

AN ABSTRACT OF THE THESIS OF

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Patricia A. Wheeler

The flow of nitrogen through microbial communities sampled from Yaquina Bay, Oregon was examined in three incubation experiments using ^{15}N -labeled NH_4^+ and NO_3^- . Comparison of rates of nutrient uptake and regeneration, as well as the change in particulate nitrogen (PN) provided estimates of the nutrient flow between PN, inorganic nitrogen and dissolved organic nitrogen (DON). Comparisons between the changes in the nutrient and PN over specific time intervals provided independent evidence for the fate of the nutrient in the microplankton.

Results for cultures supplemented with Thalassiosira weissflogii were not different than results for control cultures. The rates of nutrient depletion and assimilation, and increase in PN agreed reasonably well in two out of three experiments. In the middle experiment, NH_4^+ regeneration was significant in the NH_4^+ -supplemented cultures and accounted for most of the nutrient taken up. Accumulation of DON was inferred from rate discrepancies in two sets of cultures.

In all incubations, uptake of nitrogen by the microplankton as estimated by biomass-normalized rates of nutrient depletion, was dependent on the form of inorganic nutrient added. Uptake of NH_4^+ was positively correlated with the exponential growth constants for

PN (K_{pn}). This suggested that the NH_4^+ uptake was associated with total microbial growth. Uptake of NO_3^- was closely correlated with the exponential growth constants for in vivo fluorescence. This indicated that NO_3^- uptake was associated exclusively with autotrophic growth.

NITROGEN FLUXES THROUGH MICROBIAL COMMUNITIES
FROM YAQUINA BAY (OREGON)

by

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Professor of Oceanography in charge of major

Redacted for Privacy

Dean of College of Oceanography

Redacted for Privacy

Dean of Graduate School

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Typed by Saturnino J. Jamerlan for Saturnino J. Jamerlan

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FROM YAQUINA BAY (OREGON)

Chapter I

INTRODUCTION

1. Background

Nitrogen may be the most limiting nutrient for primary production in the marine environment (Ryther and Dunstan 1971). The dominant utilizable forms are NH_4^+ , NO_3^- and NO_2^- which supply the bulk of the nitrogen requirements of phytoplankton. Certain forms of dissolved organic nitrogen (DON) can also contribute a minor portion of the nitrogen supply for primary production. Generally, primary production occurs within the upper 100 meters of the water column where there is adequate light to support photosynthesis. In this upper layer of the ocean, light and nutrient availability are major factors determining the growth of phytoplankton. Hence, import to and loss of utilizable nitrogen from the euphotic zone could control the level of primary production.

The supply and loss of utilizable nitrogen in the euphotic zone are determined by different processes. The mode by which nitrogen is supplied into the euphotic zone partly depends on its form. Nitrate and NO_2^- are generally introduced into the euphotic zone by upward advection or diffusion of nutrient-rich water from below the nitracline (Dugdale and Goering 1967, Jackson and Williams 1985, Smith et al. 1986), where nitrification is significant. Biological processes within the euphotic zone such as

excretion and predation by heterotrophs (Dagg 1974, Eppley and Peterson 1979, Copping and Lorenzen 1980, Glibert 1982, Roman et al. 1988) contribute the major portion of NH_4^+ and labile DON. Nitrogen fixation converts dissolved N_2 gas to NH_4^+ , but the process is limited and probably insignificant in most marine water columns (Carpenter 1983). Marine rains import small amounts of free amino acids (Mopper and Zika 1987) into the surface waters and thereby contribute a minor portion of the DFAA pool. Terrestrial inputs could contribute significantly to the dissolved nitrogen in coastal waters (Gardner and Stephens 1978). In contrast to the variety of processes determining rates of nitrogen supply, loss of nitrogen from the euphotic zone occurs primarily through sedimentation of particulate nitrogen (McCave 1975). Sinking PN is consumed by heterotrophs and a major fraction is remineralized into NH_4^+ or converted to DON and smaller suspended particles (Karl et al. 1988).

Certain processes that control the supply and loss of nitrogen in the euphotic zone are biologically mediated fluxes between the dissolved and particulate nitrogen. The supply of nitrogen is partly determined by the rates at which dissolved nitrogen is produced from PN through remineralization, and from N_2 through nitrogen fixation. Loss of nitrogen from the euphotic zone through sedimentation is directly affected by primary production (Pace et al. 1988). Phytoplankton control some of these processes (i.e., primary production, DON excretion) and therefore can affect nitrogen cycling in the marine environment.

The predominant process by which nitrogen is incorporated into PN in the marine environment is by assimilation of inorganic nutrients by primary producers. Heterotrophic bacteria can utilize

a significant portion of NH_4^+ (Laws et al. 1985, Wheeler and Kirchman 1986, Fuhrman et al. 1988). Nitrogen can also be incorporated into the particulate fraction through uptake of DON. Bacteria are widely believed to be the most efficient consumers of DON in marine environments (Paul 1983, Wheeler and Kirchman 1986). However, phytoplankton can take up some forms of DON (i.e., urea, DFAA) at natural concentrations (McCarthy 1972, Wheeler et al. 1974) and may use these to support part of primary production seasonally (Flynn and Butler 1986). Thus, fluxes of dissolved nitrogen into PN is controlled mainly by phytoplankton and bacteria, through uptake of inorganic nitrogen and DON.

Nitrogen fixation can introduce dissolved N_2 into the particulate fraction but it is generally restricted to O_2 -depleted microzones on suspended particles. During cyanobacterial blooms, nitrogen fixation may contribute as much as 79% of the nitrogen supply for the $>10 \mu\text{m}$ PN fraction (Sörensson and Sahlsten 1987). Generally, however, N_2 fixation appears to be a minor component of nitrogen cycle in the marine environment (Carpenter 1983).

Dissolved nitrogen is released from PN mainly through NH_4^+ remineralization, which is controlled by protozoans (Caron and Goldman in press) and bacteria (Cho and Azam 1988). Significant amounts of dissolved nitrogen may also be released through excretion of DON. Phytoplankton appear to dominate excretion of DON in the water column (Hellebust 1974, Hammer and Brockman 1983, Eberlein et al. 1985, Slawyk and Rodier 1986). Changes in the concentrations of certain DFAA observed in phytoplankton cultures (Admiraal et al. 1986) and natural blooms (Hammer and Katner 1986) have been attributed to excretion of DON by phytoplankton and disintegration of dead cells. Estimates of DON release in natural

phytoplankton populations range from 10% (Schell 1974) to 40% (Laws 1984) of the nitrogen assimilated, but larger amounts are reported following blooms of certain haptophyceans (Eberlein et al. 1985).

In summary, phytoplankton play important roles in controlling certain fluxes of nitrogen between the particulate and dissolved pools in the water column. Assimilation of inorganic nitrogen and DON into the particulate fraction is associated with autotrophic activity. The flux from the PN into DON pools also appears to be caused primarily by phytoplankton excretion. The processes which are not significantly affected by phytoplankton activity include regeneration of NH_4^+ , excretion of certain forms of DON (i.e., urea) and denitrification.

Early studies of nitrogen fluxes in the microplankton involved measurements of autotrophic uptake of nitrogen. Nutrient uptake is measured as the decrease in inorganic nitrogen ("nutrient depletion") or the accumulation of ^{15}N -labeled NH_4^+ or NO_3^- in the particulate fraction ("nutrient assimilation"). These two estimates of nitrogen uptake are not equivalent when processes such as NH_4^+ regeneration, DON excretion and heterotrophic uptake of NH_4^+ are significant in the water column.

Studies investigating nitrogen assimilation by phytoplankton often report a discrepancy between the amount of ^{15}N assimilated in the particulate fraction and the amount of inorganic ^{15}N depleted from the pool of dissolved nutrients. One possible cause of the "missing" nitrogen is excretion of ^{15}N -DON by phytoplankton (Laws 1984). This excretion of DON by natural phytoplankton assemblages could account for as much as 40% of the assimilated nutrient.

Bacterial uptake of NH_4^+ observed in some studies (Laws et al. 1985, Wheeler and Kirchman 1986, Fuhrman et al. 1988) could

also cause discrepancies between the changes in the inorganic nutrient and particulate nitrogen pools because bacterial biomass is only partly retained in the "particulate fraction". Studies measuring nutrient uptake typically use glass-fiber filters (nominal pore size=0.8 μm) to collect the particulate fraction. Lee and Fuhrman (1987) found that approximately 47% of bacterial biomass passes through these filters and remains in the "dissolved" fraction. Thus, a significant portion of ^{15}N assimilation by bacteria would not be measured by current techniques. If bacteria are responsible for a significant portion of total inorganic nitrogen assimilation by the microplankton, inefficient collection of bacterial biomass on glass-fiber filters could be the cause of "missing nitrogen" in ^{15}N tracer experiments.

2. Statement of Objectives

The general aims of this study were to determine the fate of nitrogen in a microbial community, and to assess the role of autotrophs on nitrogen fluxes. Standard methods were used for measuring nutrient depletion, assimilation and regeneration. Relatively high additions of ^{15}N tracers were made to maximize changes among the different nitrogen pools.

The following hypotheses were tested:

1) Inorganic nitrogen depleted from the medium but not recovered in the particulate fraction, has been metabolized then released as DON.

2) Depletion of NH_4^+ depends on the activities of both autotrophs and heterotrophs, and is thus better correlated with total microbial biomass and activity than with autotrophic biomass and activity alone.

3) Depletion of NO_3^- is better correlated with phytoplankton activity and biomass than with total microbial activity and biomass.

In each experiment, nitrogen fluxes through a microplankton community were studied by monitoring the three nitrogen pools (DON, PN and inorganic nitrogen). The DON pool was measured during the course of the incubations, to determine whether it is an important "source" or "sink" of nitrogen for the microplankton. The changes in the three nitrogen pools during the periods of NH_4^+ and NO_3^- uptake were also compared.

Chapter II

METHODS

A series of ^{15}N incubation experiments were conducted on natural microbial assemblages to trace the fluxes of nitrogen among the three nutrient pools (inorganic, particulate and dissolved organic nitrogen). Chemical and isotopic methods were used to measure these fluxes. Since the assemblages were isolated from a nutrient-rich environment, the uptake rates measured in these incubation were probably not nutrient-limited. Each incubation involved a high ^{15}N enrichment to facilitate isotopic measurement of the fluxes. In each experiment, half of the carboys were inoculated with a diatom culture in an attempt to enhance DON excretion.

1. Seawater Collection

Water was collected from different sites on lower Yaquina Bay, Oregon, on three dates. The sites and dates of each collection for Experiments 1-3 are as follows; from the shore at the beach in front of the Hatfield Marine Science Center (HMSC) (7 May 1987), from a dock near the entrance to the South Beach Marina (29 May 1987) and from a small boat in the middle of the bay opposite HMSC (1 July 1987). Each collection was scheduled within 2 hours of the occurrence of the highest high tide for the day. Tidal currents were ebbing during the first collection, and flooding during the two other samplings. Surface water was sampled using plastic buckets, and then filtered through a Nitex screen (200 μm). Four white polyethylene carboys (diameter=35.6 cm, height=67.3 cm, neck diameter=10.2 cm), which were previously acid-

washed and rinsed with deionized water, were individually rinsed and then filled with 50 l of the collected seawater.

Within 3 h after collection, the carboys were transported to Corvallis and placed in walk-in cold rooms. The light banks in both cold rooms had the same photoperiod (14 h light, 10 h dark) and illuminated the carboys at the top and on one side. Light intensities measured inside the carboys were 80 and 60 $\mu\text{Einst. m}^{-2}\text{s}^{-1}$ for the NH_4^+ - and NO_3^- -supplemented cultures (see below), respectively. Temperatures in the cold rooms were 19°C and 15°C for the NH_4^+ - and NO_3^- -supplemented cultures (see below), respectively.

2. Experimental Sampling Scheme

Initial ($T=0$) samples of ~1.75 l were drawn from each carboy, and then one culture from each pair (designated as + Diatom) was inoculated with 50 ml of an exponentially growing (1 week old) non-axenic culture of Thalassiosira weissflogii in f/2 medium (Guillard and Ryther 1962). Immediately after inoculation, the cell density of the T. weissflogii in the + Diatom carboy ($\sim 10^2$ cells ml^{-1}) was within the range of cell densities typical for estuarine waters (23-6700 cells ml^{-1} , Raymont 1980). The nitrogen source in each inoculum was identical to the ^{15}N -labelled nutrient to be added in the carboy, but did not measurably increase nutrient concentrations in the + Diatom cultures. The other carboy in each pair served as a control. Labeled $(\text{NH}_4)_2\text{SO}_4$ (99.7 atom % ^{15}N) or NaNO_3 (98.8 atom % ^{15}N) (MSD Isotopes) was then added to each pair of carboys. At the start of the incubation, ^{15}N concentrations in Experiments 1, 2 and 3 were as follows; 7.8, 3.2 and 12.7 μM for the $^{15}\text{NH}_4^+$ -supplemented cultures, and 3.6, 3.7 and 18.8 μM for $^{15}\text{NO}_3^-$ -supplemented cultures. Nitrogen concentrations at the beginning of

the experiments are reported in the next chapter (see Table III.1). After nitrogen supplementation, the carboys were capped, agitated and quickly sampled (within 10 minutes) for initial experimental time points. Subsequent samplings were made at 8-16 h intervals, with the exception of the last time point in Experiment 3 which was 24 h after the previous sampling. Before each sampling, the carboys were shaken until any settled material was resuspended. Sampling was terminated when the concentration of inorganic nitrogen became undetectable (4-5 days). The volume remaining in each culture was determined at the end of the experiment for calculation of the nutrient addition.

3. Sample Analysis

Microbial biomass and growth were estimated from particulate nitrogen (PN) and the changes in PN. Microbial growth on the walls of the carboys could have led to underestimation of PN. However, total nitrogen concentrations in all incubations were constant over time, indicating that practically all of the nitrogen initially measured could be accounted during the incubations. Particulate material was collected under gentle vacuum pressure (50 mm Hg) onto precombusted (500°C, 20 min.) glass-fiber filters (2.4 cm Whatman GF/F; nominal pore size=0.8 μm). Separate filter samples were taken for analyses of PN and atom % ^{15}N in the PN. Both sets of samples were stored frozen for subsequent analysis.

Autotrophic biomass and growth were estimated from in vivo fluorescence (IVF) measurements. Three 40-ml subsamples for each time point were measured for in vivo fluorescence with a Turner Designs fluorometer. The fluorometer was set to zero with filtered (0.2 μm Nuclepore) seawater blanks, and then calibrated with a coproporphyrin standard solution (0.05 $\mu\text{g}/\text{l}=20$ units).

Concentrations of NH_4^+ , and $\text{NO}_3^- + \text{NO}_2^-$ in the filtrate were determined. An additional 36-ml of each filtrate was also stored frozen for subsequent assay of total dissolved nitrogen (TDN). Fifty milliliter fractions of the filtrates were stored frozen for determination of atom % ^{15}N . Prior to isotopic analysis, these were thawed and divided into 25-ml portions, which were swirled and frozen onto the surfaces of 125-ml Erlenmeyer flasks and then freeze-dried. The samples were then transferred to plastic grinding vials and dried in an oven (60°C) for at least 48 h.

For the NH_4^+ -supplemented cultures, dissolved NH_4^+ was extracted from the remaining filtrate (600-900 ml) using a modification of procedures described by Dudek et al. (1986) and Selmer and Sörensson (1986). Ammonium was converted into indophenol using the phenolhypochlorite reaction. The indophenol was absorbed onto an Octadecyl (C18) column (Baker) and then eluted with HPLC grade acetone (Baker Analyzed). The eluate was spotted onto a combusted (500°C , 20 min) 4.7 cm Whatman GF/C glass fiber filter, dried in a vacuum oven at 80°C overnight and stored in a desiccator for subsequent analysis.

4. Nutrient and Biomass Assays

Ammonium was determined by the phenolhypochlorite reaction (Strickland and Parsons 1972) scaled down for 10-ml samples. Ammonium chloride (Baker) was used as the standard and absorbance at 640 nm was measured with a Spectronic 70 (Bausch and Lomb) spectrophotometer using 10 cm cells. Combined nitrate and nitrite was determined by reducing NO_3^- in copper-cadmium columns and then forming a diazo dye from the resulting NO_2^- as described by Strickland and Parsons (1972). To insure good reduction efficiencies, the copper-cadmium columns were recharged at the end

of each experiment. Reagent grade sodium nitrate (Baker) was used as the standard and absorbance at 543 nm was measured with a Spectronic 1001 (Bausch and Lomb) spectrophotometer. One centimeter plastic cells were used on samples with high concentrations and 10 cm glass cells were used for concentrations less than 1 μ M.

Nitrite concentration was not measured separately and thus could not be distinguished from NO_3^- . Nitrate was assumed to comprise the major fraction of the $\text{NO}_3^- + \text{NO}_2^-$ concentration because NO_2^- typically accounts for less than 10% of the sum in natural marine samples (Strickland and Parsons 1972). The addition of labeled NO_3^- (18-74 % of ambient levels) further decreased the relative abundance of NO_2^- in NO_3^- -supplemented cultures.

The samples for particulate (PN) and total dissolved nitrogen (TDN) concentrations were thawed, and oxidized with potassium persulphate (Baker) in a highly basic (pH>11) medium under high heat (100°C) and pressure (15 psi). Under these conditions, nitrogen is oxidized to nitrate (Koroleff 1983). After slow cooling, the samples were acidified and pH was adjusted to 8.0-8.4 for subsequent analysis of NO_3^- . An accompanying series of bovine gamma-globulin (Sigma) solutions with known nitrogen concentrations and reagent blanks were used as standards. For reading absorbance, a Spectronic 1001 (Bausch and Lomb) spectrophotometer was used in the first two experiments and a Lambda Array 3840 (Perkin-Elmer) spectrophotometer was used in Experiment 3. Dissolved organic nitrogen (DON) concentrations were calculated from the difference between the TDN and the summed inorganic nitrogen. Total nitrogen (TN) concentrations were calculated as the sum of TDN and PN.

5. Determination of Isotopic Ratio

Isotopic enrichment of dried samples was determined by emission spectrometry (Fiedler and Proksch 1975). Prior to isotopic analysis, the PN samples were oven-dried (60°C) for about 48 h. Samples were ground with a copper catalyst (Cuprox), vacuum sealed (<10 μ Torr) in glass tubes (OD=5 mm) with calcium oxide, and combusted at 500°C for at least 12 h. Relative atom % ^{15}N was determined from 3 scans of each sample using a Jasco N150 emission spectrometer. Labeled N_2 gas standards were used for instrument calibration. All atom % ^{15}N estimates were based on linear regression equations calculated from four standards bracketing the sample value.

To determine effects of background contaminants and recovery for the $^{15}\text{NH}_4^+$ samples, 6 solutions of labeled (5 atom % ^{15}N) NH_4Cl (5 μM) were processed as samples for NH_4^+ extraction. The resulting mean atom % ^{15}N was 4.17% (SD=0.14%) indicating a reduction of 0.83 atom % ^{15}N . All $^{15}\text{N-NH}_4^+$ measurements were corrected for this dilution (19.90%) which resulted from reagent additions and sample processing. For the $^{15}\text{N-TDN}$ samples, 3 standard solutions of labeled ($4.19 \pm 0.09\%$ ^{15}N) alanine (40 μM) were freeze-dried and analyzed for ^{15}N enrichment. A mean atom % ^{15}N of 3.92% (SD=0.34%) was measured, and all $^{15}\text{N-TDN}$ samples were corrected for 6.89% dilution.

6. Calculations

Concentrations of ^{15}N in PN, TDN and the NH_4^+ fractions were calculated as products of atom % ^{15}N and concentration of PN, TDN or NH_4^+ . The atom % ^{15}N for the NO_3^- fraction was calculated from the known isotope addition and was assumed constant throughout each incubation. Total ^{15}N were calculated as the sum of $^{15}\text{N-TDN}$ and

^{15}N -PN. When ^{15}N -TDN was underestimated, the total ^{15}N was calculated as ^{15}N -PN plus inorganic ^{15}N .

Rates of nutrient depletion were calculated from least square linear regressions of nutrient concentrations versus time. Similarly, rates of increase in biomass were calculated from linear segments of plots of PN or IVF against time. Since the amount of biomass varied in all cultures, changes in nutrient concentration were also normalized to PN and IVF values corresponding to the midpoint of the period of nutrient depletion (i.e., "median" PN and IVF).

