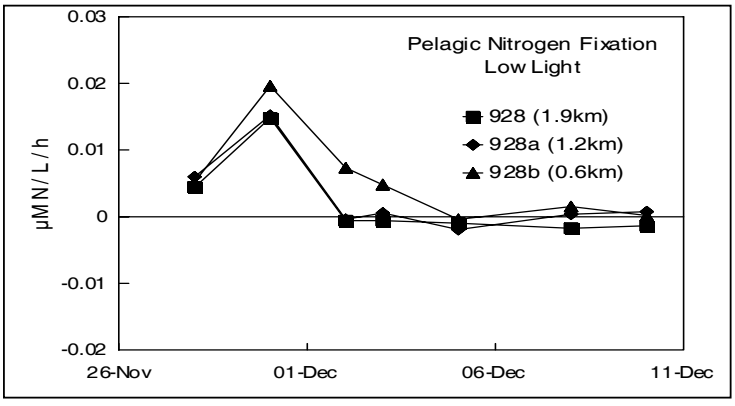

Fig. 6.34b. Pelagic nitrogen fixation rates at low light.

Table 6.1. Benthic and pelagic N and P Debts.
Benthic and pelagic water samples from near the Maleri Islands
Each benthic sand sample consisted of 63.68 cm2 of surface area or 95.52 cm3 sample volume.
Station 913 and 915 are pelagic samples from the whole lake cruise.
Values > 0.15 and 0.075 µM N or P respectively indicate N or P deficiency.

Location	Depth (m)	Date	Chl a µg/L	P Debt µM P/24h	P Debt µM P/µg Chla/24h	N Debt µM N/24h	N Debt µM N/µg Chla/24h
Benthic 1	2	11-Nov-96	75.33	-0.048	-0.001		
Benthic 2	2	11-Nov-96	176.2	-0.439	-0.002		
Pelagic	2	11-Nov-96	0.8	-0.976	-1.22		
Benthic 1	5	12-Nov-96	57.95	-10.788	-0.186		
Benthic 2	5	12-Nov-96	122.7	-10.352	-0.084		
Pelagic	5	12-Nov-96	0.55	-0.044	-0.08		
Benthic 1	10	14-Nov-96	94.36	1.942	0.021	2.019	0.021
Benthic 2	10	14-Nov-96	70.46	1.778	0.025	1.593	0.023
Pelagic	10	14-Nov-96	0.44	0.04	0.091	-0.204	-0.464
Station 913	1	22-Nov-96	0.715	0	0	1.181	1.652
	20		0.392	0	0	-0.822	-2.097
	35		0.486	-0.001	-0.002	0.564	1.16
	60		0.658	-0.002	-0.003	1.335	2.029
	80		0.166	-0.005	-0.03	-0.257	-1.548
Staton 915	5	22-Nov-96	1.2	0.004	0.003	0.205	0.171

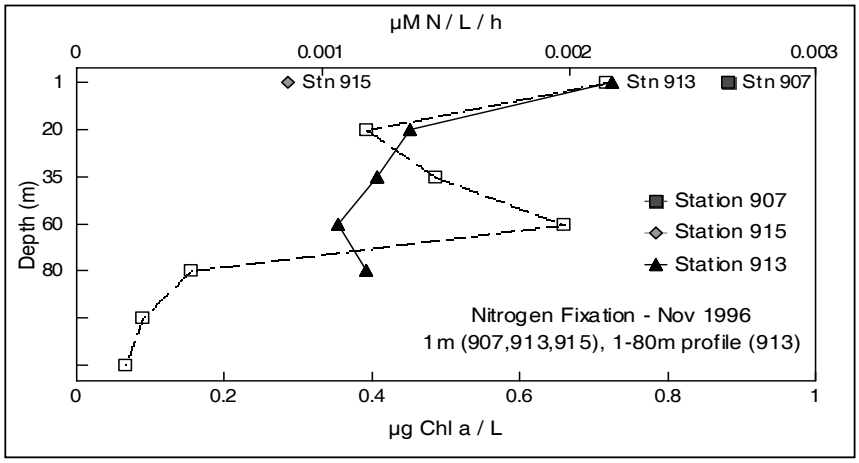

Figure 6.35. Pelagic nitrogen fixation rates at Stations 913, 915, 907.

measured in some of the 915 profile sample, an analytical problem was suspected. Nutrient composition ratios of C:P, C:N and N:P of particulate samples from the three off-shore stations at Senga Bay (Figure 6.36) indicated only moderate levels of either nitrogen or phosphorus deficiency based on indicator value of these ratios as described by Healey and Hendzel, 1980. On the three occasions that alkaline phosphatase activity was measured, rates at all three stations were extremely low and appear to increase slightly at the deeper off-shore stations (Table 6.2).

