To the Graduate Council:

I am submitting herewith a thesis written by Deborah Lynn Muggli entitled "The Uptake of Nitrogenous Nutrients by Phytoplankton in the Waters of the Fram Strait during Spring 1989." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Walker O. Smith, Jr., Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

THE UPTAKE OF NITROGENOUS NUTRIENTS BY PHYTOPLANKTON IN THE WATERS OF THE FRAM STRAIT DURING SPRING 1989

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

Three different aspects of the nitrogenous nutrition of phytoplankton in the Fram Strait were examined: the effect of irradiance on nitrate and ammonium uptake rates, the effect of nutrient (nitrate, ammonium) concentration on nutrient (nitrate, ammonium) uptake rates, and the effect of ammonium concentration on nitrate uptake rates. All experiments were performed with natural assemblages of phytoplankton. Labelled nutrients were added in tracer amounts, and incubations were carried out under natural light conditions. Both nitrate and ammonium uptake rates were strongly dependent on irradiance, and the relationship followed the model used by Priscu (1989). Ammonium uptake rates were always inhibited by surface irradiance levels. The phytoplankton present at this time of year were able to utilize nitrate at lower irradiance levels than ammonium, with the average optimal percentage of surface irradiance for nitrate and ammonium uptake being 18.0 and 77.8%, respectively. The relationship between nutrient concentration and nutrient uptake could be characterized by the Michaelis-Menton model. Lastly, there was a definite negative relationship between ammonium concentration and nitrate uptake rates. The average maximal extent of inhibition of nitrate uptake rates by ammonium was 40%, and occured at ammonium concentrations equal to or greater than ca. 2.5 μM. Ambient ammonium concentrations encountered during this study in the Fram Strait were capable of suppressing in situ nitrate uptake rates.

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CHAPTER I

INTRODUCTION

Scientists have been seeking to identify and quantify the processes which regulate algal production in natural waters throughout history (McCarthy 1980). The large quantities of carbon fixed by marine phytoplankton (55×10^9 dry tons of carbon per year, Whitaker 1970) play a critical role in maintaining our atmospheric carbon dioxide level, as well as serving as the primary food source for the rich and diverse life found in the world's oceans. Planktonic algae are similar to higher plants in that they require adequate light and nutrients to maintain themselves and grow. Nitrate, ammonium, phosphate, and in some cases silicic acid, are all nutrients required by marine phytoplankton. Both light and nutrients can limit the growth of these organisms, but it has been found that for most of the world's oceans, nitrogen is the nutrient that limits the total production in the upper ocean (Eppley & Peterson 1979).

Nitrogen is available to phytoplankton in different forms and via different mechanisms. Dissolved forms of nitrogen present in the ocean that phytoplankton are able to utilize include nitrate, nitrite, ammonium, urea, and disolved amino acids. Nitrate is the most common inorganic form of nitrogen found in the ocean, and ambient concentrations of nitrate range from 0.01 to 50.0 μM (Parsons et al. 1984). Nitrite is normally present in the

euphotic zone in low concentrations, from undetectable to 5.0 μM (Parsons et al. 1984). Ammonium may be very abundant in productive (especially shallow) waters. In oceanic waters, ammonium concentrations range from undetectable to 5.0 μM. The concentrations of these inorganic forms of nitrogen vary greatly from region to region, and depend on both biological and physical processes. Organic forms of nitrogen present in the water column include dissolved amino acids and urea. The amount of dissolved organic nitrogen (DON) present in the water column often greatly exceeds the amount of inorganic nitrogen, but most of the DON cannot be directly utilized by phytoplankton. Amino acids and urea comprise a small part of the DON, and range from 0.025 to 1.4 μM and up to 8.9 μM, respectively (McCarthy 1980). In the open ocean, nitrite, urea, and amino acids are generally found in very low concentrations (less than 0.1 μM), whereas nitrate and ammonium can be more abundant and can reach concentrations of over 50 μM and 5 μM, respectively (Parsons et al. 1984).

The way in which nitrogenous nutrients are generated and made available to phytoplankton differs, and Dugdale & Goering (1967) catagorized nitrogenous nutrients as either 'new' or 'regenerated'. New forms of nitrogen are made available to phytoplankton in the upper ocean by predominantly physical processes such as upwelling or deep vertical mixing, with the most common form brought up from depth being nitrate. Regenerated nitrogen is nitrogen that is formed within the upper layer of the

water column, and cycles or is regenerated without flux to depth. Ammonium is formed either by zooplankton excretion or bacterial ammonification, and any urea or amino acids formed by heterotrophic organisms are all considered regenerated forms of nitrogen. Eppley & Peterson (1979) elaborated on this concept, and labelled production resulting from nitrate as new production, and ammonium-based production as regenerated production.