Linear regression parameters were also calculated for particulate atom % ^{15}N versus time. Specific assimilation rates were then calculated using the equation for constant uptake rates (Dugdale and Wilkerson 1986);

$$V_c = 1/T \times \text{LN}[(R - (F)) / (R - {}^{15}\text{N}_{\text{PN}})]$$

where,

T = time

R = atom % ^{15}N in nutrient (calculated for NO_3^-)

F = natural ^{15}N enrichment (0.367 %)

${}^{15}\text{N}_{\text{PN}}$ = final atom % ^{15}N in PN.

In the NH_4^+ -supplemented cultures, the parameter R was measured and a statistical mean of all values was used. If R decreased with time (i.e., isotope dilution due to NH_4^+ regeneration), the calculated enrichment at the midpoint of incubation period was used. The assimilation rate (ρ_c) was calculated from the product of V_c and the "median" PN for the time interval.

Ammonium regeneration (R) rates were calculated using the equations of Glibert et al. (1982);

$$R = k \times P \quad \text{and} \quad k = -\text{LN}(R_t/R_0)/T$$

where,

P = mean NH_4^+ concentration during incubation

R_0 = initial atom % ^{15}N in NH_4^+

R_t = final atom % ^{15}N in NH_4^+

T = time.

Ammonium regeneration (D) was also calculated using the "mass balance" approach (Fisher et al. 1981);

$$D = \text{ND} - \text{rho}_c$$

where,

ND = rate of nutrient depletion

rho_c = nutrient assimilation rate.

Regeneration in NO_3^- -supplemented cultures could not be estimated directly because the atom % ^{15}N in the NH_4^+ fraction was not measured.

Exponential growth constants were calculated using the following equations;

$$K_{rf} = \ln(\text{IVF}_f/\text{IVF}_i)/T$$

$$K_{pn} = \ln(\text{PN}_f/\text{PN}_i)/T$$

where,

IVF_f , IVF_i = in vivo fluorescence at the end and at the beginning of the growth period

PN_f , PN_i = the ratio of PN at the end and at the beginning of the growth period

T = time.

7. Statistical Tests

The constants K_{pn} and K_{rf} , and the rates of change in nutrient and biomass were slopes of regression equations. The standard errors for these values were the square roots of the variances for the calculated slopes (Neter et al. 1983). The majority of estimates (nutrient and PN concentration, atom % ^{15}N) were calculated from standard curves. The errors for these estimates were calculated from the SD (CV<10%, n=2-3) of the replicates and the standard errors of the regression parameters from the standard curves. Equations for the propagation of errors were based from Bevington (1969).

Rates and variances were compared using two-tailed t-tests for slopes of linear regression equations and variances (Neter et al. 1983), respectively. Estimates calculated from rates were compared using a general t-test for difference (Zar 1984) and their propagated errors were considered as their standard errors (Bevington 1969). All statistical tests were conducted at a 95% level of significance (P=0.05).

Chapter III

RESULTS

1. Initial Nutrient and Biomass Concentrations

Ambient NH_4^+ concentrations were generally low (1.2-1.7 μM) relative to NO_3^- and similar in all three experiments (Table III.1). Ammonium additions ranged from 5-10 μM resulting in mean initial concentrations ranging from 5.0-13.8 μM . Ambient $\text{NO}_3^- + \text{NO}_2^-$ concentration was lowest in Experiment 1 (1.6 μM , Table III.1) compared to 9.97 μM and 17.37 μM for Experiments 2 and 3. Presumably the flooding tides during the last two collections brought in NO_3^- -enriched offshore water. Nitrate additions (range of 4-20 μM) increased the mean initial NO_3^- concentrations to 5.3, 13.7 and 36.5 μM , respectively for Experiments 1-3. Total dissolved inorganic nitrogen ranged from 6-17 μM for all cultures in the first two experiments. In Experiment 3, inorganic nitrogen was 2-4 times higher (range of 31-39 μM) than in the two preceding incubations.

All cultures had similar initial biomass concentrations, despite the Thalassiosira weissflogii inocula for the + Diatom cultures. Initial PN was approximately 10 μM in the first two experiments, and was 50% lower in Experiment 3 (Table III.1). Mean initial in vivo fluorescence was similar ($P > 0.05$) in all three experiments, ranging from 5.08-7.93 fluorescence units (FU) (Table III.1).

Table III.1. Ambient and initial nutrient and biomass conditions.

a. Ambient nutrient and PN concentrations

Experiment	NH_4^+ (μM)	$\text{NO}_3^- + \text{NO}_2^-$ (μM)	PN (μM)
1	1.60 ± 0.08	1.60 ± 0.28	9.55 ± 1.90
2	1.72 ± 0.30	9.97 ± 1.48	10.75 ± 1.10
3	1.23 ± 0.13	17.37 ± 1.02	4.83 ± 0.55

b. Initial nutrient concentrations in (N-supplemented cultures) and ambient In Vivo fluorescence

Experiment	NH_4^+ (μM)	NO_3^- (μM)	Fluorescence (relative units)
1	9.35 ± 0.78	5.25 ± 0.21	6.23 ± 0.44
2	5.05 ± 0.64	13.7 ± 1.55	7.93 ± 0.78
3	13.85 ± 0.07	36.45 ± 2.33	5.08 ± 0.59

2. Changes in Nutrient and Biomass Concentrations

By the end of each incubation, all inorganic nutrients were depleted. The plankton showed a preference for NH_4^+ over NO_3^- , and NO_3^- uptake generally started within 8 h after NH_4^+ depletion (Figs. III.1-6). No lag period preceded NH_4^+ uptake except in the last experiment (Figs. III.5, III.6).

Increases in PN and IVF coincided in each pair of cultures (control and + Diatom), and were associated with depletion of inorganic nitrogen. In all NH_4^+ -supplemented cultures and in the NO_3^- -supplemented cultures in Experiment 2, PN reached a maximum in the middle of the incubation and then apparently decreased. These decreases in PN were not significant ($P > 0.05$) and have to be independently verified. In two NO_3^- -supplemented cultures, maximum change in PN occurred at the end of incubation. Accumulation of ^{15}N in the particulate fraction coincided with the depletion of the labeled nutrient. In NH_4^+ -supplemented cultures with high ambient NO_3^- , the atom % ^{15}N of PN decreased after NH_4^+ depletion as a result of uptake of unlabeled NO_3^- .

3. Rate Measurements

Inorganic nitrogen was taken up at similar rates ($P > 0.05$) for each pair of control and + Diatom cultures. Growth constants and rates of PN increase were also similar ($P > 0.05$) for these paired cultures. Since the addition of *Thalassiosira weissflogii* had no significant effect, results from the two cultures were pooled. Mean and standard deviations are given in Tables III.2-8, and the complete data are given in the Appendix.

A. Rates of Nutrient Depletion and Assimilation

Rates of NH_4^+ and NO_3^- depletion (in the respectively supplemented cultures) ranged from 0.107-0.584 $\mu\text{M h}^{-1}$, and did not

Figure III.1. Changes in nutrient, biomass and particulate atom % ^{15}N in NH_4^+ -supplemented cultures of Experiment 1. Data for control (panels A, C and E) and + Diatom cultures (panels B, D and F) (see page 20). Linear segments used for calculation of rates are indicated. A and B. NH_4^+ (open circles), $\text{NO}_3^- + \text{NO}_2^-$ (closed circles). C and D. Particulate nitrogen (open circles), and in vivo fluorescence (closed circles). E and F. Labeled particulate nitrogen (open circles), and atom % ^{15}N in particulate nitrogen (closed circles).

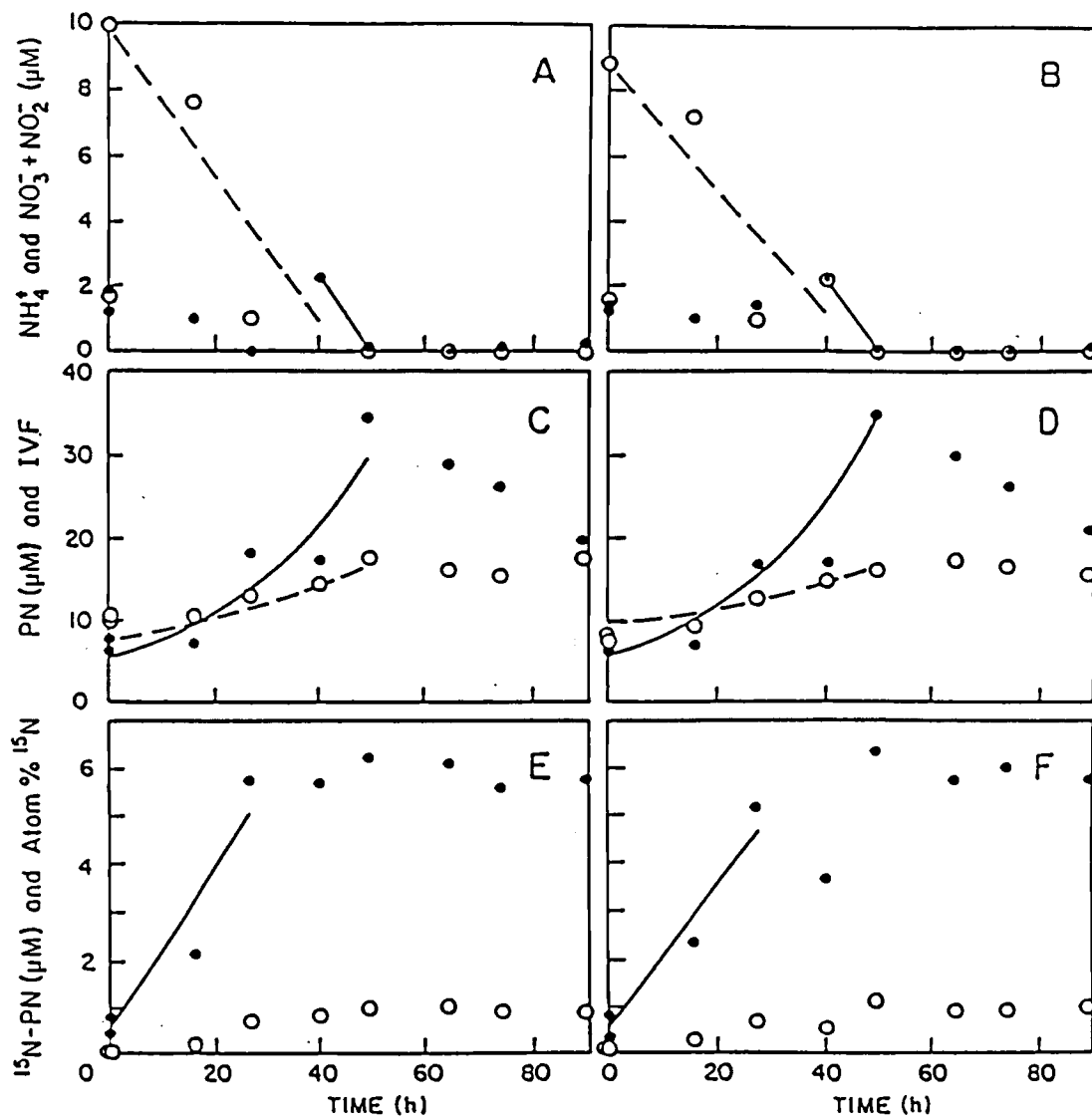


Figure III.1

Figure III.2. Changes in nutrient, biomass and particulate atom % ^{15}N in NO_3^- -supplemented cultures of Experiment 1. Data for control (panels A, C and E) and + Diatom cultures (panels B, D and F) (see page 22). Linear segments used for calculation of rates are indicated. A and B. $\text{NO}_3^- + \text{NO}_2^-$ (open circles) and NH_4^+ (closed circles). C and D. Particulate nitrogen (open circles), and in vivo fluorescence (closed circles). E and F. Labeled particulate nitrogen (open circles), and atom % ^{15}N in particulate nitrogen (closed circles).

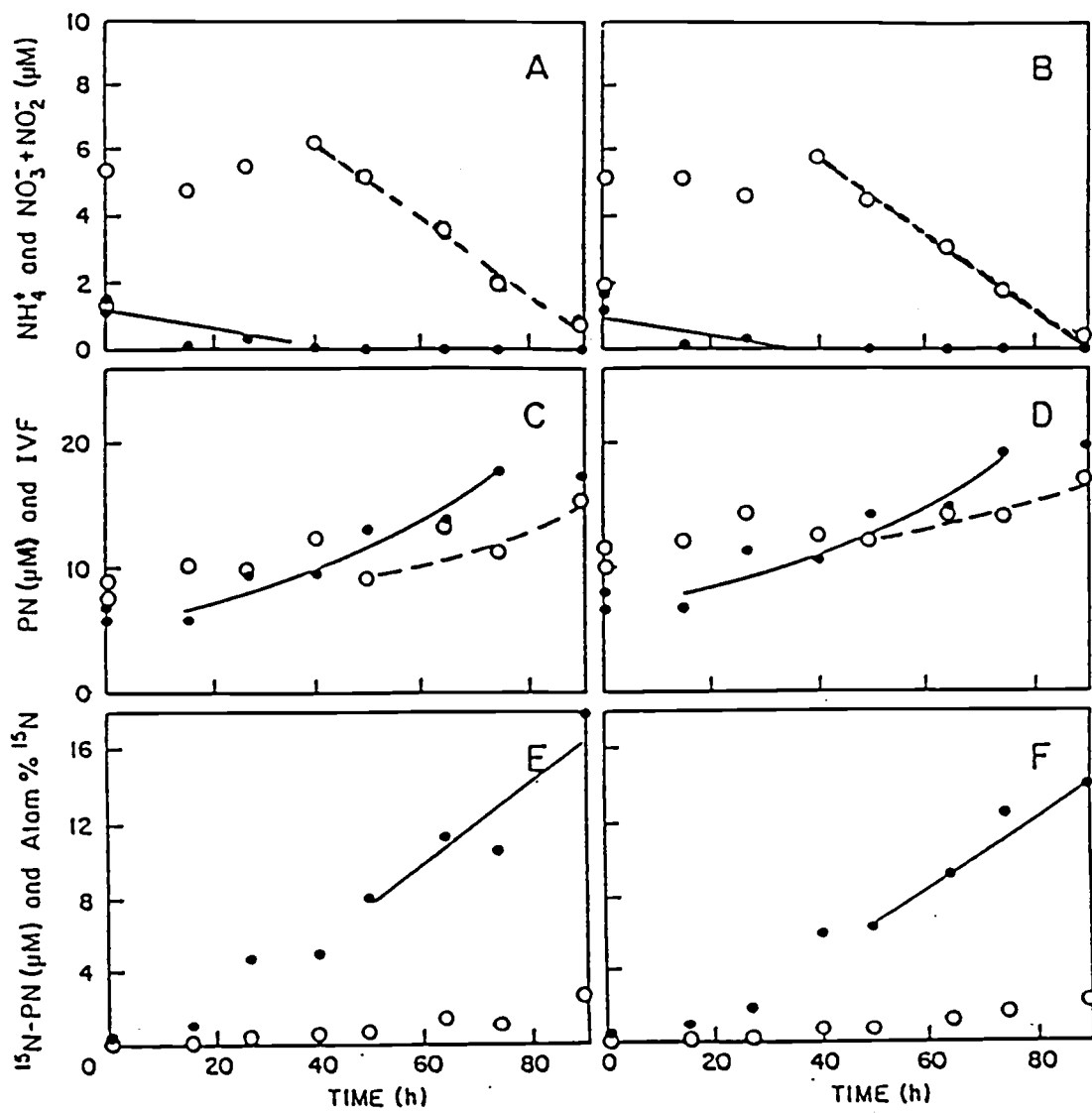


Figure III.2

Figure III.3. Changes in nutrient, biomass and particulate atom % ^{15}N in NH_4^+ -supplemented cultures of Experiment 2. (as in Figure III.1) (see page 24).

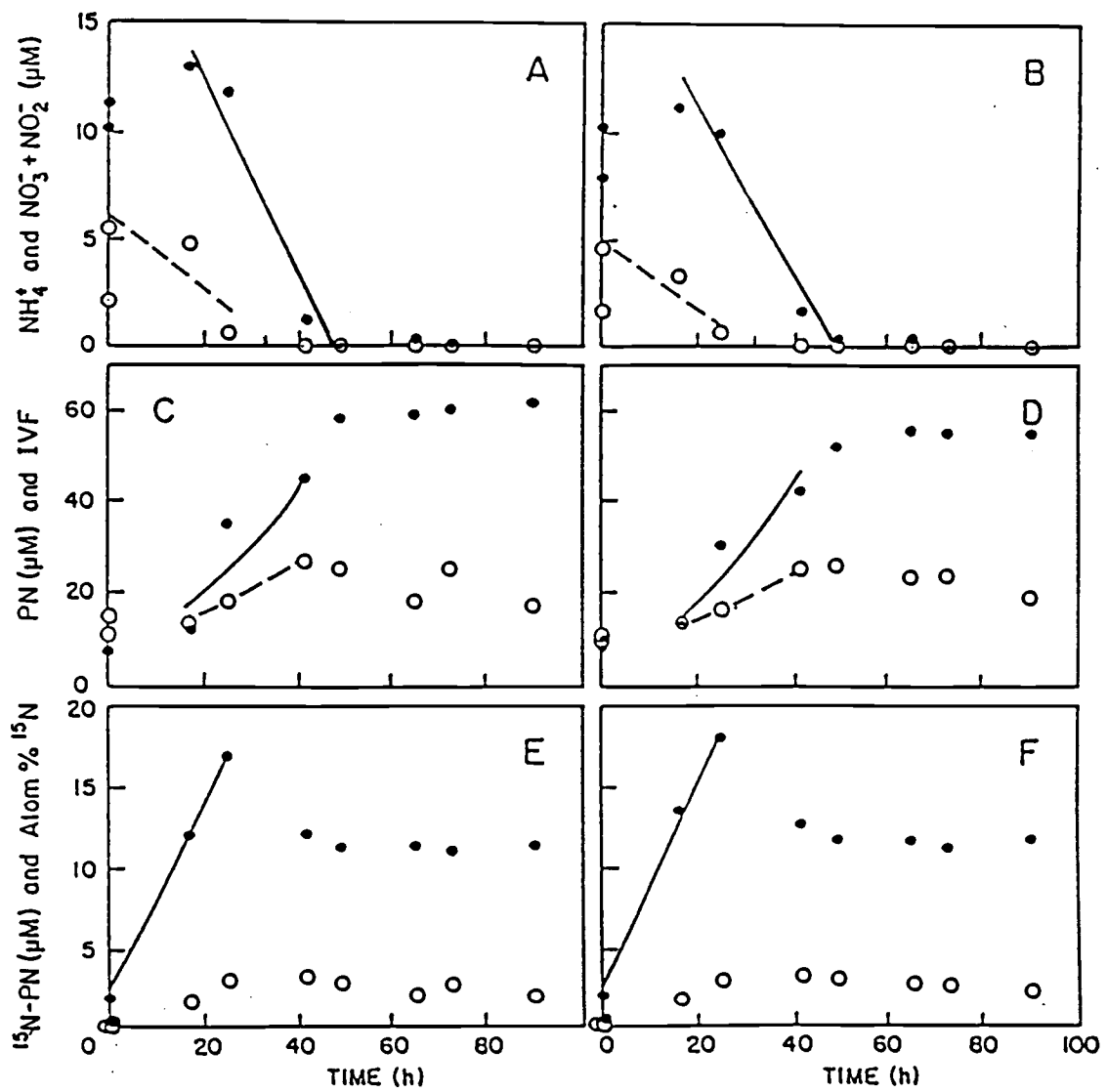


Figure III.3

Figure III.4. Changes in nutrient, biomass and particulate atom % ^{15}N in NO_3^- -supplemented cultures of Experiment 2 (as in Figure III.2) (see page 26).