Discussion

The data indicate that nitrogen fixation in Lake Malawi is occurring within both the benthic and the pelagic algal community but that certain physical and chemical factors appear to constrain the amount of nitrogen being fixed. This hypothesis is based on two possible limiting interactions. One that suggests that reduced mean irradiance levels are maintained at pelagic stations by deep mixing of the mixed layer (Sterner 1990) and that deep mixing results in increased nutrient regeneration (Fee et al, 1994) and enhanced nutrient exchange from deeper, nutrient-rich waters (Hecky et al, 1996). While light limitation as a result of mixing depth was shown (Guildford et al, 1994) not to be the case in temperate great lakes, there are certain conditions where increased mixing depth in large lakes has resulted in increasing light extinction with depth (Sterner 1990). While this is thought to be the case in the deep, mixed pelagic zone of Lake Malawi it is believed that phytoplankton and benthic algae, occupying the relatively shallower waters which comprise the fringe of the lake, are somewhat more nutrient deficient. This is due to the net removal and deposition of nitrogen and phosphorus to deeper waters and also the higher, mean irradiance of this near-shore mixed layer. As evidence, nitrogen fixation rates measured at deep, pelagic stations (Station 915, 913, and 907) were up to an order of magnitude lower (Figure 6.33, 6.34, and 6.35) than those measured in near-shore pelagic waters (station 928, 928a, and 928b) and shallower littoral sites such as seen at the Malari Islands. Phosphorus and nitrogen debt measurements (Table 6.1) indicate that these deep pelagic stations are more P sufficient while being variably N sufficient/deficient. This suggests greater efficiency by the benthic, littoral cyanobacteria (Figure 34, plate a and b, station 928b) than pelagic assemblages (Figure 6.34, plate a and b, station 928, 928a) in fixing nitrogen at similar light intensities. This is not to suggest that the input of nitrogen to the lake by pelagic nitrogen fixation could not be significant. High particulate C:N ratios and low particulate N:P (Figure 6.36) and TN:TP ratios suggest that nitrogen deficiency within the phytoplankton is a chronic occurrence (Hecky et al, 1996) whereby the lakes uses nitrogen fixation as the primary route to meet the nitrogen demands of the phytoplankton (Hendzel et al, 1994). Surface blooms consisting of large patches of vacuolated cyanobacteria have been observed as occurring at various times over different areas of the lake (R.E. Hecky and A. Ribbink - personal communication) and is suggested to be the major component accounting for the input of fixed nitrogen to the pelagic waters of Lake Malawi (Hecky at al, 1996). However quantifying the contribution of this component to the lake's nitrogen budget will be difficult based on the likelihood that pelagic nitrogen fixation will be a localized or zonal event.

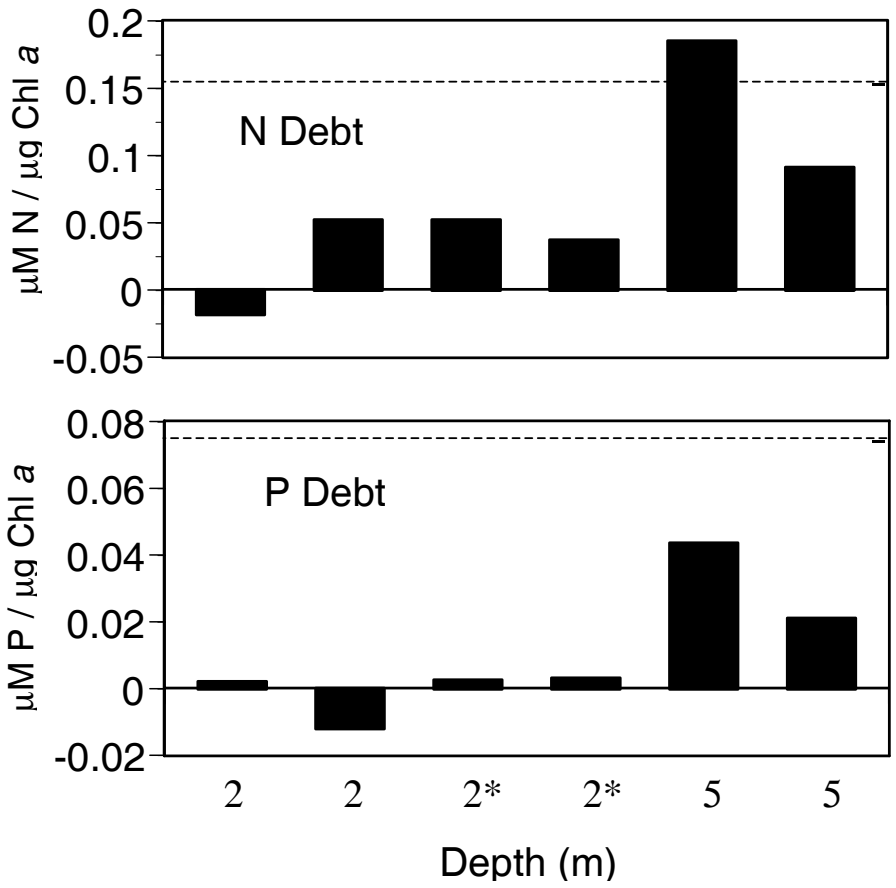

Figure 6.36. N and P debt measurements on the sand at 2 and 5m. * = fish feces on the sand surface. Values above the dashed lines are indicative of nutrient deficiency.