Because ammonium is a more reduced form of nitrogen than nitrate, it would be more efficient energetically for phytoplankton to utilize ammonium before nitrate when both are present (McCarthy & Carpenter 1983). In natural waters, it has been found by numerous researchers that marine phytoplankton prefer ammonium over nitrate when nonlimiting amounts of both nutrients are available (Dugdale & Goering 1967, Eppley et al. 1969, MacIsaac & Dugdale 1972, McCarthy et al. 1977, Hains & Wheeler 1978, Glibert et al. 1982, Terry 1982). However, when ammonium concentrations are reduced, nitrate is the form utilized. This phenomenon is generally observed throughout the plant kingdom, namely, that nitrate is not utilized until the concentration of ammonium is greatly reduced or totally exhausted (Syrett & Morris 1963, Bayley et al. 1972, Moore & Black 1979). The actual concentration of these nutrients before a change in utilization by natural phytoplankton assemblages occurs is variable and changes with species composition, light regime, and other nutrients. Ammonium concentrations as low as 0.5 μM have

been found to supress the uptake of nitrate (MacIsaac & Dugdale 1972).

The actual mechanism for the inhibition of nitrate uptake by ammonium is still not known, but many possibilities have been examined. Nitrate is transported across the plasma membrane (uptake) into the cell, where nitrate reductase then reduces nitrate to nitrite. There is generally a nitrate 'pool' within the cell, indicating that nitrate is transported into the cell across a negative concentration gradient. Nitrite is then reduced to ammonium by nitrite reductase. Ammonium is the most reduced form of nitrogen and is incorporated into organic compounds by way of the glutamate dehydrogenase pathway and/or the glutamine synthetase-glutamate synthase pathway (Lea & Mifflin 1979). In 1962 Syrett & Morris found that the inhibition of nitrate uptake was not due to the presence of ammonium alone, but to ammonium assimilation. They also concluded that inhibition acted on the reduction of nitrate to nitrite step. The reduction of nitrate to nitrite is still thought to be the reaction inhibited by ammonium in the reduction process of nitrogen (Guerrero et al. 1981), since the accumulation of nitrite is seldom observed.

Although ammonium can cause the inactivation or repression of nitrate reductase, the presence of ammonium causes the more immediate inhibition of nitrate transport into the cell (Syrett & Morris 1963, Vennesland & Guerrero 1979, Losada et al. 1981). The addition of low concentrations of ammonium causes a prompt

cessation of nitrate uptake (Thacker & Syrett 1972, Ohmori et al. 1977, Tischner & Lorenzen 1979, Ullrich 1981) without a significant change in the cellular level of nitrate reductase activity. The ability of the cells to utilize nitrate is restored immediately after exhaustion of ammonium in the outer medium (Thacker & Syrett 1972, Tischner & Lorenzen 1979, Ullrich 1981). That the nitrate transport step (uptake) is the target of short-term ammonium inhibition has been demonstrated by Cresswell & Syrett (1972) using the diatom Phaeodactylum tricornutum.

The actual transport of nitrate into the cell is different for different organisms. However, one unifying fact is that they all appear to be mediated by specific carriers and are all dependent on metabolic energy (Losada et al. 1981, Ullrich 1981). Falkowski (1985) has reported a (NO_3^-,Cl^-)-activated adenosine trisphosphatase responsible for nitrate transport in Skeletonema costatum. Irradiance and temperature greatly influenced the ATP pool and hence the uptake of nitrate in this species.

Various factors can control or regulate the ability of phytoplankton to utilize the nitrogenous nutrients available to them. The ambient concentration of the available nitrogenous nutrients, irradiance, and nutrients other than nitrate or ammonium may all effect the uptake and assimilation of nitrogen by phytoplankton. The uptake of a nitrogenous nutrient can depend on the ambient concentration of that nutrient. This relationship was first characterized in Dugdale (1967), in which he related the

rate of nutrient uptake to nutrient availability, and mathematically described the relationship by a hyperbolic equation. The form of the equation is essentially the same as the Monod equation (Monod 1942) used to describe the relationship between substrate-limited bacterial growth rates and substrate concentration, as well as the Michaelis-Menton equation used to describe enzyme-substrate kinetics. The initial slope of the curve describes the uptake of the nutrient while that nutrient is limiting, and can be used for comparative and predictive purposes. If a given phytoplankter can utilize a nutrient at a lower concentration than another phytoplankter, the first will be able to maintain itself at steady-state and proliferate at a lower nutrient concentration, surviving and perhaps outcompeting the second. Also, if the ambient concentration of the nutrient is known, and given the uptake curve for that particular set of conditions, the rate of uptake by the phytoplankton can be estimated along with whether the phytoplankton's growth is being limited by that particular nutrient.