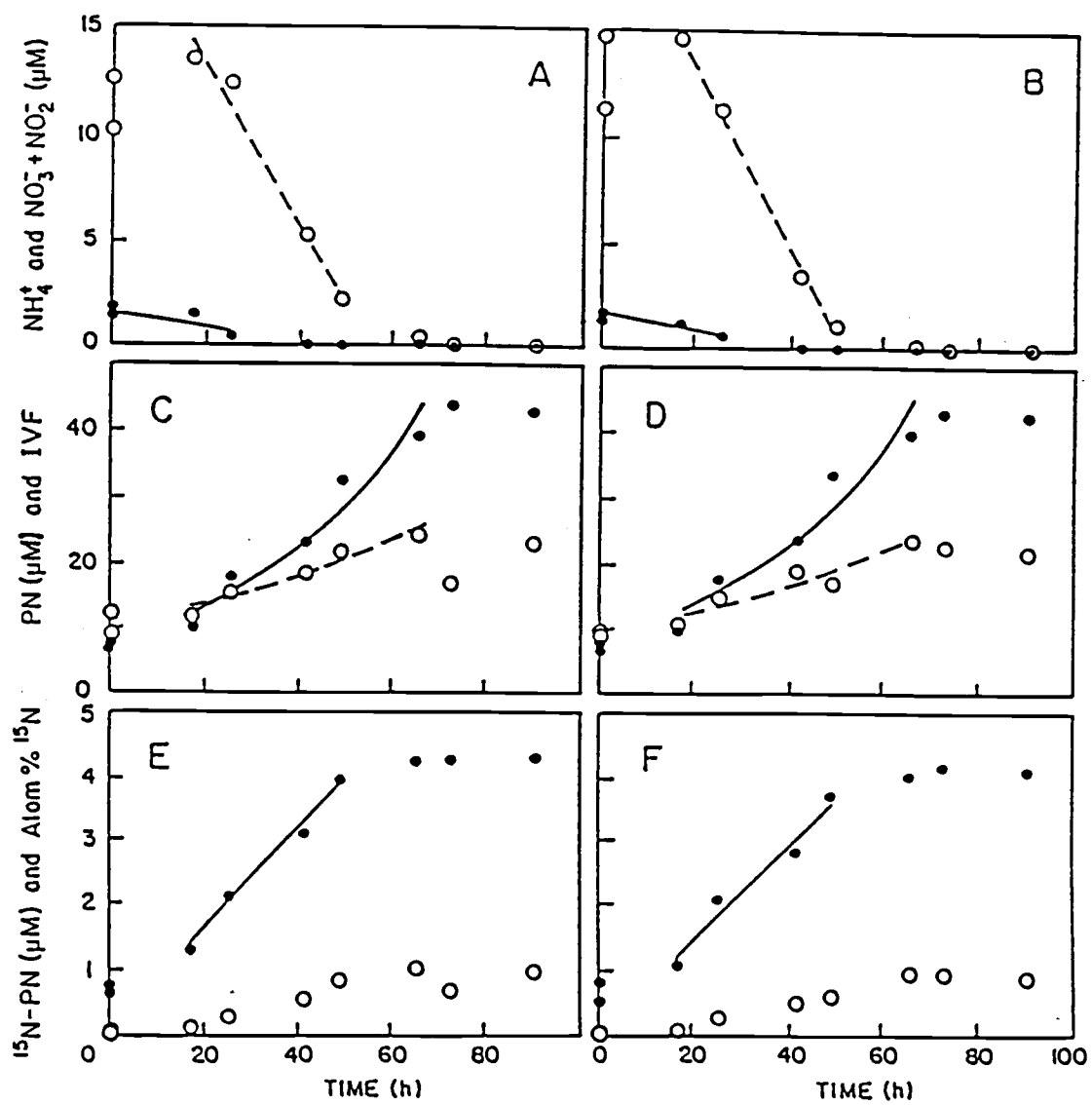


Figure III.4

Figure III.5. Changes in nutrient, biomass and particulate atom % ^{15}N in NH_4^+ -supplemented cultures of Experiment 3 (as in Figure III.1) (see page 28).

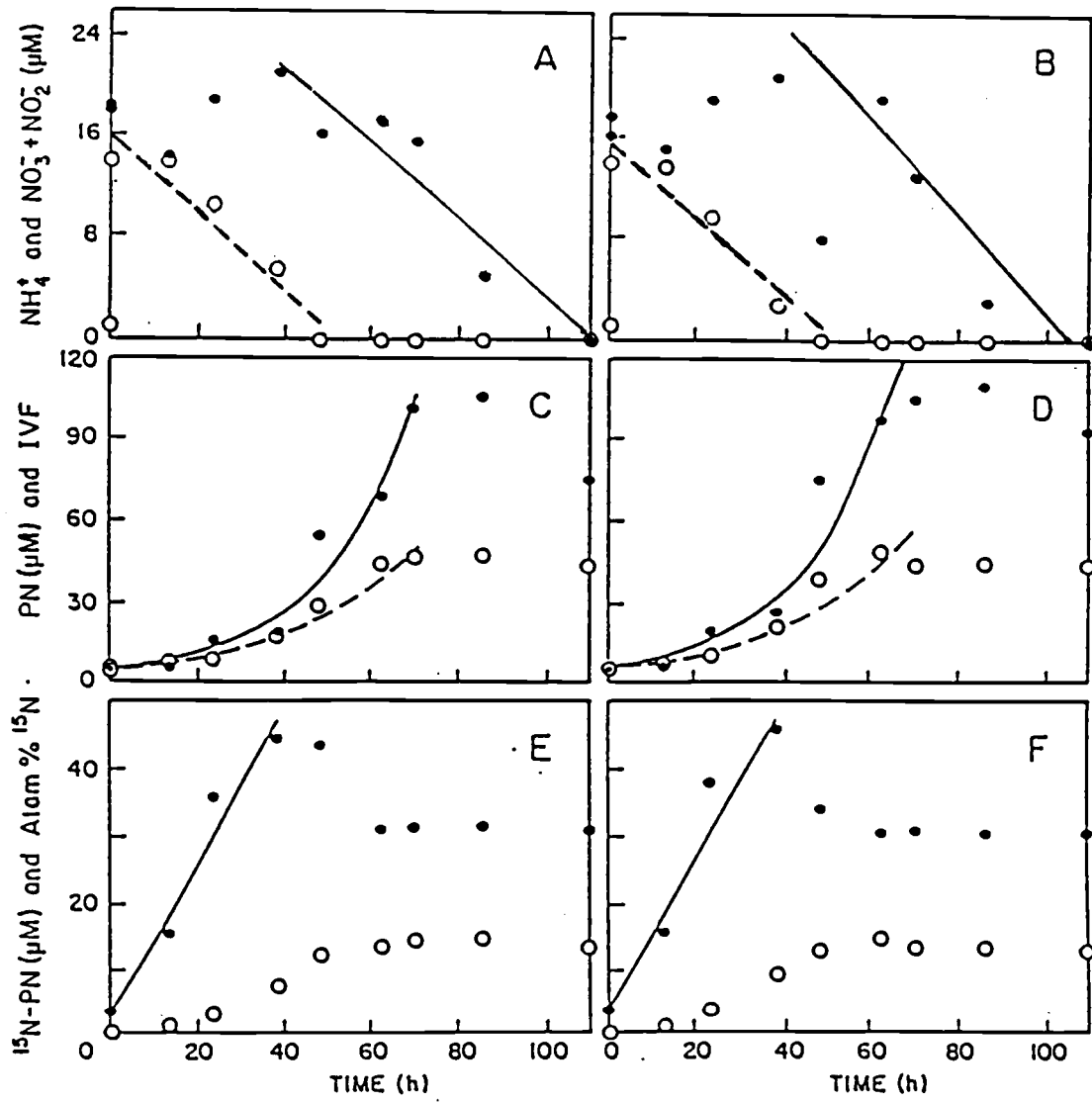


Figure III.5

Figure III.6. Changes in nutrient, biomass and particulate atom % ^{15}N in NO_3^- -supplemented cultures of Experiment 3 (as in Figure III.2) (see page 30).

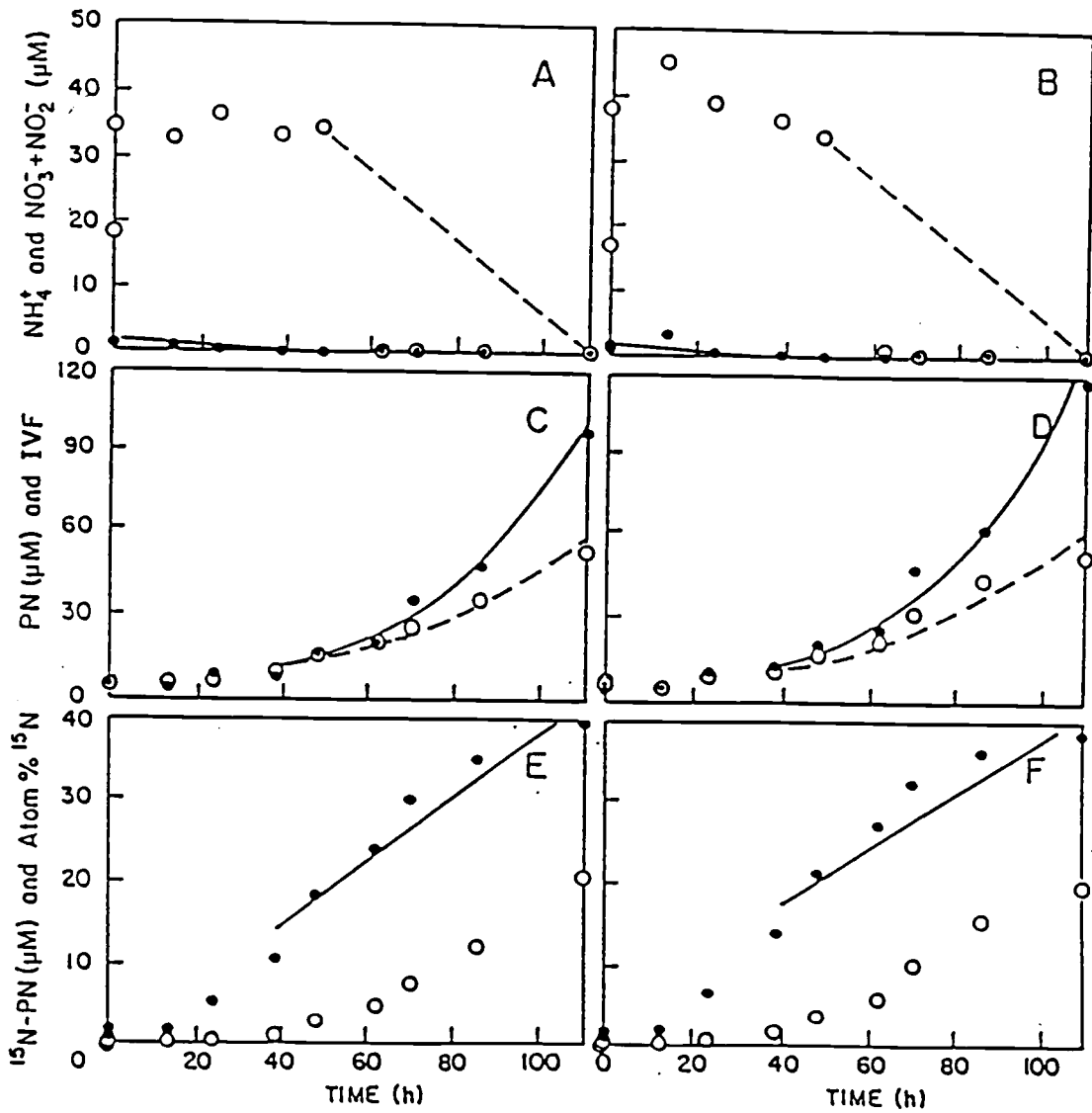


Figure III.6

show a close correspondence to rates of ^{15}N assimilation which ranged from 0.139-0.712 $\mu\text{M h}^{-1}$ (Table III.2). Nitrogen-specific depletion rates for supplemented nutrients ranged from 0.008-0.129 h^{-1} , while in the absence of a supplement, rates ranged from 0.002-0.023 h^{-1} (Tables III.3, III.4). Likewise, depletion rates normalized to IVF ranged from 0.007-0.116 $\mu\text{M h}^{-1} \text{FU}^{-1}$ in the respectively supplemented cultures, and from 0.003-0.014 $\mu\text{M h}^{-1} \text{FU}^{-1}$ (Tables III.3, III.4) when the nutrient was not supplemented. In both cases, the higher rates for the supplemented cultures simply reflects the effect of nutrient concentration on depletion rates.

Rate discrepancies in Experiment 2 indicate excretion of DON and/or NH_4^+ regeneration (Table III.2). In the NH_4^+ -supplemented cultures, NH_4^+ depletion was only 31% of $^{15}\text{N-NH}_4^+$ assimilation ($P < 0.05$), and changes in the atom % ^{15}N of the NH_4^+ indicated that the discrepancy was due to regeneration. For the NO_3^- -supplemented cultures, rates of NO_3^- depletion were 89% faster than the rates of NO_3^- assimilation which indicated DON excretion (Table III.2).

In Experiment 3, there was a dramatic decrease in NO_3^- (Figure III.6a, b) between 48 and 62 h ($2.377 \pm 0.065 \mu\text{M h}^{-1}$, Table III.4) for the NO_3^- -supplemented cultures. This decrease is about 4 times faster than the corresponding increase in PN ($0.594 \pm 0.004 \mu\text{M h}^{-1}$, Table III.2), which was constant from 39 to 110 h. However, $^{15}\text{N-NO}_3^-$ was constant during 48 to 110 h (Fig. III.6e, f), indicating that NO_3^- should decrease at a constant rate during this interval. Furthermore, the average rate of decrease in NO_3^- for the period 48-110 h is $0.584 \pm 0.007 \mu\text{M NO}_3^-$ (Table III.4), which is close to the rate of PN increase. Nutrient concentrations between 62 and 80 h were probably underestimated, thus NO_3^- depletion was assumed to occur between 48 and 110 h.

Table III.2. Changes in nutrient and PN concentrations compared with rates of nitrogen assimilation (averaged for paired cultures).

Exp't. / Treatment	ΔNutrients ($\mu\text{M h}^{-1}$) SE	ΔPN ($\mu\text{M h}^{-1}$) SE	Assimilation Rate ($\mu\text{M h}^{-1}$) SE	ΔNutrients: Assimilation Rate	ΔPN: Assimilation Rate
Experiment 1					
Ammonium Supplemented Cultures					
	0.211 \pm 0.021	0.154 \pm 0.049	0.194 \pm 0.006	1.088	0.794
Nitrate Supplemented Cultures					
	0.107 \pm 0.008	0.127 \pm 0.011	0.139 \pm 0.001	0.770	0.914
Experiment 2					
Ammonium Supplemented Cultures					
	0.166 \pm 0.018	0.146 \pm 0.072	0.543 \pm 0.049	0.306	0.269
Nitrate Supplemented Cultures					
	0.401 \pm 0.045	0.244 \pm 0.052	0.212 \pm 0.005	1.892	1.151
Experiment 3					
Ammonium Supplemented Cultures					
	0.389 \pm 0.007	0.732 \pm 0.194	0.236 \pm 0.040	1.572	3.102
Nitrate Supplemented Cultures					
	0.584 \pm 0.007	0.606 \pm 0.013	0.712 \pm 0.006	0.820	0.851

Table III.3. Changes in NH_4^+ concentration normalized to PN and IVF (averaged for paired cultures).

Exp't. / Treatment	ΔNH_4^+ ($\mu\text{M h}^{-1}$) SE	PN_{nd} (μM) SE	$\Delta\text{NH}_4^+/\text{PN}$ (h^{-1}) SE	IVF_{nd} (FU) SE	$\Delta\text{NH}_4^+/\text{IVF}$ ($\mu\text{M h}^{-1}\text{FU}^{-1}$) SE
Experiment 1					
Ammonium Supplemented Cultures (0-40 h)					
	0.211 \pm 0.021	11.49 \pm 0.77	0.018 \pm 0.003	11.87 \pm 0.54	0.018 \pm 0.003
Nitrate Supplemented Cultures (0-49 h)					
	0.023 \pm 0.000	10.93 \pm 1.64	0.002 \pm 0.000	10.06 \pm 0.00	0.002 \pm 0.000
Experiment 2					
Ammonium Supplemented Cultures (0-25 h)					
	0.166 \pm 0.018	14.35 \pm 1.66	0.012 \pm 0.000	16.75 \pm 0.45	0.010 \pm 0.001
Nitrate Supplemented Cultures (0-25 h)					
	0.037 \pm 0.004	11.41 \pm 0.42	0.003 \pm 0.000	11.05 \pm 0.01	0.003 \pm 0.000
Experiment 3					
Ammonium Supplemented Cultures (13-38 h)					
	0.389 \pm 0.007	11.66 \pm 1.43	0.034 \pm 0.004	14.87 \pm 3.21	0.027 \pm 0.005
Nitrate Supplemented Cultures (0-39 h)					
	0.027 \pm 0.005	7.61 \pm 0.87	0.004 \pm 0.001	7.57 \pm 1.14	0.004 \pm 0.001

Note: FU - Fluorescence units in calibrated fluorometer.

Table III.4. Changes in NO_3^- concentration normalized to PN and IVF (averaged for paired cultures).

Exp't./ Treatment	ΔNO_3^- ($\mu\text{M h}^{-1}$) SE	PN _{nd} (μM) SE	$\Delta\text{NO}_3^-/\text{PN}$ (h^{-1}) SE	IVF _{nd} (FU) SE	$\Delta\text{NO}_3^-/\text{IVF}$ ($\mu\text{M h}^{-1}\text{FU}^{-1}$) SE
Experiment 1					
Ammonium Supplemented Cultures (40-64 h)					
	0.083 ± 0.000	16.17 ± 0.06	0.005 ± 0.000	27.51 ± 0.21	0.003 ± 0.000
Nitrate Supplemented Cultures (49-89 h)					
	0.110 ± 0.005	13.27 ± 0.45	0.008 ± 0.001	16.22 ± 0.99	0.007 ± 0.001
Experiment 2					
Ammonium Supplemented Cultures (16-41 h)					
	0.411 ± 0.055	19.51 ± 0.93	0.021 ± 0.002	31.16 ± 1.52	0.013 ± 0.001
Nitrate Supplemented Cultures (16-49 h)					
	0.401 ± 0.045	15.98 ± 1.05	0.025 ± 0.004	20.79 ± 0.31	0.019 ± 0.002
Experiment 3					
Ammonium Supplemented Cultures (62-41 h)					
	0.306 ± 0.014	45.91 ± 0.12	0.007 ± 0.001	98.99 ± 8.27	0.003 ± 0.000
Nitrate Supplemented Cultures (26-48 h, 48-62 h, 48-110 h)					
	0.147 ± 0.072	11.45 ± 1.14	0.013 ± 0.005	12.53 ± 2.28	0.012 ± 0.004
	2.377 ± 0.061	18.86 ± 0.86	0.129 ± 0.009	20.78 ± 3.43	0.116 ± 0.023
	0.584 ± 0.007	33.83 ± 2.09	0.017 ± 0.001	54.11 ± 8.46	0.011 ± 0.002

Note: FU - Fluorescence units in the calibrated fluorometer.

B. Changes in Biomass

The specific growth constants for in vivo fluorescence (K_{rf}) were always higher than the specific growth constants for PN (K_{pn}) within each experiment. The ratio $K_{rf}:K_{pn}$ in the three experiments ranged from 1.34-5.71 (Table III.5). The faster doubling of IVF could be due to the increase of the cellular chlorophyll content, a faster replication of autotrophs and/or incomplete recovery of PN during filtration.

The coefficients of determination (r^2) indicated good fit of data for all linear slopes of PN increases except for the NH_4^+ -supplemented cultures of Experiment 2 ($r^2=0.575$), and for all exponential growth constants (Table III.5). In NH_4^+ -supplemented cultures of Experiment 3, increases in PN between 0 and 70 h were well described by an exponential curve and two linear equations over the periods 0-38 h and 38-70 h. Since, first order rate constants could be generally used to describe PN increase, changes in nutrient and PN concentrations can be directly compared.

C. Comparison Between Changes in Inorganic and Particulate Nitrogen

i. During NH_4^+ Depletion

In the NH_4^+ -supplemented cultures of the first two experiments (Table III.2) the corresponding decreases in NH_4^+ and increases in PN were similar ($P>0.005$). In the NH_4^+ -supplemented cultures of Experiment 3, increases in PN exceeded decreases in NH_4^+ suggesting uptake of $\sim 8.6 \mu M$ DON. As shown by mass balance calculations, however, this discrepancy may have been due to overestimation of PN concentrations (see below).