Table 6.2. Alkaline Phosphatase Activity at stations near and away from shore. * indicates questionable result.

Date	Station	A-Pase(S) FUnits/h	A-Pase(T) FUnits/h	A-Pase(S) µMP/hr	A-Pase(T) µMP/hr	A-Pase(C) µMP/µgChl/hr	Chl a µg/L	
Dec 5/97	928	0.000	40.080	0.00000	0.02738	0.02976	0.92	*
Dec 8/97	928	9.408	16.455	0.00899	0.01321	0.00469	0.90	
Dec 10/97	928	5.505	8.250	0.00665	0.00830	0.00176	0.94	
Dec 5/97	928a	64.680	10.680	0.04213	0.00975	-0.03722	0.87	*
Dec 8/97	928a	5.664	4.260	0.00675	0.00590	-0.00087	0.98	*
Dec 10/97	928a	1.215	9.855	0.00408	0.00926	0.00563	0.92	
Dec 5/97	928b	5.220	10.020	0.00648	0.00936	0.00242	1.19	
Dec 8/97	928b	4.728	9.870	0.00618	0.00927	0.00245	1.26	
Dec 10/97	928b	0.990	2.610	0.00394	0.00491	0.00126	0.77	

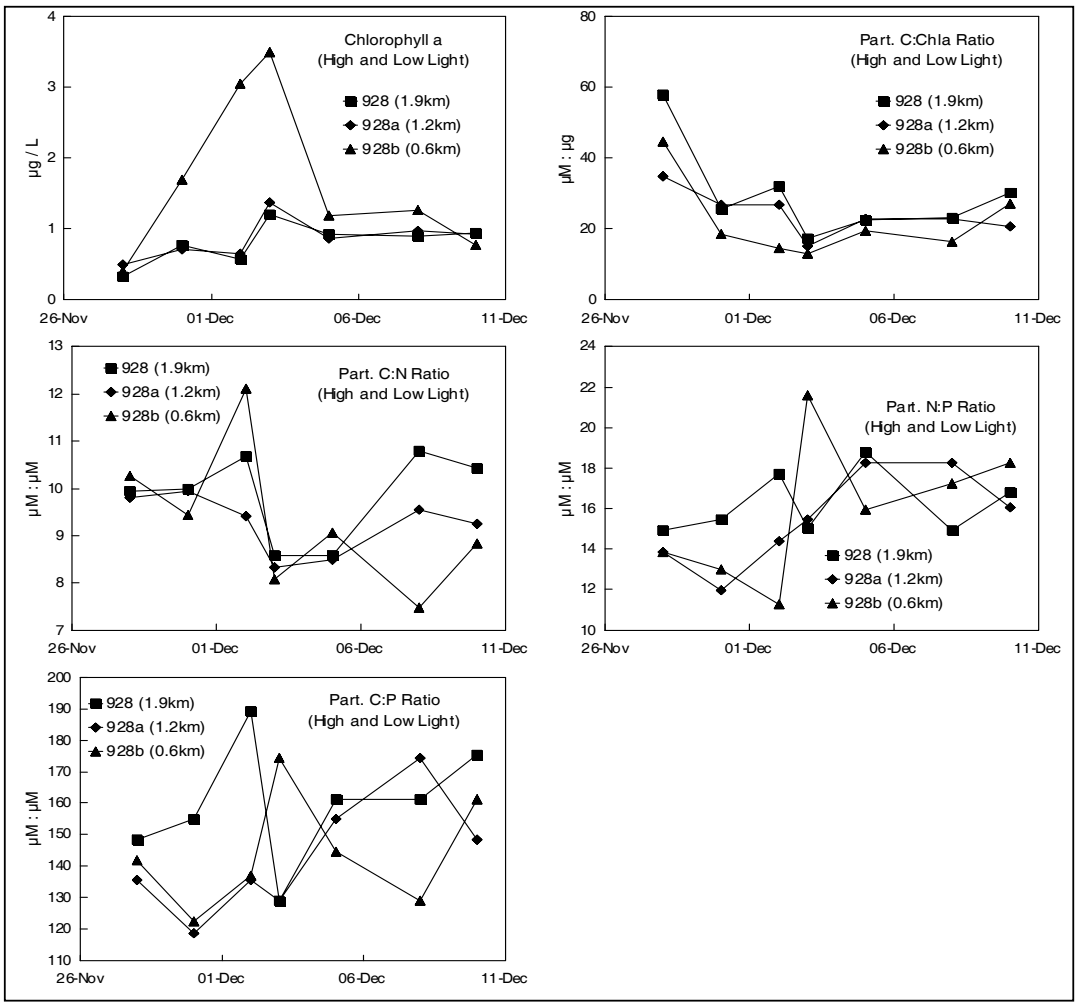

Figure 6.37. Particulate composition ratios for Stations 928, 928a, 928b, 1997.

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