In the NO_3^- -supplemented cultures of the first experiment, NH_4^+ depletion was similar ($P>0.05$) to PN increase. In the last

Table III.5. Linear increases in biomass and exponential growth constants. Coefficients of determination are enclosed in parentheses (averaged for paired cultures).

Exp't./ Treatment	Linear Increase		Exponential Increase		K_{rf}/K_{pa}
	m ($\mu M h^{-1}$)	SE	K_{pa} (h^{-1})	K_{rf} (h^{-1})	
Experiment 1					
Ammonium Supplemented Cultures (0-49 h)					
	0.189 ± 0.013 (0.953)		0.014 ± 0.003 (0.962)	0.034 ± 0.001 (0.894)	2.43
Nitrate Supplemented Cultures (49-89 h)					
	0.107 ± 0.008 (0.820)		0.010 ± 0.002 (0.925)	0.016 ± 0.001 (0.901)	1.60
Experiment 2					
Ammonium Supplemented Cultures (16-41 h)					
	0.146 ± 0.072 (0.575)		0.027 ± 0.001 (0.995)	0.045 ± 0.002 (0.790)	1.67
Nitrate Supplemented Cultures (16-45 h)					
	0.401 ± 0.045 (0.863)		0.014 ± 0.000 (0.908)	0.080 ± 0.003 (0.968)	5.71
Experiment 3					
Ammonium Supplemented Cultures					
(0-38 h, growth constants are for 0-70 h)					
	0.732 ± 0.194 (0.886)		0.035 ± 0.001 (0.963)	0.047 ± 0.001 (0.948)	1.34
(38-70 h)					
	0.854 ± 0.147 (0.857)				
Nitrate Supplemented Cultures (39-110 h)					
	0.594 ± 0.004 (0.970)		0.022 ± 0.000 (0.950)	0.031 ± 0.001 (0.974)	1.41

two experiments, PN increases were 4-7 times faster than the corresponding rates of NH_4^+ depletion (see Appendix, Table A.14). This suggests that 77-86% of the PN increase during NH_4^+ depletion was due to uptake of NO_3^- or DON. Alternatively, these discrepancies could be due to systematic errors in measuring PN.

ii. During NO_3^- Depletion

Increases in PN were similar to the rates of NO_3^- depletion in the NH_4^+ -supplemented cultures of the first 2 experiments (see Appendix, Table A.15). In the NH_4^+ -supplemented cultures of the last experiment, increases in PN during NO_3^- depletion were only 43% ($P < 0.05$) of the nutrient decrease suggesting that NO_3^- was converted to DON. Increase of DON in these cultures was estimated to average $9.74 \mu\text{M}$ during NO_3^- depletion.

In the NO_3^- -supplemented cultures of Experiments 1 and 3, increase of PN was similar to NO_3^- depletion ($P > 0.05$). For the second experiment, increase of PN was only 62% of NO_3^- depletion (see Appendix, Table A.15). For these NO_3^- -supplemented cultures, calculated increase in DON was $5.18 \mu\text{M}$.

D. Rates of Ammonium Regeneration

Rates of increases in PN and nutrient assimilation were generally similar ($P > 0.05$) except in the NH_4^+ -supplemented cultures of Experiments 2 and 3. Discrepancies between these rates indicate either NH_4^+ regeneration, DON excretion or systematic errors in estimating PN. In Experiment 2, the slower rates of increase in PN relative to the rates of $^{15}\text{N-NH}_4^+$ assimilation, and the significant decrease in atom % $^{15}\text{N-NH}_4^+$ with time (see Appendix, Table A.7) strongly indicate NH_4^+ regeneration. From the change in the atom % ^{15}N of NH_4^+ , a mean rate of $0.527 \mu\text{M NH}_4^+ \text{ h}^{-1}$ was determined. Regeneration was also estimated from the difference between rates

of NH_4^+ depletion and ^{15}N assimilation, and averaged $0.377 \mu\text{M h}^{-1}$. Thus, the rate of regeneration in these cultures was 69-97% of the rate of ^{15}N assimilation, indicating that a major fraction of the assimilated NH_4^+ was being regenerated.

No change in the atom % $^{15}\text{NH}_4^+$ was observed in the third experiment. Thus, the discrepancies between increases in PN and nutrient assimilation was not due to NH_4^+ regeneration. Mass balance calculations indicate that overestimation of PN rather than DON excretion caused the rate discrepancies in these cultures (see below).

4. Mass Balance

Total nitrogen and total ^{15}N were relatively constant during the incubations (Table III.6 and Appendix, Table A.20). Hence, any differences between the changes in inorganic nitrogen and PN indicate changes in DON, or systematic errors in PN, NH_4^+ or NO_3^- estimates.

Discrepancies between changes in PN and nutrient concentrations were apparent (Table III.7), but were generally not statistically significant ($P > 0.05$). Thus, changes in DON have to be verified from differences in rate measurements. In the first two experiments, the ratio $\Delta\text{PN}/\Delta\text{nutrient}$ ranged from 0.357-0.972 at the end of incubation but the discrepancies were not statistically significant ($P > 0.05$). Maximum increases in PN were also similar ($P > 0.05$) to final increases.

In the last experiment, the changes in PN were consistently higher ($P < 0.05$) than the changes in inorganic nitrogen. Increases in PN exceeded the decrease in nutrients by 21-40% in the NH_4^+ -supplemented cultures (Table III.7). Changes in ^{15}N -PN were 21-35% higher than the depleted inorganic ^{15}N (see Appendix, Table A.21).

Table III.6. Summary of mean total nitrogen and the range of propagated errors (PE) associated with replicates (μM).

Exp't./Treatment	Mean TN	SD	Range of PE
Experiment 1 (data from Table A2)			
Ammonium Supplemented			
Control	37.49	8.54	5.88 - 13.43
+ Diatom	35.30	6.59	4.94 - 11.95
Nitrate Supplemented			
Control	32.94	7.90	5.22 - 12.16
+ Diatom	32.30	6.91	4.98 - 11.75
Experiment 2 (data from Table A6)			
Ammonium Supplemented			
Control	53.79	7.12	11.58 - 26.87
+ Diatom	56.32	11.96	10.45 - 31.59
Nitrate Supplemented			
Control	54.27	4.44	14.14 - 22.13
+ Diatom	56.07	5.07	9.97 - 21.87
Experiment 3 (data from Table A10)			
Ammonium Supplemented			
Control	54.46	5.42	5.97 - 16.86
+ Diatom	60.90	4.92	5.91 - 23.65
Nitrate Supplemented			
Control	65.73	3.52	7.00 - 18.45
+ Diatom	67.44	3.84	5.85 - 16.21

Table III.7. Changes in nutrient concentrations and biomass.

Exp't./ Treatment	Incubation Nutrient Concentration (μM) SE		Increase in Particulate N (μM)				PN Nut. Conc.	
	Max	SE	Final	SE	Max	Final		
Experiment 1								
Ammonium Supplemented								
Control	11.10 \pm 1.53		10.10 \pm 2.04		8.43 \pm 2.62		0.910	0.759
+ Diatom	10.20 \pm 1.32		7.17 \pm 3.36		7.00 \pm 3.09		0.703	0.686
Nitrate Supplemented								
Control	6.68 \pm 0.87		6.49 \pm 2.28		6.49 \pm 2.28		0.972	0.972
+ Diatom	6.38 \pm 1.60		5.54 \pm 1.43		5.54 \pm 1.43		0.868	0.868
Experiment 2								
Ammonium Supplemented								
Control	16.89 \pm 3.34		15.41 \pm 5.40		6.03 \pm 7.43		0.912	0.357
+ Diatom	14.85 \pm 3.43		16.05 \pm 3.93		9.55 \pm 3.87		1.081	0.643
Nitrate Supplemented								
Control	13.99 \pm 3.24		12.20 \pm 4.59		10.95 \pm 5.07		0.872	0.783
+ Diatom	16.37 \pm 3.23		13.78 \pm 3.82		11.90 \pm 4.02		0.842	0.727
Experiment 3								
Ammonium Supplemented								
Control	32.17 \pm 1.03		42.90 \pm 3.78		38.96 \pm 3.59		1.334	1.211
+ Diatom	31.40 \pm 1.18		43.93 \pm 4.45		39.39 \pm 3.91		1.399	1.254
Nitrate Supplemented								
Control	35.94 \pm 1.34		48.37 \pm 3.28		48.37 \pm 3.28		1.346	1.346
+ Diatom	39.18 \pm 1.32		46.32 \pm 9.45		46.32 \pm 9.45		1.182	1.182

In the NO_3^- -supplemented cultures, the increase of PN was 18-35% higher than the initial amount of nutrients (Table III.7), and the increase in labeled PN (see Appendix, Table A.21) was 7-26% higher than the initial ^{15}N spikes. Because there was no additional ^{15}N source, these discrepancies were probably due to errors in estimates of PN.

Possible effects of systematic errors in estimates of increases in PN and nutrient uptake rates need to be assessed. If PN was overestimated by as much as 35%, assimilation rates in Experiment 3 would range from $0.072\text{-}0.093 \mu\text{M NH}_4^+ \text{ h}^{-1}$ and $0.246\text{-}0.253 \mu\text{M NO}_3^- \text{ h}^{-1}$. These values would still be comparable to rates reported in the literature.

5. Comparison Between Rates of Nutrient Depletion, Growth Constants and Nutrient Concentrations

Ammonium depletion seemed to be dependent on the initial concentration of the nutrient (Fig. III.7). Nitrogen-specific and IVF-normalized rates of NH_4^+ depletion were faster in NH_4^+ than in NO_3^- -supplemented cultures. Initial NH_4^+ concentration was closely correlated with the nitrogen-specific rates of NH_4^+ depletion ($r^2=0.976$, $n=12$) and NH_4^+ depletion rates normalized to IVF ($r^2=0.988$, $n=12$). The reason behind such a correlation is not known and should be investigated.

All four cultures within each experiment had similar IVF-normalized and nitrogen-specific rates of NO_3^- depletion (Table III.4). There were large differences in rates for each water collection, indicating that the rates of NO_3^- uptake could depend on the microbial assemblage. The IVF-normalized and nitrogen-specific rates of NO_3^- were apparently independent of initial NO_3^- concentration (Fig. III.8). Generally, NH_4^+ -supplemented and

Figure III.7. Rates of NH_4^+ depletion normalized to particulate nitrogen and in vivo fluorescence as a function of NH_4^+ concentration. A. Nitrogen-specific rates of NH_4^+ depletion (h^{-1}). B. Rates of NH_4^+ depletion normalized to in vivo fluorescence ($\mu\text{M NH}_4^+ \text{h}^{-1}$ fluorescence unit $^{-1}$). Ammonium-supplemented cultures are represented as squares (control) and crosses (+ Diatom), and NO_3^- -supplemented cultures are represented as diamonds (control) and triangles (+ Diatom) (see page 43).

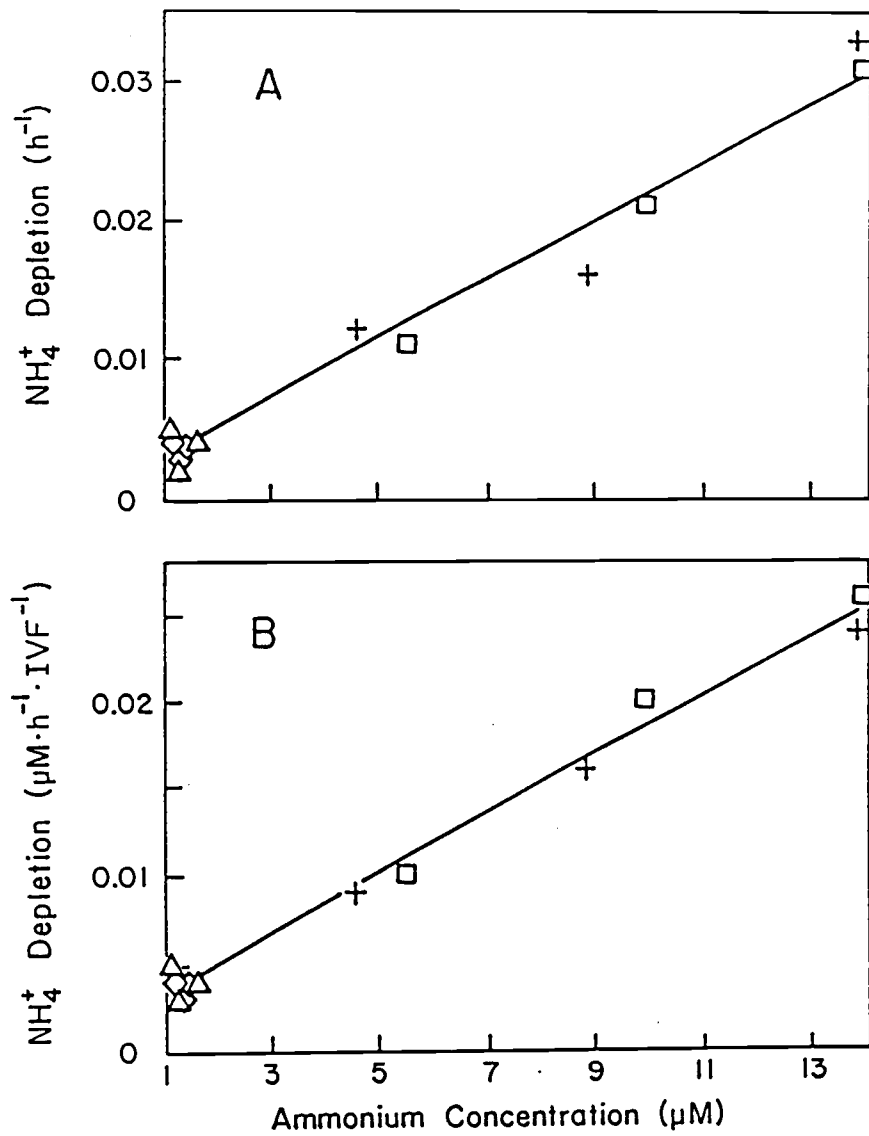


Figure III.7

Figure III.8. Rates of nitrate depletion normalized to particulate nitrogen and in vivo fluorescence as a function of NO_3^- concentration. A. Nitrogen-specific rates of NO_3^- depletion (h^{-1}). B. Rates of NO_3^- depletion normalized to in vivo fluorescence ($\mu\text{M NO}_3^- \text{ h}^{-1}$ fluorescence unit $^{-1}$). Ammonium-supplemented cultures are represented as squares (control) and crosses (+ Diatom), and NO_3^- -supplemented cultures are represented as diamonds (control) and triangles (+ Diatom) (see page 45).

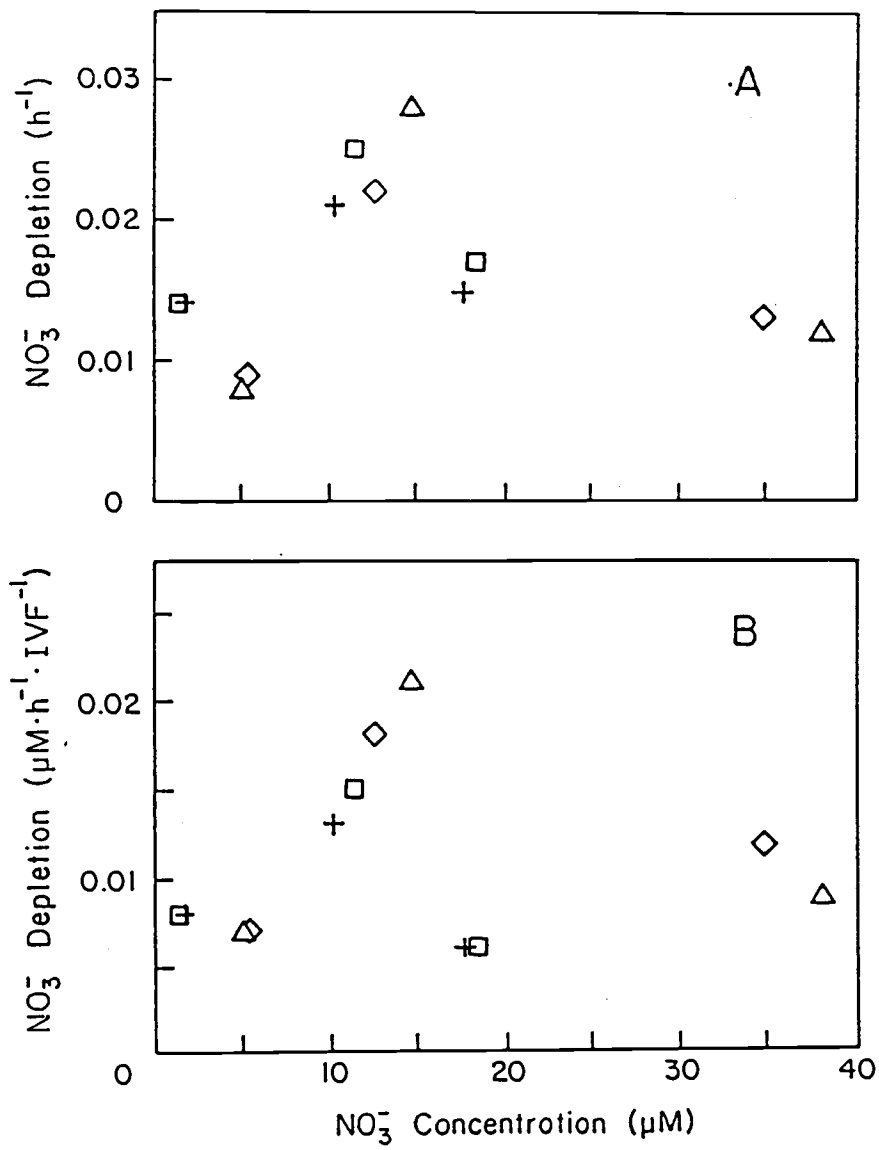


Figure III.8

NO_3^- -supplemented cultures had similar nitrogen-specific and IVF normalized rates of NO_3^- depletion ($P > 0.005$). Thus, initial NO_3^- concentration seem to have no effect on the rates of NO_3^- depletion.

The growth constants K_{pn} in the NH_4^+ -supplemented cultures were closely correlated ($r^2 = 0.767$, $n = 6$) with nitrogen-specific rates of NH_4^+ depletion (Fig. III.9.a). The K_{pn} in NO_3^- -supplemented cultures was not compared with the corresponding rate of NH_4^+ depletion because periods of NH_4^+ and NO_3^- decrease were not distinct. In these cultures, increases in PN during the periods of NH_4^+ decrease could have been partly due to NO_3^- or DON uptake. In contrast to K_{pn} , K_{rf} was poorly correlated with the nitrogen-specific rates of NH_4^+ depletion ($r^2 = 0.007$, $n = 12$). Nitrogen-specific rates of NO_3^- depletion were not closely correlated with K_{pn} (Fig. III.9.b), but were correlated ($r^2 = 0.726$, $n = 12$) with K_{rf} (Fig. III.9.c). The rates of depletion for NH_4^+ and NO_3^- were correlated with different growth constants, suggesting that different fractions of the microplankton are responsible for the uptake of each nutrient.

Figure III.9. Nitrogen-specific rates of nutrient depletion as a function of exponential growth constants.

A. Nitrogen-specific rates of NH_4^+ depletion (h^{-1}).

B and C. Nitrogen-specific rate of NO_3^- depletion (h^{-1}). Ammonium-supplemented cultures are

represented as squares (control) and crosses

(+ Diatom), and NO_3^- -supplemented cultures are

represented as diamonds (control) and triangles

(+ Diatom) (see page 48).

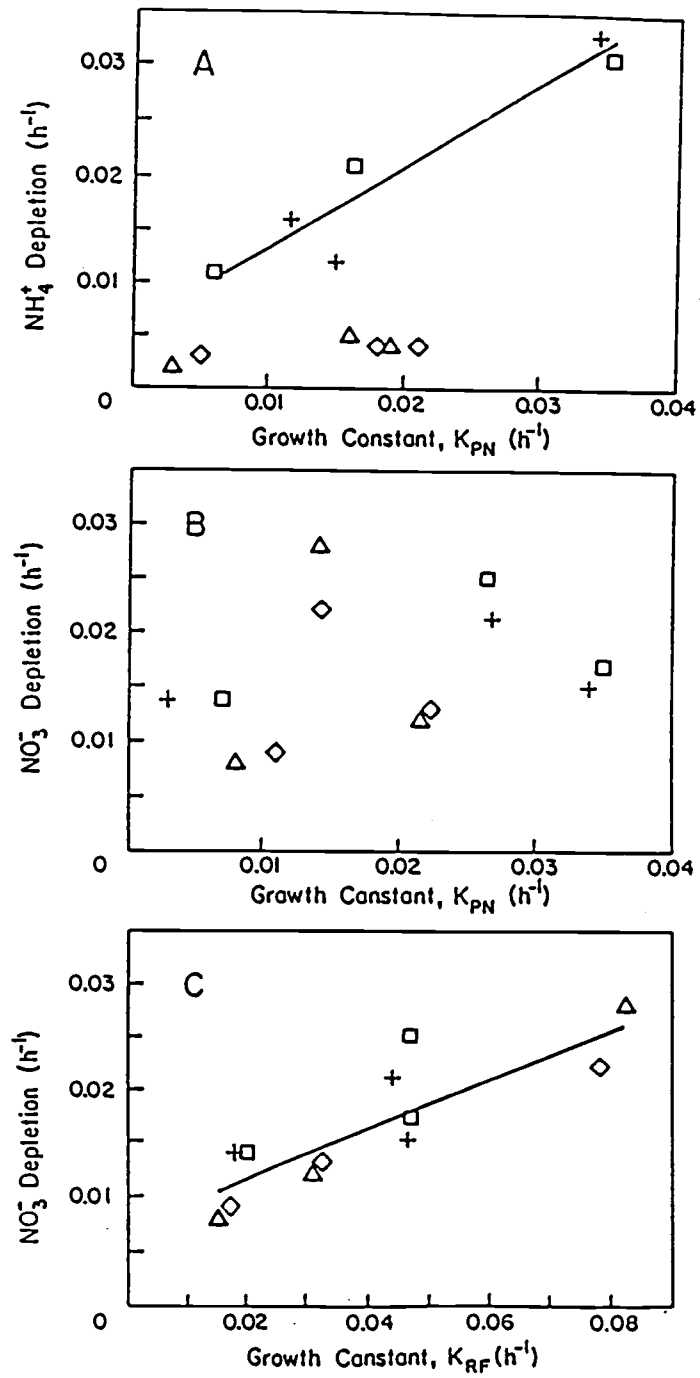


Figure III.9

Chapter IV

DISCUSSION

Statistically similar rates of nutrient depletion and assimilation, which were observed in some of these cultures, indicate that most of the inorganic nutrient was assimilated into particulate nitrogen. When discrepancies between these rates occurred, they can be attributed to DON excretion and NH_4^+ regeneration. Comparisons of nitrogen-specific rates of nutrient depletion and exponential growth constants suggest that uptake of NO_3^- is most closely correlated with increases in autotrophic biomass, while uptake of NH_4^+ is better correlated with general increases in particulate nitrogen. In the following sections, the hypotheses presented in Chapter 1 are examined in light of the experimental results, the distribution of nitrogen biomass is estimated, and the general flow of nitrogen through the microbial community is discussed.

1. Assessment of Original Hypotheses

- A. Excretion of Dissolved Organic Nitrogen

Excretion of DON occurred in two of the six experiments conducted and represented 39-57% of the inorganic nitrogen initially supplied. Reports in the literature suggest that 10-95% of inorganic nitrogen utilized may be excreted as DON (Table IV.1). Some of these estimates, however, have been dismissed as overestimates resulting from use of high vacuum pressures and rinsing procedures (Fuhrman and Bell 1985, Goldman and Dennett 1985). In this study such potential artifacts were minimized by

Table IV.1. Review of literature reporting "missing" nitrogen.

Reference	Unrecovered N (%)
Sörensson et al. (1988)	35-47
Kokkinakis and Wheeler (1987)	15
Dugdale and Wilkerson (1996)	23-34
Slawyk and Rodier (1986)	56
Laws et al. (1984)	40
Chan and Campbell (1978)	60
Schell (1974)	> 10

eliminating the rinsing step and maintaining low filtration pressures (50 mm Hg).

Although my results suggest that DON excretion does occur, this apparent release of DON may actually represent uptake of inorganic nitrogen by organisms that pass through a GF/F filter. Picoplankton (organisms < 1 μm) comprise 29-56% of total microbial biomass (Harrison and Wood 1988), but to a certain extent pass through filters normally used in assimilation studies (Lee and Fuhrman 1987).

B. Ammonium Assimilation by Autotrophic and Heterotrophic Organisms

Nitrogen-specific ammonium uptake rates were associated with the exponential increase in PN, but not with the exponential increase in relative fluorescence. This relation suggests that depletion of NH_4^+ may be associated with growth of both autotrophs and heterotrophs. In previous studies (Wheeler and Kirchman 1986, Harrison and Wood 1988), the picoplankton size fraction showed a preferential use of NH_4^+ , indicating that heterotrophic bacteria can utilize a significant fraction of NH_4^+ . My results are consistent with uptake of NH_4^+ by both autotrophic and heterotrophic organisms.

Mean rates of NH_4^+ assimilation in this study were higher than in most short-term low nutrient incubations (Table IV.2) but similar to assimilation rates reported for eutrophic environments such as the Carmans River estuary (Carpenter and Dunham 1985) and Chesapeake Bay (Glibert et al. 1982). For past studies reviewed here, rates of NH_4^+ assimilation were correlated ($r^2=0.701$, $n=13$) with mean PN (Fig. IV.1.A).

Table IV.2. Mean specific and absolute uptake rates from the literature.

Region	Absolute Rate (nM h ⁻¹)	Specific Rate (h ⁻¹)	PN (μM)	Reference
Ammonium Uptake				
Yaquina Bay	324 ± 174	0.026 ± 0.009	11.7 ± 2.3	this study
Washington/ Oregon	90 ± 66	0.018 ± 0.008	5.8 ± 5.4	Kokkinakis and Wheeler (1987)
Benguela Upwelling	56 ± 42	0.007 ± 0.005	7.0 ± 2.0	Probyn (1987)
Baltic Sea	52 ± 11	0.020 ± 0.003	2.6 ± 0.2	Sörensson and Sahlsten (1987)
Peru	129 ± 79	0.029 ± 0.005	4.5 ± 3.0	Dugdale and Wilkerson (1986)
Sapelo Island	64 ± 23	0.007 ± 0.002	9.7 ± 4.9	Wheeler and Kirchman (1986)
Gulf Stream	5 ± 2	0.005 ± 0.008	1.0 ± 0.5	ditto
Carmans River Estuary	229 ± 90	0.010 ± 0.004	22.6 ± 1.8	Carpenter and Dunham (1985)
N. Pacific	12 ± 5	0.331 ± 0.016	0.4 ± 0.2	Laws et al. (1985)
Sargasso Sea	6 ± 6	0.009 ± 0.003	0.5 ± 0.1	Glibert et al. (1982)
Chesapeake Bay	659 ± 715	0.025 ± 0.015	21.3 ± 15.4	ditto
Nitrate Uptake				
Yaquina Bay	352 ± 277	0.015 ± 0.006	20.1 ± 8.7	this study
Washington/ Oregon	402 ± 409	0.061 ± 0.039	5.8 ± 5.4	Kokkinakis and Wheeler (1987)
Benguela Upwelling	278 ± 113	0.047 ± 0.037	7.0 ± 2.0	Probyn (1987)
Baltic Sea	6 ± 1	0.002 ± 0.000	2.6 ± 0.2	Sörensson and Sahlsten (1987)
Peru Upwelling	121 ± 149	0.022 ± 0.017	4.5 ± 3.0	Dugdale and Wilkerson (1986)
Carmans River Estuary	325 ± 304	0.014 ± 0.041	22.6 ± 1.8	Carpenter and Dunham (1985)

Figure IV.1. Rates of nutrient assimilation as a function of particulate nitrogen. A. Ammonium. B. Nitrate. Data taken from the literature (see Table IV.2). Hyperbolic curve in B was defined by:
$$\text{NO}_3^- \text{ assimilation} = 0.369 - (0.641/\text{PN})$$

(see page 54).

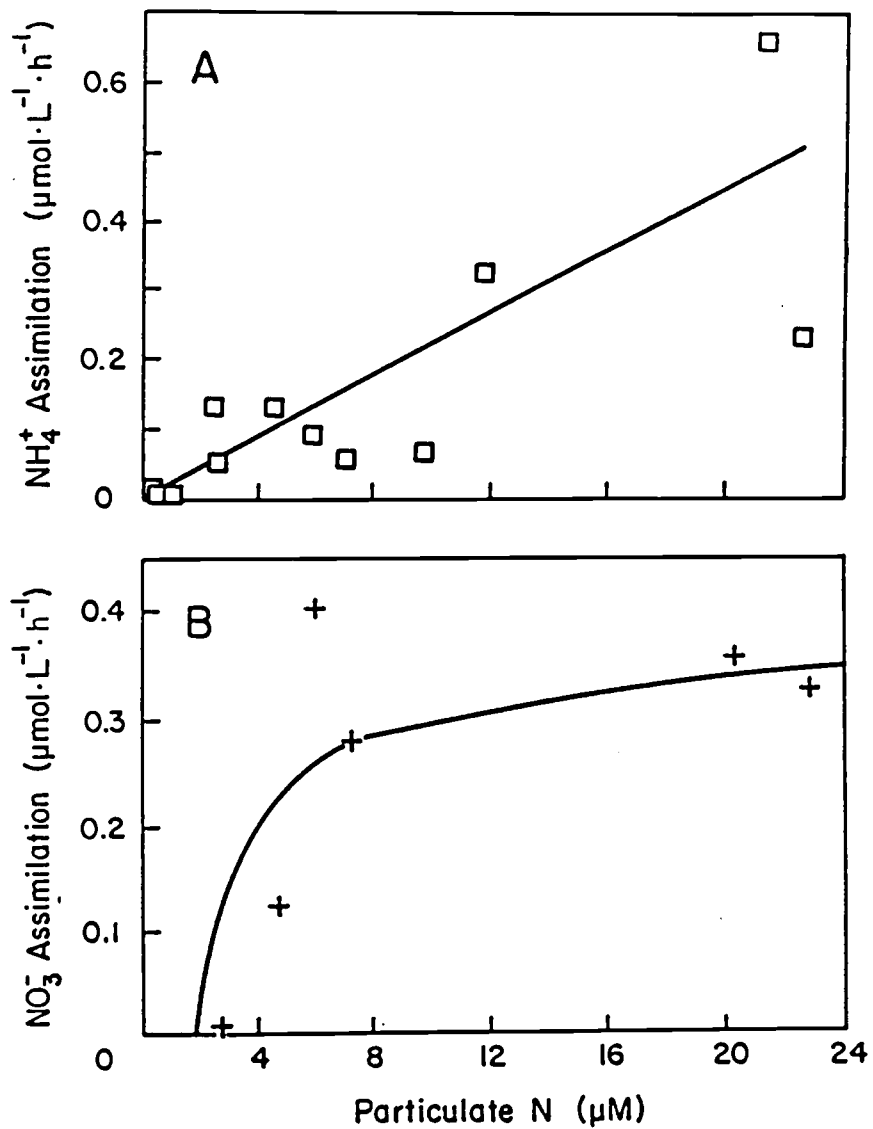


Figure IV.1

C. Nitrate Assimilation by Autotrophic Organisms

Nitrogen-specific nitrate uptake rates were positively correlated with the exponential increase in relative fluorescence, but not with the exponential increase in PN. This suggests that most NO_3^- uptake is associated with autotrophic organisms and that autotrophic biomass is a variable fraction of total particulate nitrogen.

The mean rate of NO_3^- assimilation in this study was similar to those measured in other eutrophic environments and was higher than those calculated for the Baltic Sea (Table IV.2). The hyperbolic relationship between PN concentration and NO_3^- assimilation rates (Fig. IV.1.b) may result from a systematic variation in relative autotrophic biomass. For example, Kokkinakis and Wheeler (1987) found a hyperbolic relationship between Chl:PN and NO_3^- in coastal water off Oregon. Thus, the highest rates of NO_3^- assimilation would be expected when PN and Chl/PN are both maximized.

2. Flow of Nitrogen Through the Microplankton

Uptake of inorganic nitrogen accounted for most of the nitrogen flux into particulate nitrogen. Nitrogen was released from the particulate nitrogen pool by NH_4^+ regeneration and excretion of DON. Excretion of DON occurred during two experiments, and comprised up to 57% of initial inorganic nitrogen in the cultures. Release of dissolved nitrogen from the particulate nitrogen pool as NH_4^+ and as DON are both important processes. The relative importance of each type of release is variable and may depend on the composition of the microbial assemblage and nutrient regime.

3. Conclusions

Results presented here indicate that autotrophic microorganisms play a major role in assimilating NO_3^- . Assimilation of NH_4^+ , on the other hand, is better correlated with total microbial biomass (autotrophs and heterotrophs). Release of DON does occur, but could not be distinguished from bacterial assimilation in this study.

The relative roles of the different microbial factions in the marine environment will be better understood if biomass-specific rates of heterotrophic and autotrophic activities are compared. Heterotrophic microorganisms play important roles in certain processes which were previously believed to be dominated by phytoplankton. The contribution of heterotrophs to total NH_4^+ uptake in some studies have been estimated, and were found to be potentially significant. Since microbial composition varies, comparison between heterotrophic and autotrophic uptake of inorganic nitrogen should be normalized to the biomass of each faction. Greater accuracy of estimating biomass of the different microbial factions is now possible through improved laboratory techniques (i.e., fluorescence microscopy) and more precise estimates of cell carbon or nitrogen for natural assemblages of phytoplankton, bacteria and protozoa.

The most serious problem encountered in this study was the lack of accuracy and precision for the DON analysis. There is increasing evidence that DOM may play an important (but underestimated) role in the upper portion of the water column, and analysis of the concentration and turnover rates of DON and DOC is currently being investigated. Unfortunately, there are conflicting reports about the accuracy of past and recent concentration

measurements (Sharp 1973, Suzuki et al. 1985, Sugimura and Suzuki 1988). Thus, the cycling of DOM cannot be addressed adequately until the accuracy and precision for DON and DOC measurements are established.

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APPENDIX

Table A.1. Nutrient concentrations with associated standard errors (SE) for Experiment 1. [NH₄]=ammonium, TDN=total dissolved nitrogen, [N+N]=nitrate + nitrite, DON=dissolved organic nitrogen.

CUM. TIME (hours)	[NH ₄] (μ M)	SE (μ M)	TDN (μ M)	SE (μ M)	[N+N] (μ M)	SE (μ M)	DON (μ M)	SE (μ M)
Ammonium Grown Control								
0.0	1.648	0.160	27.294	16.500	1.600	0.740	24.046	16.517
0.1	9.900	1.300	57.713	14.300	1.200	0.800	46.613	14.381
15.5	7.600	1.300	14.796	6.600	1.000	0.760	6.196	6.770
26.8	0.980	0.140	NA	NA	NA	NA	NA	NA
40.1	2.150	0.350	18.288	5.500	2.200	0.500	13.938	5.534
49.4	0.000	0.000	19.573	13.400	0.100	0.245	19.473	13.402
64.3	0.000	0.000	30.695	9.700	0.000	0.048	30.695	9.700
74.1	0.000	0.000	27.846	6.800	0.080	0.048	27.766	6.800
89.4	0.000	0.000	24.170	11.400	0.250	0.741	23.920	11.424
Ammonium Grown Experimental								
0.0	1.550	0.140	71.682	18.600	1.400	0.600	68.732	18.610
0.1	8.800	0.900	52.567	5.700	1.400	0.960	42.367	5.850
15.5	7.200	1.300	13.785	8.300	1.000	0.620	5.585	8.424
26.8	0.940	0.190	15.255	11.800	1.400	0.600	12.915	11.817
40.1	2.150	1.300	23.710	8.400	2.200	0.570	19.360	8.519
49.4	0.000	0.000	18.380	5.900	0.050	0.230	18.330	5.904
64.3	0.000	0.000	23.710	5.600	0.000	0.048	23.710	5.600
74.1	0.000	0.000	21.413	4.500	0.080	0.049	21.333	4.500
89.4	0.000	0.000	25.548	4.800	0.170	0.335	25.378	4.812
Nitrate Grown Control								
0.0	1.540	0.180	56.519	8.700	1.400	0.680	53.579	8.728
0.2	1.300	0.100	60.930	12.500	5.380	0.860	54.250	12.530
14.9	0.170	0.160	13.785	10.300	4.800	0.660	8.815	10.322
26.3	0.320	0.110	15.164	9.700	5.500	0.370	9.344	9.708
39.5	0.060	0.140	20.586	8.300	6.250	0.555	14.276	8.320
49.1	0.000	0.000	28.213	5.500	5.200	0.305	23.013	5.508
63.9	0.000	0.000	34.187	12.100	3.619	0.120	30.568	12.101
74.1	0.000	0.000	21.597	6.900	2.000	0.077	19.597	6.900
89.4	0.000	0.000	15.715	5.100	0.793	0.276	14.922	5.107
Nitrate Grown Experimental								
0.0	1.670	0.160	59.276	7.600	1.960	0.800	55.646	7.644
0.2	1.240	0.220	55.416	14.200	5.140	1.580	49.036	14.289
14.9	0.170	0.160	20.861	9.900	5.100	0.660	15.591	9.923
26.3	0.340	0.110	13.693	4.600	4.580	0.370	8.773	4.616
39.5	-0.030	0.070	20.953	5.300	5.765	0.335	15.218	5.311
49.1	0.000	0.000	24.721	7.600	4.460	0.335	20.261	7.607
63.9	0.000	0.000	29.684	6.700	3.082	0.149	26.602	6.702
74.1	0.000	0.000	15.899	11.600	1.820	0.075	14.079	11.600
89.4	0.000	0.000	4.779	10.900	0.453	0.319	4.326	10.905

Table A.2. Biomass measurements with associated standard errors (SE) for Experiment 1. PN=particulate nitrogen, TN=total nitrogen, In vivo Fluor.=in vivo fluorescence, SD=standard deviation, NA=not available.

CUM. TIME (hours)	PN (μ M)	SE (μ M)	TN (μ M)	SE (μ M)	In Vivo Fluor.	SD	PN (μ M)	SE (μ M)	TN (μ M)	SE (μ M)	In Vivo Fluor.	SD
Ammonium Grown Control						Ammonium Grown Experimental						
0.0	7.205	1.170	34.499	16.541	6.000	0.100	10.587	2.750	82.269	18.802	7.800	0.300
0.1	7.490	2.040	65.203	14.445	5.900	0.100	10.045	1.430	62.611	5.877	6.500	0.100
15.5	9.337	2.090	24.133	6.923	7.000	0.100	10.679	1.940	24.464	8.524	7.400	0.200
26.8	12.609	2.440	NA	NA	16.700	0.300	13.096	1.870	28.351	11.947	18.300	0.300
40.1	14.732	2.070	33.020	5.877	17.000	0.000	14.539	1.970	38.249	8.628	17.500	0.000
49.4	16.083	0.880	35.657	13.429	34.700	0.300	17.764	1.930	36.144	6.208	34.500	0.500
64.3	17.296	1.670	47.990	9.843	30.000	1.000	16.211	1.050	39.921	5.698	29.000	1.000
74.1	16.496	2.250	44.342	7.163	26.200	0.600	15.430	2.030	36.843	4.937	26.300	0.300
89.4	15.632	2.340	39.802	11.638	21.000	0.000	17.590	1.410	43.138	5.003	20.000	0.900
Nitrate Grown Control						Nitrate Grown Experimental						
0.0	8.923	1.980	65.442	8.922	6.800	0.200	11.533	0.910	70.809	7.654	8.100	0.150
0.2	7.609	0.660	68.539	12.517	5.800	0.100	10.045	1.600	65.460	14.290	6.700	0.100
14.9	10.146	0.900	23.931	10.339	5.900	0.100	12.011	1.040	32.873	9.954	6.900	0.100
26.3	9.852	0.750	25.015	9.729	9.300	0.100	14.245	1.910	27.938	4.981	11.300	0.600
39.5	12.416	4.150	33.001	9.280	9.600	0.400	12.462	1.090	33.415	5.411	10.500	0.500
49.1	9.172	1.930	37.385	5.829	13.100	0.400	11.975	0.770	36.696	7.639	14.100	0.300
63.9	13.169	1.190	47.356	12.158	13.800	0.400	14.079	1.960	43.763	6.981	14.800	0.300
74.1	11.184	1.980	32.781	7.178	17.700	0.800	14.006	1.870	29.904	11.750	19.000	0.000
89.4	15.412	1.130	31.127	5.224	17.400	0.200	17.075	1.100	21.854	10.955	19.700	0.600

Table A.3. Atom % enrichments with associated standard errors (SE) for Experiment 1. Inorg. N=inorganic nitrogen, TDN=total dissolved nitrogen, DON=dissolved organic nitrogen, TN=total nitrogen, NA=not available, *=value calculated indirectly.

CUM. TIME (hours)	Inorg. N	SE	TDN	SE	DON	SE	PN	SE	TN	SE
Ammonium Grow Control										
0.0	0.497	0.011	0.1230	0.074	0.000	0.000	0.439	0.071	0.092	0.473
0.1	15.145	0.291	2.2532	0.559	0.000	0.000	0.825	0.019	2.393	1.051
15.5	12.192	0.291	3.5573	1.587	7.016	16.048	2.128	0.054	6.464	4.119
26.8	21.092	0.324	NA	NA	NA	NA	5.754	0.033	NA	NA
40.1	-0.188	0.000	2.1246	0.639	5.197	3.015	5.700	0.084	4.724	1.323
49.4	0.000	0.000	1.6822	1.152	2.873	3.413	6.221	0.135	4.375	2.247
64.3	0.000	0.000	0.6861	0.061	0.686	0.313	6.095	0.027	2.635	0.595
74.1	0.000	0.000	1.3048	0.255	1.309	0.541	5.586	0.107	2.898	0.624
89.4	0.000	0.000	1.3910	0.160	1.406	0.957	5.743	0.013	3.100	1.064
Ammonium Grow Experimental										
0.0	0.591	0.023	0.0454	0.012	0.000	0.000	0.301	0.025	0.039	0.316
0.1	13.443	0.293	0.8365	0.081	-0.207 *	2.828	0.871	0.019	2.029 *	0.356
15.5	14.899	0.292	2.8103	1.692	1.158	17.775	2.356	0.074	5.678	4.488
26.8	23.756	0.296	2.0130	1.557	3.791	6.972	5.163	0.047	4.899	3.476
40.1	-0.188	0.000	0.7915	0.091	0.990	0.566	3.620	0.035	1.867	0.580
49.4	0.000	0.000	0.9120	0.293	1.470	0.818	6.302	0.083	3.843	0.801
64.3	0.000	0.000	0.5298	0.029	0.530	0.179	5.733	0.033	2.643	0.418
74.1	0.000	0.000	0.8326	0.097	0.836	0.267	6.022	0.003	3.006	0.551
89.4	0.000	0.000	0.6792	0.207	0.684	0.277	5.728	0.018	2.738	0.395
Nitrate Grow Control										
0.0	0.4	0.0	0.7472	0.405	0.000	0.000	0.517	0.042	0.716	0.507
0.2	48.9	0.4	12.2069	0.614	0.000	0.000	0.504	0.052	3.893	0.947
14.9	48.9	0.3	13.7863	0.722	1.947 *	6.507	1.103	0.051	10.272 *	4.653
26.3	48.9	0.2	10.8695	0.581	-5.673 *	7.707	4.785	0.054	12.632 *	4.975
39.5	48.9	0.3	11.1670	0.102	-7.348 *	6.012	5.024	0.218	11.147 *	3.396
49.4	48.9	0.1	10.7274	0.086	2.107	2.694	8.169	0.027	10.100	2.300
63.9	48.9	0.1	6.2660	0.203	1.221	2.544	11.419	0.005	7.699	2.555
74.1	48.9	0.0	5.2235	0.277	0.769	1.894	10.617	0.028	7.064	1.982
89.4	48.9	0.1	2.6057	0.048	0.147	1.271	17.893	0.052	10.175	1.776
Nitrate Grow Experimental										
0.0	0.4	0.0	0.6702	0.036	0.000	0.000	0.466	0.070	0.637	0.153
0.2	43.6	0.7	11.6774	0.091	0.000	0.000	0.533	0.010	3.503	1.323
14.9	43.6	0.3	12.2060	0.380	2.080	8.092	0.963	0.004	8.098	4.433
26.3	43.6	0.2	12.7560	0.386	-0.348 *	8.205	1.927	0.021	8.125 *	1.632
39.5	43.6	0.1	9.1344	0.416	-6.749 *	5.221	6.057	0.046	9.776 *	1.663
49.1	43.6	0.1	11.2359	0.109	4.118	4.549	6.416	0.078	9.663	3.082
63.9	43.6	0.1	6.3194	0.072	2.004	1.689	9.324	0.039	7.286	1.546
74.1	43.6	0.0	4.5130	0.080	-0.536 *	3.753	12.578	0.035	8.543 *	3.388
89.4	43.6	0.1	1.8485	0.045	-8.121 *	26.171	14.017	0.080	11.855 *	5.984

Table A.4. Concentrations of ^{15}N with associated standard errors (SE) for Experiment 1. Inorg. N=inorganic ^{15}N , TDN=total dissolved ^{15}N , PN=particulate ^{15}N , TN=total ^{15}N , DON=dissolved organic ^{15}N , *=value calculated indirectly.

CUM. TIME (hours)	Inorg. N (μM)	SE (μM)	TDN (μM)	SE (μM)	PN (μM)	SE (μM)	TN (μM)	SE (μM)	DON (μM)	SE (μM)
Ammonium Grown Control										
0.0	0.008	0.001	0.000	0.000	0.032	0.162	0.032	0.162	-0.008	0.001
0.1	1.499	0.199	1.498	0.525	0.062	0.272	1.560	0.591	-0.001	0.561
15.5	0.927	0.160	1.361	0.859	0.199	0.224	1.560	0.887	0.435	0.874
26.8	0.207	0.030	0.834	NR	0.726	0.194	NR	NR	NR	NR
40.1	-0.004	0.001	0.720	0.306	0.840	0.141	1.560	0.337	0.724	0.306
49.4	0.000	0.000	0.560	0.542	1.000	0.059	1.560	0.545	0.560	0.542
64.3	0.000	0.000	0.211	0.069	1.054	0.097	1.265	0.119	0.211	0.069
74.1	0.000	0.000	0.363	0.121	0.921	0.138	1.285	0.183	0.363	0.121
89.4	0.000	0.000	0.336	0.163	0.898	0.150	1.234	0.221	0.336	0.163
Ammonium Grown Experimental										
0.0	0.009	0.001	0.000	0.000	0.032	0.260	0.032	0.260	-0.009	0.001
0.1	1.183	0.124	0.440	0.064	0.087	0.142	1.270 *	0.189	0.000 *	0.267
15.5	1.073	0.195	1.137	0.969	0.252	0.182	1.389	0.985	0.065	0.988
26.8	0.223	0.045	0.713	0.780	0.676	0.143	1.389	0.793	0.490	0.781
40.1	-0.004	0.002	0.188	0.070	0.526	0.136	0.714	0.153	0.192	0.070
49.4	0.000	0.000	0.269	0.122	1.120	0.110	1.389	0.164	0.269	0.122
64.3	0.000	0.000	0.126	0.030	0.929	0.065	1.055	0.072	0.126	0.030
74.1	0.000	0.000	0.178	0.043	0.929	0.132	1.107	0.138	0.178	0.043
89.4	0.000	0.000	0.174	0.062	1.008	0.080	1.181	0.101	0.174	0.062
Nitrate Grown Control										
0.0	1.400	0.680	0.422	0.238	0.046	0.222	0.468	0.325	0.417	0.238
0.2	5.380	0.860	7.438	1.571	0.038	0.087	2.668 *	0.429	0.000 *	0.607
14.9	4.800	0.660	1.900	1.423	0.112	0.089	2.458 *	0.335	0.210 *	0.544
26.3	5.500	0.370	1.648	1.058	0.471	0.076	3.160 *	0.196	-0.492 *	0.472
39.5	6.250	0.555	2.299	0.927	0.624	0.335	3.679 *	0.431	-1.011 *	0.609
49.1	5.200	0.305	3.027	0.591	0.749	0.210	3.776	0.627	0.485	0.609
63.9	3.619	0.120	2.142	0.761	1.504	0.090	3.646	0.767	0.373	0.764
74.1	2.000	0.077	1.128	0.365	1.187	0.177	2.316	0.406	0.151	0.367
89.4	0.793	0.276	0.409	0.133	2.758	0.074	3.167	0.152	0.022	0.190
Nitrate Grown Experimental										
0.0	1.960	0.800	0.397	0.055	0.054	0.079	0.451	0.097	0.397	0.055
0.2	5.140	1.580	6.471	1.639	0.054	0.159	2.293 *	0.707	0.000 *	0.999
14.9	5.100	0.660	2.546	1.211	0.116	0.087	2.662	1.214	0.324	1.245
26.3	4.580	0.370	1.747	0.589	0.274	0.134	2.270 *	0.210	0.023 *	0.737
39.5	5.765	0.335	1.914	0.492	0.755	0.088	3.267 *	0.170	-0.974 *	0.727
49.1	4.460	0.335	2.778	0.854	0.768	0.065	3.546	0.857	0.834	0.867
63.9	3.082	0.149	1.876	0.424	1.313	0.139	3.189	0.446	0.533	0.429
74.1	1.820	0.075	0.718	0.524	1.762	0.134	2.555 *	0.138	-0.262 *	0.720
89.4	0.453	0.319	0.088	0.202	2.393	0.066	2.591 *	0.154	-0.298 *	0.723

Table A.5. Nutrient concentrations with associated standard errors (SE) for Experiment 2. [NH₄]=ammonium, TDN=total dissolved nitrogen, [N+N]=nitrate + nitrite, DON=dissolved organic nitrogen.

CUM. TIME (hours)	[NH ₄] (μ M)	SE (μ M)	TDN (μ M)	SE (μ M)	[N+N] (μ M)	SE (μ M)	DON (μ M)	SE (μ M)
Ammonium Grown Control								
0.0	2.110	2.250	33.213	14.084	10.250	3.750	22.853	14.747
0.1	5.510	0.600	40.329	15.654	11.380	3.290	23.439	16.007
16.4	4.820	0.460	42.948	18.732	12.950	3.460	25.178	19.055
24.7	0.605	0.485	29.331	11.993	11.830	3.150	16.896	12.409
41.1	0.000	0.000	38.154	12.276	1.215	0.845	36.939	12.305
48.8	0.000	0.000	35.213	26.705	0.000	0.845	35.213	26.718
64.9	0.000	0.000	30.641	14.551	0.285	0.840	30.356	14.575
72.6	0.000	0.000	28.986	14.548	0.059	0.840	28.927	14.572
90.1	0.000	0.000	25.740	9.205	0.078	0.170	25.662	9.207
Ammonium Grown Experimental								
0.0	1.620	0.700	31.705	26.069	7.900	2.170	22.185	26.168
0.1	4.600	1.400	40.763	21.466	10.250	3.130	25.915	21.738
16.4	3.235	0.440	49.266	20.241	11.230	3.190	34.801	20.496
24.7	0.575	1.090	39.134	31.484	10.030	3.300	28.529	31.675
41.1	0.000	0.000	37.824	9.948	1.700	0.850	36.124	9.984
48.8	0.000	0.000	53.402	16.052	0.305	0.830	53.097	16.073
64.9	0.000	0.000	28.351	10.821	0.360	0.825	27.991	10.853
72.6	0.000	0.000	16.545	18.602	0.072	0.167	16.473	18.603
90.1	0.000	0.000	27.264	12.912	0.018	0.165	27.246	12.913
Nitrate Grown Control								
0.0	1.840	1.600	39.785	12.238	10.250	3.750	27.695	12.899
0.1	1.410	0.500	37.503	17.308	12.580	3.200	23.513	17.608
16.4	1.475	0.600	42.726	21.926	13.550	3.210	27.701	22.168
24.8	0.430	1.275	42.948	15.730	12.430	3.200	30.068	16.103
41.1	0.000	0.000	39.241	21.068	5.250	0.930	33.991	21.089
48.8	0.000	0.000	37.939	13.747	2.170	0.865	35.769	13.774
65.5	0.000	0.000	30.963	20.440	0.390	0.835	30.573	20.457
72.8	0.000	0.000	33.145	21.757	0.057	0.160	33.088	21.758
90.3	0.000	0.000	29.661	19.276	0.053	0.160	29.608	19.277
Nitrate Grown Experimental								
0.0	1.410	0.600	36.415	16.534	11.380	3.580	23.625	16.928
0.1	1.620	0.580	48.393	21.681	14.750	3.180	32.023	21.920
16.4	1.235	0.530	48.937	20.302	14.680	3.220	33.022	20.563
24.8	0.575	0.715	47.734	21.727	11.300	3.190	35.859	21.971
41.1	0.000	0.000	30.312	9.535	3.460	0.895	26.852	9.577
48.8	0.000	0.000	38.368	17.660	1.065	0.840	37.303	17.680
65.5	0.000	0.000	37.503	11.388	0.190	0.820	37.313	11.417
72.8	0.000	0.000	26.391	19.069	0.000	0.176	26.391	19.070
90.3	0.000	0.000	33.145	17.698	0.057	0.166	33.088	17.699

Table A.6. Biomass measurements with associated standard errors (SE) for Experiment 2. PN=particulate nitrogen, TN=total nitrogen, In vivo Fluor.=in vivo fluorescence, SD=standard deviation.

CUM. TIME (hours)	PN (μ M)	SE (μ M)	TN (μ M)	SE (μ M)	In Vivo Fluor.	SD	PN (μ M)	SE (μ M)	TN (μ M)	SE (μ M)	In Vivo Fluor.	SD
Ammonium Grown Control						Ammonium Grown Experimental						
0.0	11.226	2.416	46.440	14.289	8.0	0.2	9.871	3.099	41.576	26.253	8.1	0.3
0.1	15.118	2.529	53.446	15.857	8.0	0.2	11.100	2.259	51.865	21.585	9.0	0.3
16.4	13.663	2.627	56.611	18.916	12.4	0.5	12.963	3.045	62.229	20.469	13.1	0.2
24.7	18.173	2.829	47.505	12.322	34.7	0.3	16.267	2.581	53.401	31.590	30.3	0.6
41.1	26.645	4.827	64.798	13.191	44.7	0.6	25.162	3.203	62.987	10.451	42.3	0.6
48.8	25.078	3.013	60.291	26.874	58.0	1.0	25.925	3.205	79.327	16.369	52.0	0.0
64.9	18.173	4.465	48.814	15.221	58.7	0.3	23.532	3.722	51.883	11.443	55.5	0.9
72.6	24.909	3.251	53.895	14.907	60.0	1.0	23.659	2.896	40.204	18.826	55.0	0.0
90.1	17.262	7.031	43.002	11.583	61.2	0.8	19.423	3.145	46.687	13.289	55.0	1.0
Nitrate Grown Control						Nitrate Grown Experimental						
0.0	12.053	3.400	51.838	12.702	7.5	0.3	9.786	2.276	46.202	16.690	7.4	0.2
0.1	8.992	2.070	46.495	17.431	7.3	0.2	8.876	2.506	57.269	21.825	7.4	0.1
16.4	11.778	2.981	54.504	22.128	9.7	0.3	10.653	2.286	59.592	20.431	9.9	0.1
24.8	15.335	2.558	58.283	15.937	17.7	0.7	14.679	2.453	62.414	21.865	17.4	0.1
41.1	18.364	2.638	57.606	21.233	23.0	0.7	18.915	2.919	49.227	9.971	23.5	0.5
48.8	21.604	3.293	59.543	14.136	32.3	0.6	16.871	3.160	55.239	17.941	33.7	0.6
65.5	24.251	3.086	55.214	20.672	39.0	1.0	23.574	3.065	61.077	11.793	39.7	0.6
72.8	16.744	3.148	49.889	21.984	43.5	0.5	22.472	3.478	48.863	19.384	42.8	1.0
90.3	23.002	3.762	52.662	19.640	42.3	0.6	21.689	3.312	54.835	18.005	42.3	0.6

Table A.7. Atom % enrichments with associated standard errors (SE) for Experiment 2. Inorg. N=inorganic nitrogen, TDN=total dissolved nitrogen, DON=dissolved organic nitrogen, TN=total nitrogen, *=value calculated indirectly.

CUM. TIME (hours)	Inorg. N	SE	TDN	SE	DON	SE	PN	SE	TN	SE
Ammonium Grown Control										
0.0	0.675	0.074	0.391	0.060	0.537	0.306	0.495	0.022	0.416	0.163
0.1	46.951	0.303	2.360	0.062	0.000 *	0.000	1.760	0.032	5.106	1.410
16.4	37.031	0.295	3.764	0.092	-2.288 *	1.588	12.099	0.127	6.031	1.965
24.7	10.349	0.331	1.122	0.092	1.563	0.973	16.932	0.136	7.102	1.894
41.1	0.000	0.000	0.768	0.041	0.793	0.223	12.150	0.132	5.417	1.319
48.8	0.000	0.000	3.077	0.096	3.077	2.219	11.341	0.126	6.487	3.106
64.9	0.000	0.000	1.725	0.115	1.741	0.719	11.362	0.132	5.275	1.827
72.6	0.000	0.000	1.311	0.069	1.314	0.574	11.038	0.136	5.778	1.583
90.1	0.000	0.000	1.570	0.059	1.575	0.433	11.307	0.131	5.426	2.229
Ammonium Grown Experimental										
0.0	0.553	0.013	0.349	0.043	0.429	0.148	0.517	0.014	0.382	0.120
0.1	48.473	0.303	0.280	0.054	0.000 *	0.000	1.888	0.034	4.665	2.237
16.4	40.346	0.295	3.058	0.080	0.601	0.328	13.642	0.128	5.252	1.968
24.7	10.684	0.331	0.791	0.014	0.868	0.920	18.137	0.155	5.844	3.340
41.1	0.000	0.000	1.013	0.032	1.060	0.224	12.731	0.130	5.669	0.992
48.8	0.000	0.000	1.387	0.082	1.395	0.375	11.785	0.140	4.774	1.033
64.9	0.000	0.000	1.895	0.137	1.917	0.799	11.736	0.129	6.120	1.753
72.6	0.000	0.000	1.793	0.118	1.797	0.951	11.276	0.136	5.753	1.965
90.1	0.000	0.000	1.460	0.067	1.463	1.465	11.790	0.136	7.959	3.334
Nitrate Grown Control										
0.0	0.369	0.014	0.341	0.070	0.353	0.140	0.759	0.014	0.437	0.135
0.1	11.520	0.369	1.842	0.045	0.000 *	0.000	0.672	0.020	3.216	1.355
16.4	11.520	0.370	1.939	0.035	-0.733 *	0.548	1.314	0.014	3.125	1.371
24.8	11.520	0.369	2.550	0.071	-0.806 *	0.387	2.109	0.025	2.992	0.971
41.1	11.520	0.107	1.929	0.146	0.466	0.270	3.114	0.051	2.304	1.049
48.8	11.520	0.100	1.506	0.115	0.906	0.304	3.952	0.124	2.387	0.630
65.5	11.520	0.096	0.911	0.081	0.778	0.484	4.285	0.125	2.379	0.928
72.8	11.520	0.018	1.196	0.085	1.178	0.725	4.287	0.123	2.223	1.080
90.3	11.520	0.018	1.372	0.458	1.353	0.783	4.306	0.124	2.656	1.068
Nitrate Grown Experimental										
0.0	0.369	0.013	0.356	0.064	0.370	0.240	0.805	0.028	0.450	0.198
0.1	10.360	0.329	2.044	0.108	0.000 *	0.000	0.540	0.024	2.736	1.131
16.4	10.360	0.334	2.253	0.171	-0.179 *	2.103	1.079	0.025	2.730	1.033
24.8	10.360	0.330	3.492	0.149	1.404	0.805	2.062	0.073	3.158	1.545
41.1	10.360	0.093	1.929	0.085	0.864	0.237	2.785	0.034	2.254	0.494
48.8	10.360	0.087	0.921	0.087	0.655	0.284	3.672	0.123	1.755	0.630
65.5	10.360	0.085	0.661	0.076	0.612	0.154	3.989	0.123	1.936	0.389
72.8	10.360	0.018	0.843	0.100	0.843	0.563	4.117	0.129	2.331	0.965
90.3	10.360	0.017	0.729	0.058	0.713	0.349	4.033	0.124	2.024	0.697

Table A.8. Concentrations of ^{15}N with associated standard errors (SE) for Experiment 2. Inorg. N=inorganic ^{15}N , TDN=total dissolved ^{15}N , PN=particulate ^{15}N , TN=total ^{15}N , DON=dissolved organic ^{15}N , *=value calculated indirectly .

CUM.TIME (hours)	Inorg.N (μM)	SE (μM)	TDN (μM)	SE (μM)	PN (μM)	SE (μM)	TN (μM)	SE (μM)	DON (μM)	SE (μM)
Ammonium Growth Control										
0.0	0.014	0.015	0.139	0.054	0.056	0.012	0.195	0.053	0.125	0.056
0.1	2.587	0.282	0.962	0.333	0.266	0.045	2.853 *	0.286	-0.266 *	0.402
16.4	1.785	0.171	1.631	0.656	1.653	0.318	3.438 *	0.361	-0.851 *	0.458
24.7	0.063	0.050	0.335	0.120	3.077	0.480	3.412	0.494	0.273	0.130
41.1	0.000	0.000	0.297	0.082	3.237	0.587	3.534	0.593	0.297	0.082
48.8	0.000	0.000	1.098	0.792	2.844	0.343	3.942	0.863	1.098	0.792
64.9	0.000	0.000	0.538	0.222	2.065	0.508	2.603	0.554	0.538	0.222
72.6	0.000	0.000	0.385	0.169	2.749	0.360	3.134	0.398	0.385	0.169
90.1	0.000	0.000	0.413	0.114	1.952	0.795	2.365	0.804	0.413	0.114
Ammonium Growth Experimental										
0.0	0.009	0.004	0.140	0.040	0.051	0.016	0.192	0.043	0.132	0.040
0.1	2.230	0.679	0.115	0.061	0.210	0.043	2.439 *	0.680	-0.210 *	0.961
16.4	1.305	0.178	1.516	0.578	1.768	0.416	3.285	0.712	0.211	0.605
24.7	0.061	0.116	0.313	0.241	2.950	0.469	3.263	0.527	0.252	0.268
41.1	0.000	0.000	0.388	0.079	3.208	0.410	3.596	0.417	0.388	0.079
48.8	0.000	0.000	0.745	0.203	3.055	0.380	3.800	0.431	0.745	0.203
64.9	0.000	0.000	0.593	0.247	2.762	0.438	3.354	0.503	0.593	0.247
72.6	0.000	0.000	0.592	0.315	2.668	0.328	3.259	0.455	0.592	0.315
90.1	0.000	0.000	0.167	0.167	2.290	0.372	2.457	0.408	0.167	0.167
Nitrate Growth Control										
0.0	0.038	0.014	0.137	0.045	0.091	0.026	0.229	0.052	0.099	0.047
0.1	1.449	0.369	0.699	0.293	0.060	0.014	1.510 *	0.369	-0.021 *	0.621
16.4	1.561	0.370	0.836	0.402	0.155	0.039	1.716 *	0.372	-0.181 *	0.705
24.8	1.432	0.369	1.105	0.363	0.323	0.054	1.755 *	0.373	0.696 *	1.328
41.1	0.605	0.107	0.765	0.388	0.572	0.083	1.337	0.396	0.160	0.402
48.8	0.250	0.100	0.578	0.188	0.854	0.133	1.432	0.230	0.328	0.213
65.5	0.045	0.096	0.287	0.178	1.039	0.136	1.326	0.224	0.242	0.202
72.8	0.007	0.018	0.402	0.249	0.718	0.136	1.120	0.284	0.396	0.249
90.3	0.006	0.018	0.405	0.270	0.990	0.164	1.396	0.316	0.399	0.271
Nitrate Growth Experimental										
0.0	0.042	0.013	0.131	0.059	0.079	0.019	0.210	0.062	0.089	0.060
0.1	1.528	0.329	0.996	0.420	0.048	0.014	1.576 *	0.330	-0.134 *	0.668
16.4	1.521	0.334	1.110	0.435	0.115	0.025	1.636 *	0.335	0.184 *	0.625
24.8	1.171	0.330	1.679	0.717	0.303	0.052	1.982	0.719	0.508	0.790
41.1	0.358	0.093	0.595	0.146	0.527	0.082	1.122	0.167	0.237	0.173
48.8	0.110	0.087	0.358	0.154	0.620	0.118	0.977	0.194	0.247	0.177
65.5	0.020	0.085	0.251	0.069	0.940	0.126	1.191	0.143	0.231	0.109
72.8	0.000	0.018	0.227	0.154	0.925	0.146	1.153	0.212	0.227	0.153
90.3	0.006	0.017	0.245	0.122	0.875	0.136	1.120	0.183	0.239	0.123

Table A.9. Nutrient concentrations with associated standard errors (SE) for Experiment 3. [NH₄]=ammonium, TDN=total dissolved nitrogen, [N+N]=nitrate + nitrite, DON=dissolved organic nitrogen.

CULTURE TIME (hours)	[NH ₄] (μM)	SE (μM)	[NH ₄] (μM)	SE (μM)	TDN (μM)	SE (μM)	DON (μM)	SE (μM)
Ammonium Grown Control								
0.0	18.130	1.160	1.079	0.533	52.980	21.091	33.771	21.130
0.1	18.270	1.010	13.902	0.224	48.873	13.931	16.703	13.969
12.8	14.250	9.280	13.866	0.212	47.443	16.779	19.327	19.176
23.6	18.830	1.020	10.460	0.632	43.744	9.604	14.454	9.678
38.4	21.060	3.120	5.553	0.125	45.184	13.953	18.571	14.299
48.0	16.120	2.940	0.000	0.000	30.603	13.364	14.483	13.683
62.3	17.116	0.988	0.000	0.000	17.461	7.252	0.345	7.319
70.1	13.540	0.982	0.000	0.000	21.773	9.389	6.233	9.440
86.0	5.100	0.407	0.000	0.000	18.694	4.894	13.594	4.911
110.0	0.207	0.251	0.000	0.000	15.822	4.832	15.615	4.839
Ammonium Grown Experimental								
0.0	16.050	0.980	1.180	0.078	36.561	15.615	19.331	15.646
0.1	17.580	1.160	13.820	0.222	46.210	6.900	14.810	7.001
12.8	14.940	1.550	13.470	0.184	51.548	5.774	23.138	5.982
23.6	18.970	1.170	9.580	0.782	46.823	10.783	18.273	10.874
38.4	20.800	3.100	2.859	0.158	37.587	7.406	13.928	8.030
48.0	7.900	2.730	0.000	0.000	23.626	9.795	15.726	10.168
62.3	19.030	1.032	0.000	0.000	15.200	10.921	-3.830	10.969
70.1	12.732	0.900	0.000	0.000	24.032	22.761	11.300	22.778
86.0	3.090	0.347	0.000	0.000	16.029	5.368	12.939	5.380
110.0	0.207	0.363	0.000	0.000	20.540	15.968	20.333	15.972
Nitrate Grown Control								
0.0	18.270	1.010	1.235	0.158	37.174	8.263	17.669	8.326
0.1	34.780	1.290	1.164	0.382	53.446	6.946	19.502	7.075
13.0	32.970	1.520	0.966	0.214	59.965	7.452	26.029	7.608
23.7	36.720	1.300	0.568	0.222	56.473	9.956	19.185	10.043
38.6	33.560	3.590	0.045	0.133	52.574	8.516	18.969	9.243
48.2	34.640	3.590	0.000	0.000	50.315	10.507	15.675	11.104
62.4	0.238	0.252	0.000	0.000	43.951	5.637	43.713	5.642
70.3	0.269	0.253	0.000	0.000	44.158	18.166	43.889	18.167
86.2	0.192	0.232	0.000	0.000	36.561	15.615	36.369	15.617
110.0	0.223	0.298	0.000	0.000	13.969	8.171	13.746	8.177
Nitrate Grown Experimental								
0.0	17.030	1.160	1.399	0.286	40.459	10.446	22.030	10.514
0.1	38.100	1.310	1.084	0.192	56.679	11.388	17.495	11.465
13.0	45.040	1.370	3.290	0.252	80.910	27.034	32.580	27.070
23.7	38.940	1.830	0.568	0.222	56.373	5.529	16.865	5.829
38.6	36.500	3.800	0.203	0.900	51.341	5.774	14.638	6.971
48.2	34.030	3.700	0.017	0.080	51.341	7.429	17.294	8.299
62.4	0.887	0.276	0.000	0.000	45.184	7.743	44.297	7.747
70.3	0.223	0.234	0.000	0.000	41.632	16.121	41.469	16.122
86.2	0.192	0.298	0.000	0.000	28.757	5.866	28.565	5.874
110.0	0.238	0.252	0.000	0.000	15.615	9.948	15.377	9.951

Table A.10. Biomass measurements with associated standard errors (SE) for Experiment 3. PN=particulate nitrogen, TN=total nitrogen, In vivo Fluor.=in vivo fluorescence, SD=standard deviation.

CUM. TIME (hours)	PN (µM)	SE (µM)	TN (µM)	SE (µM)	In Vivo Fluor.	SD	PN (µM)	SE (µM)	TN (µM)	SE (µM)	In Vivo Fluor.	SD
Ammonium Grown Control						Ammonium Grown Experimental						
0.0	4.116	0.784	57.097	21.106	4.8	0.0	5.167	1.097	41.727	15.654	5.6	0.3
0.1	4.816	1.869	53.692	14.055	4.7	0.2	5.625	1.240	51.836	7.011	5.8	0.2
12.8	7.027	1.683	54.470	16.863	4.9	0.1	7.296	1.281	58.844	5.915	6.2	0.2
23.6	8.427	2.809	52.172	10.006	15.0	0.0	10.502	0.954	57.325	10.825	19.4	0.4
38.4	16.888	1.360	62.073	14.020	18.4	0.1	20.742	2.990	58.329	7.986	26.6	0.2
48.0	28.313	1.499	58.916	13.448	54.2	1.3	39.254	2.772	62.880	10.180	73.3	0.3
62.3	43.592	5.924	61.053	9.364	68.2	0.8	49.103	4.313	64.303	11.742	97.5	0.9
70.1	46.341	2.026	68.113	9.605	100.7	1.2	44.265	6.428	68.297	23.651	105.0	0.0
86.0	47.023	3.703	65.717	6.137	105.0	0.0	45.182	6.594	61.211	8.503	110.0	0.0
110.0	43.080	3.500	58.902	5.966	73.8	0.3	44.562	3.753	65.102	16.403	93.8	1.3
Nitrate Grown Control						Nitrate Grown Experimental						
0.0	4.709	1.113	41.883	8.338	4.4	0.2	5.328	2.480	45.787	10.736	5.1	0.1
0.1	5.140	2.000	60.586	7.228	4.5	0.1	6.595	1.822	63.274	11.533	5.3	0.1
13.0	5.706	0.845	65.671	7.499	4.8	0.3	5.679	0.844	86.590	27.047	5.0	0.1
23.7	6.837	0.968	63.310	10.003	8.6	0.2	9.236	1.921	65.609	5.853	10.3	0.2
38.6	10.071	2.751	62.646	8.950	8.9	0.2	11.122	0.979	62.463	5.857	12.5	0.3
48.2	15.959	3.853	66.275	11.192	16.0	0.0	17.212	8.148	68.553	11.026	20.7	0.3
62.4	20.553	4.158	64.505	7.004	20.7	0.8	21.739	2.164	66.923	8.039	25.7	0.6
70.3	25.538	3.196	69.696	18.445	34.7	0.3	31.493	1.671	73.185	16.207	46.7	1.5
86.2	35.320	2.038	71.881	15.748	47.2	0.3	43.484	3.738	72.241	6.956	61.2	0.3
110.0	53.078	3.086	67.047	8.735	97.5	0.5	51.649	9.125	67.264	13.499	117.0	2.6

Table A.11. Atom % enrichments with associated standard errors (SE) for Experiment 3. Inorg. N=inorganic nitrogen, TDN=total dissolved nitrogen, DON=dissolved organic nitrogen, TN=total nitrogen.

CUM. TIME (hours)	Inorg.N	SE	TDN	SE	DON	SE	PN	SE	TN	SE
Ammonium Grown Control										
0.0	0.761	0.026	0.385	0.037	0.580	0.440	0.697	0.031	0.408	0.210
0.1	77.323	0.310	12.286	0.202	0.000	1.586	3.030	0.097	20.292	5.324
12.8	79.944	0.310	16.797	0.195	-6.620	6.836	15.510	0.160	22.351	6.944
23.6	76.189	0.305	3.747	0.092	-0.449	7.779	33.491	0.170	21.008	4.554
38.4	76.060	0.306	8.713	0.136	-4.217	4.723	44.142	0.176	18.814	4.361
48.0	0.000	0.000	2.020	0.061	4.268	4.444	43.118	0.181	21.770	5.110
62.3	0.000	0.000	4.319	0.104	218	4638	30.907	0.165	23.303	4.695
70.1	0.000	0.000	5.441	0.147	19.008	29.940	31.197	0.168	22.964	3.453
86.0	0.000	0.000	5.557	0.197	7.642	3.420	31.197	0.168	23.903	2.874
110.0	0.000	0.000	6.616	0.199	6.704	2.924	30.757	0.169	24.272	3.114
Ammonium Grown Experimental										
0.0	0.470	0.012	0.399	0.047	0.726	0.676	0.954	0.025	0.418	0.221
0.1	79.320	0.306	7.796	0.166	0.000	1.789	3.670	0.155	21.599	2.944
12.8	74.546	0.305	12.586	0.157	-0.007	1.346	15.848	0.166	19.029	1.959
23.6	75.701	0.306	2.906	0.068	-0.043	3.930	37.631	0.170	19.545	3.884
38.4	78.819	0.305	4.492	0.093	-3.710	10.152	45.605	0.175	20.081	3.616
48.0	0.000	0.000	3.332	0.112	5.006	3.849	33.913	0.168	22.423	3.962
62.3	0.000	0.000	4.254	0.149	-16.88	49.86	30.714	0.164	24.459	4.973
70.1	0.000	0.000	4.714	0.077	10.025	22.328	30.873	0.190	21.668	8.200
86.0	0.000	0.000	4.910	0.172	6.083	3.235	30.439	0.175	23.754	4.674
110.0	0.000	0.000	5.338	0.179	5.392	5.962	30.319	0.164	22.437	6.062
Nitrate Grown Control										
0.0	0.369	0.004	0.442	0.059	0.549	0.354	0.581	0.014	0.458	0.138
0.1	47.760	0.616	26.667	0.196	0.000	4.469	0.788	0.035	27.484	3.433
13.0	47.760	0.726	28.121	0.153	4.287	8.619	1.641	0.089	25.820	4.347
23.7	47.760	0.621	27.859	0.135	-6.534	5.707	5.374	0.158	28.281	4.575
38.6	47.760	1.715	29.665	0.168	-2.388	9.799	10.686	0.165	27.303	4.788
48.2	47.760	1.715	28.489	0.424	-18.34	18.03	18.683	0.163	29.462	5.712
62.4	47.760	0.120	29.374	0.147	29.274	5.399	24.014	0.168	27.666	4.245
70.3	47.760	0.121	27.052	0.249	26.926	15.803	29.940	0.000	28.111	10.343
86.2	47.760	0.111	23.453	0.281	23.325	14.209	34.858	0.167	29.057	8.215
110.0	47.760	0.142	3.325	0.148	2.604	2.720	39.214	0.178	31.737	4.532
Nitrate Grown Experimental										
0.0	0.369	0.004	0.440	0.052	0.523	0.340	0.547	0.032	0.453	0.156
0.1	48.830	0.640	28.225	0.146	0.000	5.172	0.739	0.011	29.480	5.468
13.0	48.830	0.669	26.246	0.151	-10.53	9.20	1.619	0.000	25.505	8.004
23.7	48.830	0.894	28.774	0.192	-5.719	6.851	6.530	0.199	29.901	3.001
38.6	48.830	1.856	28.299	0.212	-4.988	13.650	14.028	0.163	31.031	4.164
48.2	48.830	1.807	28.324	0.490	-9.404	15.611	21.279	0.164	29.582	5.998
62.4	48.830	0.135	28.137	0.228	27.723	6.917	27.027	0.244	27.777	4.746
70.3	48.830	0.114	24.604	0.130	24.474	13.495	32.249	0.179	27.894	8.251
86.2	48.830	0.146	15.355	0.220	15.130	4.465	36.166	0.217	27.882	3.505
110.0	48.830	0.123	1.840	0.096	1.113	1.608	38.302	0.213	29.837	7.934

Table A.12. Concentrations of ^{15}N with associated standard errors (SE) for Experiment 3. Inorg. N=inorganic ^{15}N , TDN=total dissolved ^{15}N , PN=particulate ^{15}N , TN=total ^{15}N , DON=dissolved organic ^{15}N , *=value calculated indirectly.

CUM. TIME (hours)	INHA (μM)	SE (μM)	TDIN (μM)	SE (μM)	PIIN (μM)	SE (μM)	TIN (μM)	SE (μM)	DOIN (μM)	SE (μM)
Ammonium Grow Control										
0.0	0.008	0.004	0.204	0.084	0.029	0.006	0.233	0.084	0.196	0.084
0.1	10.749	0.178	6.005	1.714	0.146	0.057	10.895 *	0.187	0.000 *	0.265
12.8	11.085	0.175	7.969	2.820	1.090	0.261	12.175 *	0.314	-1.279 *	0.366
23.6	7.969	0.483	1.639	0.362	2.991	0.997	10.960 *	1.108	-0.065 *	1.124
38.4	4.224	0.097	3.937	1.217	7.455	0.601	11.679 *	0.609	-0.783 *	0.637
48.0	0.000	0.000	0.618	0.271	12.208	0.648	12.826	0.703	0.618	0.271
62.3	0.000	0.000	0.754	0.314	13.473	1.832	14.227	1.859	0.754	0.314
70.1	0.000	0.000	1.185	0.512	14.457	0.637	15.642	0.817	1.185	0.512
86.0	0.000	0.000	1.039	0.274	14.670	1.158	15.709	1.190	1.039	0.274
110.0	0.000	0.000	1.047	0.321	13.250	1.079	14.297	1.126	1.047	0.321
Ammonium Grow Experimental										
0.0	0.006	0.000	0.146	0.065	0.029	0.006	0.174	0.065	0.140	0.065
0.1	10.990	0.182	3.602	0.543	0.206	0.046	11.196 *	0.187	0.000 *	0.265
12.8	10.041	0.143	6.488	0.731	1.156	0.203	11.198 *	0.249	-0.002 *	0.311
23.6	7.252	0.593	1.361	0.315	3.952	0.359	11.204 *	0.693	-0.008 *	0.718
38.4	2.253	0.125	1.688	0.334	9.459	1.364	11.713 *	1.370	-0.517 *	1.382
48.0	0.000	0.000	0.787	0.327	13.312	0.942	14.099	0.998	0.787	0.327
62.3	0.000	0.000	0.647	0.465	15.082	1.327	15.728	1.406	0.647	0.465
70.1	0.000	0.000	1.133	1.073	13.666	1.986	14.799	2.258	1.133	1.073
86.0	0.000	0.000	0.787	0.265	13.753	2.009	14.540	2.026	0.787	0.265
110.0	0.000	0.000	1.096	0.853	13.511	1.140	14.607	1.424	1.096	0.853
Nitrate Grow Control										
0.0	0.067	0.004	0.164	0.043	0.027	0.006	0.192	0.043	0.097	0.043
0.1	16.611	0.616	14.786	1.855	0.041	0.016	16.651 *	0.616	0.000 *	0.872
13.0	15.746	0.726	16.862	2.097	0.094	0.015	16.956	2.097	1.116	2.220
23.7	17.537	0.621	15.733	2.775	0.367	0.053	17.905 *	0.623	-1.253 *	0.876
38.6	16.028	1.715	15.996	2.528	1.076	0.294	17.104 *	1.740	-0.453 *	1.846
48.2	16.544	1.715	14.334	3.001	2.982	0.720	19.526 *	1.860	-2.874 *	1.939
62.4	0.114	0.120	12.910	1.657	4.936	0.999	17.846	1.935	12.797	1.661
70.3	0.128	0.121	11.946	4.915	7.646	0.957	19.992	5.008	11.817	4.917
86.2	0.092	0.111	8.575	3.664	12.312	0.713	20.886	3.732	8.443	3.665
110.0	0.107	0.142	0.464	0.272	20.814	1.214	21.278	1.244	0.358	0.307
Nitrate Grow Experimental										
0.0	0.063	0.004	0.178	0.051	0.029	0.014	0.207	0.052	0.115	0.051
0.1	18.604	0.640	15.998	3.215	0.049	0.013	18.653 *	0.640	0.000 *	0.905
13.0	21.993	0.669	21.235	7.096	0.092	0.014	22.085 *	0.669	-3.432 *	0.926
23.7	19.014	0.894	16.221	1.995	0.603	0.126	19.618 *	0.902	-0.965 *	1.106
38.6	17.823	1.856	14.529	1.638	1.560	0.138	19.383 *	1.861	-0.730 *	1.968
48.2	16.617	1.807	14.542	2.119	3.663	1.734	20.279 *	2.504	-1.626 *	2.585
62.4	0.433	0.135	12.714	2.181	5.875	0.587	18.589	2.299	12.281	2.185
70.3	0.109	0.114	10.258	3.967	10.156	0.542	20.414	4.004	10.149	3.968
86.2	0.094	0.146	4.416	0.903	15.727	1.355	20.142	1.628	4.322	0.915
110.0	0.116	0.123	0.287	0.184	19.782	3.497	20.070	3.502	0.171	0.221

Table A.13. Linear increase in biomass (m) and exponential growth constants (K_{pn} , K_{rf}) with associated standard errors (SE). r^2 =coefficients of determination.

Exp't./ Treatment	Linear Increase			Exponential Increase						
	m ($\mu M \cdot h^{-1}$)	SE	r^2	K_{pn} (h^{-1})	SE	r^2	K_{rf} (h^{-1})	SE	r^2	K_{rf}/K_{pn}
Experiment 1										
Ammonium Supplemented (0-49 h)										
Control	0.189 ± 0.018		0.974	0.016 ± 0.001		0.976	0.035 ± 0.007		0.904	2.18
+ Diatom	0.119 ± 0.019		0.932	0.012 ± 0.002		0.947	0.033 ± 0.007		0.884	2.89
Nitrate Supplemented (49-89 h)										
Control	0.134 ± 0.048		0.721	0.011 ± 0.005		0.721	0.017 ± 0.002		0.925	1.49
+ Diatom	0.119 ± 0.026		0.919	0.008 ± 0.002		0.929	0.015 ± 0.003		0.877	1.77
Experiment 2										
Ammonium Supplemented (16-41 h)										
Control	0.095 ± 0.112		0.264	0.026 ± 0.003		0.990	0.047 ± 0.027		0.752	1.77
+ Diatom	0.197 ± 0.050		0.885	0.027 ± 0.000		1.000	0.044 ± 0.020		0.827	1.63
Nitrate Supplemented (16-45 h)										
Control	0.280 ± 0.027		0.972	0.014 ± 0.002		0.944	0.078 ± 0.008		0.969	5.48
+ Diatom	0.207 ± 0.068		0.753	0.014 ± 0.003		0.871	0.082 ± 0.009		0.966	5.78
Experiment 3										
Ammonium Supplemented (0-38 h, growth constants are for 0-70 h)										
Control	0.595 ± 0.065		0.884	0.035 ± 0.002		0.982	0.047 ± 0.005		0.952	1.34
+ Diatom	0.869 ± 0.181		0.887	0.034 ± 0.004		0.943	0.047 ± 0.005		0.943	1.36
Ammonium Supplemented (38-70 h)										
Control	0.958 ± 0.106		0.976							
+ Diatom	0.750 ± 0.316		0.737							
Nitrate Supplemented (39-110 h)										
Control	0.615 ± 0.013		0.982	0.022 ± 0.002		0.973	0.032 ± 0.002		0.977	1.45
+ Diatom	0.597 ± 0.062		0.958	0.022 ± 0.003		0.926	0.031 ± 0.003		0.971	1.42

Table A.14. Comparison of decreases in NH_4^+ and increases in PN with associated standard errors (SE).

Exp't./ Treatment	NH_4^+ Depletion ($\mu\text{M h}^{-1}$) SE	PN Increase ($\mu\text{M h}^{-1}$) SE	PN Inc.: NH_4^+ Depl.
Experiment 1			
Ammonium Supplemented			
Control	0.226 \pm 0.066	0.189 \pm 0.013	0.836
+ Diatom	0.196 \pm 0.063	0.119 \pm 0.019	0.607
Nitrate Supplemented			
Control	0.023 \pm 0.008	0.049 \pm 0.038	2.130
+ Diatom	0.023 \pm 0.007	0.038 \pm 0.034	1.652
Experiment 2			
Ammonium Supplemented			
Control	0.178 \pm 0.082	0.095 \pm 0.112	0.534
+ Diatom	0.153 \pm 0.042	0.197 \pm 0.050	1.288
Nitrate Supplemented			
Control	0.034 \pm 0.023	0.245 \pm 0.005	7.206
+ Diatom	0.040 \pm 0.010	0.218 \pm 0.006	5.450
Experiment 3			
Ammonium Supplemented			
Control	0.384 \pm 0.001	0.595 \pm 0.065	1.549
+ Diatom	0.394 \pm 0.016	0.869 \pm 0.181	2.206
Nitrate Supplemented			
Control	0.030 \pm 0.003	0.128 \pm 0.025	4.267
+ Diatom	0.023 \pm 0.001	0.117 \pm 0.03	5.087

Table A.15. Comparison of decreases in NO_3^- and increases in PN with associated standard errors (SE).

Exp't./ Treatment	NO_3^- Depletion ($\mu\text{M h}^{-1}$) SE	PN Increase ($\mu\text{M h}^{-1}$) SE	PN Inc.: NO_3^- Depl.
Experiment 1			
Ammonium Supplemented			
Control	0.083 \pm 0.049	0.104 \pm 0.012	1.253
+ Diatom	0.083 \pm 0.050	0.133 \pm 0.029	1.598
Nitrate Supplemented			
Control	0.113 \pm 0.023	0.134 \pm 0.048	1.186
+ Diatom	0.106 \pm 0.016	0.119 \pm 0.026	1.123
Experiment 2			
Ammonium Supplemented			
Control	0.450 \pm 0.147	0.524 \pm 0.005	1.164
+ Diatom	0.372 \pm 0.102	0.501 \pm 0.050	1.347
Nitrate Supplemented			
Control	0.369 \pm 0.033	0.280 \pm 0.027	0.759
+ Diatom	0.433 \pm 0.016	0.207 \pm 0.068	0.478
Experiment 3			
Ammonium Supplemented			
Control	0.296 \pm 0.123	0.130 \pm 0.054	0.439
+ Diatom	0.316 \pm 0.106	0.133 \pm 0.046	0.421
Nitrate Supplemented			
Control	0.589 \pm 0.172	0.615 \pm 0.013	1.044
+ Diatom	0.579 \pm 0.170	0.597 \pm 0.062	1.031

Table A.16. Changes in NH_4^+ concentration normalized to particulate nitrogen (PN) and in vivo fluorescence (IVF) with associated errors (SE). PN_{md} = median PN, IVF_{md} = median IVF.

Exp't./ Treatment	ΔNH_4^+ ($\mu\text{M h}^{-1}$) SE	PN_{md} (μM) SE	$\Delta\text{NH}_4^+/\text{PN}$ (h^{-1}) SE	IVF_{md} (FU) SE	$\Delta\text{NH}_4^+/\text{IVF}$ ($\mu\text{M h}^{-1}\text{FU}^{-1}$) SE
Experiment 1					
Ammonium Supplemented (0-40 h)					
Control	0.226 ± 0.066	10.94 ± 0.22	0.021 ± 0.006	11.48 ± 4.97	0.020 ± 0.010
+ Diatom	0.196 ± 0.063	12.03 ± 0.94	0.016 ± 0.005	12.25 ± 6.09	0.016 ± 0.009
Nitrate Supplemented (0-49 h)					
Control	0.023 ± 0.008	9.77 ± 1.80	0.002 ± 0.001	10.06 ± 2.53	0.002 ± 0.001
+ Diatom	0.023 ± 0.007	12.09 ± 0.74	0.002 ± 0.001	10.06 ± 3.01	0.002 ± 0.001
Experiment 2					
Ammonium Supplemented (0-25 h)					
Control	0.178 ± 0.082	15.52 ± 2.84	0.011 ± 0.006	17.07 ± 14.96	0.010 ± 0.010
+ Diatom	0.153 ± 0.042	13.18 ± 1.27	0.012 ± 0.003	16.43 ± 12.43	0.009 ± 0.007
Nitrate Supplemented (0-25 h)					
Control	0.034 ± 0.023	11.70 ± 0.90	0.003 ± 0.002	11.04 ± 6.80	0.003 ± 0.003
+ Diatom	0.040 ± 0.010	11.11 ± 1.83	0.004 ± 0.001	11.06 ± 6.41	0.004 ± 0.002
Experiment 3					
Ammonium Supplemented (13-38 h)					
Control	0.384 ± 0.001	10.65 ± 2.24	0.036 ± 0.008	12.60 ± 6.08	0.030 ± 0.015
+ Diatom	0.394 ± 0.016	12.67 ± 2.83	0.031 ± 0.007	17.14 ± 5.91	0.023 ± 0.008
Nitrate Supplemented (0-39 h)					
Control	0.030 ± 0.003	7.00 ± 2.24	0.004 ± 0.001	6.77 ± 2.59	0.004 ± 0.002
+ Diatom	0.023 ± 0.001	8.23 ± 2.98	0.003 ± 0.001	8.38 ± 3.02	0.003 ± 0.001

Note: FU - Fluorescence units in calibrated fluorometer.

Table A.17. Changes in NO_3^- concentration normalized to particulate nitrogen (PN) and in vivo fluorescence (IVF) with associated errors (SE). PN_{md} =median PN, IVF_{md} =median IVF.

Exp't./ Treatment	ΔNO_3^- ($\mu\text{M h}^{-1}$) SE	PN_{md} (μM) SE	$\Delta\text{NO}_3^-/\text{PN}$ (h^{-1}) SE	IVF_{md} (FU) SE	$\Delta\text{NO}_3^-/\text{IVF}$ ($\mu\text{M h}^{-1}\text{FU}^{-1}$) SE
Experiment 1					
Ammonium Supplemented (40-64 h)					
Control	0.083 \pm 0.049	16.13 \pm 0.34	0.005 \pm 0.003	27.66 \pm 37.47	0.003 \pm 0.004
+ Diatom	0.083 \pm 0.050	16.22 \pm 0.98	0.005 \pm 0.003	27.37 \pm 42.01	0.003 \pm 0.005
Nitrate Supplemented (49-89 h)					
Control	0.113 \pm 0.023	12.25 \pm 1.84	0.009 \pm 0.002	15.52 \pm 6.22	0.007 \pm 0.003
+ Diatom	0.106 \pm 0.016	14.30 \pm 0.74	0.007 \pm 0.001	16.92 \pm 5.17	0.006 \pm 0.002
Experiment 2					
Ammonium Supplemented (16-41 h)					
Control	0.450 \pm 0.147	20.20 \pm 2.91	0.022 \pm 0.005	32.23 \pm 16.48	0.014 \pm 0.008
+ Diatom	0.372 \pm 0.102	18.81 \pm 1.30	0.020 \pm 0.004	30.08 \pm 10.69	0.012 \pm 0.005
Nitrate Supplemented (16-49 h)					
Control	0.369 \pm 0.033	16.72 \pm 0.91	0.022 \pm 0.002	20.57 \pm 4.54	0.018 \pm 0.004
+ Diatom	0.433 \pm 0.016	15.24 \pm 1.85	0.028 \pm 0.004	21.01 \pm 4.55	0.021 \pm 0.005
Experiment 3					
Ammonium Supplemented (62-41 h)					
Control	0.296 \pm 0.123	45.83 \pm 2.30	0.006 \pm 0.002	93.14 \pm 67.56	0.003 \pm 0.004
+ Diatom	0.316 \pm 0.106	46.00 \pm 2.91	0.007 \pm 0.001	104.84 \pm 33.88	0.003 \pm 0.002
Nitrate Supplemented (24-48 h, 48-62 h, 48-110 h)					
Control	0.096 \pm 0.008	10.64 \pm 2.24	0.009 \pm 0.002	10.92 \pm 8.40	0.009 \pm 0.007
	2.423 NA	18.25 \pm 2.25	0.133 NA	18.35 \pm 10.18	0.132 NA
	0.589 \pm 0.172	32.35 \pm 2.26	0.018 \pm 0.005	48.13 \pm 12.28	0.012 \pm 0.005
+ Diatom	0.197 \pm 0.025	12.25 \pm 2.99	0.016 \pm 0.004	14.15 \pm 7.55	0.014 \pm 0.008
	2.331 NA	19.47 \pm 3.00	0.120 NA	23.20 \pm 10.82	0.100 NA
	0.579 \pm 0.170	35.31 \pm 3.01	0.016 \pm 0.005	60.10 \pm 13.24	0.010 \pm 0.002

Note: FU - Fluorescence units in the calibrated fluorometer.
NA - Number of replicates was too small for standard error calculations.

Table A.18. Changes in nutrient concentration (ND/PN) and of nitrogen assimilation (V_c) normalized to particulate nitrogen with associated standard errors (SE).

Exp't./ Treatment	V_c (h^{-1}) SE	ND/PN (h^{-1}) SE	(ND/PN): V_c
Experiment 1			
Ammonium Supplemented			
Control	0.020 \pm 0.000	0.021 \pm 0.006	1.00
+ Diatom	0.017 \pm 0.000	0.016 \pm 0.005	0.94
Nitrate Supplemented			
Control	0.011 \pm 0.000	0.009 \pm 0.002	0.82
+ Diatom	0.010 \pm 0.000	0.007 \pm 0.001	0.70
Experiment 2			
Ammonium Supplemented			
Control	0.037 \pm 0.002	0.011 \pm 0.006	0.30
+ Diatom	0.039 \pm 0.002	0.012 \pm 0.003	0.31
Nitrate Supplemented			
Control	0.013 \pm 0.002	0.022 \pm 0.002	1.69
+ Diatom	0.014 \pm 0.002	0.028 \pm 0.004	2.00
Experiment 3			
Ammonium Supplemented			
Control	0.020 \pm 0.001	0.028 \pm 0.009	1.40
+ Diatom	0.023 \pm 0.001	0.025 \pm 0.007	1.09
Nitrate Supplemented			
Control	0.024 \pm 0.004	0.018 \pm 0.005	0.75
+ Diatom	0.021 \pm 0.004	0.016 \pm 0.005	0.76

Table A.19. Changes in nutrient and PN concentrations compared with rates of nitrogen assimilation. Nut.D.=nutrient decrease, PN Inc.=PN increase, ρ_c =rate of nutrient assimilation.

Exp't./ Treatment	Nut.D. ($\mu\text{M h}^{-1}$) SE	PN Inc. ($\mu\text{M h}^{-1}$) SE	ρ_c ($\mu\text{M h}^{-1}$) SE	Nut.D.: ρ_c	PN Inc.: ρ_c
Experiment 1					
Ammonium Supplemented					
Control	0.226 \pm 0.066	0.189 \pm 0.018	0.198 \pm 0.013	1.141	0.955
+ Diatom	0.196 \pm 0.063	0.119 \pm 0.019	0.190 \pm 0.019	1.032	0.626
Nitrate Supplemented					
Control	0.113 \pm 0.023	0.134 \pm 0.048	0.139 \pm 0.050	0.813	0.964
+ Diatom	0.106 \pm 0.016	0.119 \pm 0.026	0.138 \pm 0.018	0.768	0.862
Experiment 2					
Ammonium Supplemented					
Control	0.178 \pm 0.082	0.095 \pm 0.112	0.578 \pm 0.129	0.308	0.164
+ Diatom	0.153 \pm 0.042	0.197 \pm 0.050	0.508 \pm 0.065	0.301	0.388
Nitrate Supplemented					
Control	0.368 \pm 0.040	0.280 \pm 0.027	0.215 \pm 0.037	1.712	1.302
+ Diatom	0.432 \pm 0.019	0.207 \pm 0.068	0.208 \pm 0.047	2.077	0.995
Experiment 3					
Ammonium Supplemented					
Control	0.384 \pm 0.001	0.595 \pm 0.065	0.207 \pm 0.059	1.855	2.874
+ Diatom	0.394 \pm 0.016	0.869 \pm 0.181	0.264 \pm 0.080	1.492	3.292
Nitrate Supplemented					
Control	0.417 \pm 0.287	0.615 \pm 0.013	0.716 \pm 0.140	0.582	0.859
+ Diatom	0.413 \pm 0.278	0.597 \pm 0.062	0.707 \pm 0.013	0.584	0.844

Table A.20. Summary of mean total ^{15}N and the ranges of standard errors (SE) associated with replicates ($\mu\text{g-atoms l}^{-1}$). SD=standard deviation of the mean total ^{15}N .

	Mean TN	SD	Range of SE
Experiment 1 (data from Table A4)			
Ammonium Supplemented			
Control	1.43	0.16	0.119 - 0.887
+ Diatom	1.17	0.25	0.072 - 0.985
Nitrate Supplemented			
Control	2.85	0.72	0.512 - 1.426
+ Diatom	2.72	0.52	0.212 - 1.214
Experiment 2 (data from Table A8)			
Ammonium Supplemented			
Control	3.18	0.54	0.398 - 0.804
+ Diatom	3.29	0.42	0.408 - 0.712
Nitrate Supplemented			
Control	1.29	0.17	0.224 - 0.404
+ Diatom	1.25	0.33	0.143 - 0.719
Experiment 3 (data from Table A12)			
Ammonium Supplemented			
Control	14.02	1.67	0.703 - 1.859
+ Diatom	14.15	1.57	0.998 - 2.258
Nitrate Supplemented			
Control	18.33	1.99	1.244 - 5.008
+ Diatom	18.63	1.98	1.600 - 7.096

Table A.21. Changes in ^{15}N inorganic nitrogen and PN with associated standard errors (SE). Max=maximum ^{15}N -PN increase, Final=final ^{15}N -PN increase.

Exp't./ Treatment	Decrease in Inorganic ^{15}N		Increase in Particulate ^{15}N (μM)				Fraction of Int.N Recovered in PN	
	(μM)	SE	Max	SE	Final	SE	Max	Final
Experiment 1								
Ammonium Supplemented								
Control	1.499 \pm 0.199		0.992 \pm 0.289		0.836 \pm 0.311		0.662	0.558
+ Diatom	1.183 \pm 0.124		1.033 \pm 0.180		0.921 \pm 0.163		0.873	0.779
Nitrate Supplemented								
Control	2.242 \pm 0.441		2.720 \pm 0.114		2.720 \pm 0.114		1.213	1.213
+ Diatom	2.042 \pm 0.702		2.339 \pm 0.172		2.339 \pm 0.172		1.145	1.145
Experiment 2								
Ammonium Supplemented								
Control	2.587 \pm 0.282		2.971 \pm 0.589		1.686 \pm 0.796		1.148	0.652
+ Diatom	2.230 \pm 0.679		2.998 \pm 0.412		2.080 \pm 0.374		1.344	0.933
Nitrate Supplemented								
Control	1.443 \pm 0.369		0.979 \pm 0.137		0.930 \pm 0.165		0.678	0.644
+ Diatom	1.522 \pm 0.349		0.892 \pm 0.127		0.827 \pm 0.137		0.586	0.543
Experiment 3								
Ammonium Supplemented								
Control	10.749 \pm 0.178		14.524 \pm 1.959		13.104 \pm 1.181		1.351	1.219
+ Diatom	10.990 \pm 0.182		14.876 \pm 2.328		13.305 \pm 1.161		1.354	1.211
Nitrate Supplemented								
Control	16.504 \pm 0.632		20.773 \pm 2.214		20.773 \pm 2.214		1.259	1.259
+ Diatom	18.488 \pm 0.652		19.733 \pm 3.497		19.733 \pm 3.497		1.067	1.067