Irradiance plays a very interesting and not fully understood role in the uptake of nitrogenous nutrients by phytoplankton. Light is and can be treated mathmatically as a necessary substrate for nitrogen utilization (Priscu 1984). The first quantitative attempt made at describing the relationship between the uptake of nitrogenous nutrients and light was by MacIsaac and Dugdale (1972). "Certain variability in natural uptake can be attributed

to nutrient concentration variations (MacIsaac & Dugdale 1969), but light intensity also is important in controlling uptake, either through photosynthesis or directly (MacIsaac & Dugdale 1972)." They described the relationship between nitrate or ammonium uptake and irradiance with the same hyperbolic equation used for substrate-limited uptake, with the parameters given in units of light irradiance rather than substrate concentration. However, whereas high concentrations of substrate have no added effect on the maximum uptake rate of that substrate, high irradiance levels can have an inhibitory effect on the uptake of nitrogenous nutrients. The initial model proposed by MacIsaac and Dugdale and used by many others does not allow for any inhibitory response of the phytoplankton. In 1984 Priscu used the Michaelis-Menton equation to describe the uptake of nitrate and ammonium by polar freshwater phytoplankton at low irradiance levels, and performed a linear regression on the higher irradiance uptake data, with the slope of the regression being an indicator as to the degree of inhibition of uptake. A few years later he applied a four-parameter model adapted from Platt et al. (1980) that more accurately characterized the relationship between irradiance and nitrate or ammonium uptake (Priscu 1989). The inhibition of nitrogen uptake by high irradiance levels has been found to occur in natural waters (Priscu 1984, Dodds & Priscu 1989, Priscu 1989) and this along with the strong dependence of nitrogen uptake on irradiance has some important ecological implications. For

example, Nelson and Conway (1979) emphasized the importance of the effect of irradiance on nutrient uptake in areas of the ocean where the depth of the mixed layer is below the euphotic zone. The sudden exposure to high irradiance levels may play a more significant role in the utilization of available nutrients by the phytoplankton than the ambient nutrient concentration regime.

The mechanisms by which irradiance regulates nitrate and ammonium uptake and assimilation are still not clear (Miflin & Lea 1977, Guerrero et al. 1981, Syrett 1981), although nitrogen assimilation is ultimately dependent upon light as an energy source. Moreover, irradiance seems to effect nitrate and ammonium uptake differently. For example, irradiance has been found to inhibit nitrate uptake more strongly than ammonium uptake in Antarctic freshwater phytoplankton assemblages (Priscu 1984, Priscu 1989). Also, it has been demonstrated that ammonium can be utilized at lower irradiance levels than nitrate by some phytoplankton assembleges (Priscu 1984). These phenomenon seem to indicate that ammonium uptake by phytoplankton is less light-dependent that nitrate uptake (Falkowski & Stone 1975, Nelson & Conway 1979, Ronner et al. 1983, Dodds & Priscu 1989). Falkowski & Stone (1975) found that the source of ATP utilized for nitrate uptake was primarily from cyclic photophosphorylation (PSI) in natural assemblages from Knight Inlet, B. C., Canada. This would account for the strong irradiance dependence of nitrate uptake found to occur in some phytoplankton assemblages. Nelson and

Conway (1979) reported that nitrate was almost never taken up in the dark by phytoplankton in the Baja California and northwest Africa upwelling systems, whereas both ammonium and silicic acid dark uptake rates ranged from undetectable to their maximum rates found at higher irradiance levels.

This study of the uptake of nitrogenous nutrients by phytoplankton was performed with natural assemblages in the Fram Strait region of the East Greenland Sea during spring, 1989. The Fram Strait is a very dynamic and complex area hydrodynamically. Polar water flows south along the east Greenland shelf forming the west side of the Arctic front, and warmer Atlantic water (3-4 °C) flows north along west Spitsbergen forming the east side of the Atlantic front (Figure 1). The Arctic water is of lower salinity than the Atlantic water (34.8-35 per mil) due to ice melt, and the large body of water between the two fronts is known as Arctic intermediate water (Paquette et al. 1975). The variations in temperature and salinity of the large water masses interacting in this region cause many mesoscale physical events (Johannessen et al. 1983, Wadhams & Squire 1983). In particular, eddies seem to be an episodic but prevalent feature in both the frontal regions and the marginal ice zone. The biological enhancement brought about by these features has been the topic of recent research (McRoy & Goering 1974, Alexander 1980, Smith et al. 1985, Smith et al. 1987, Niebauer & Smith 1989), and the specific region of study for this research, the Fram Strait, has been found to exhibit

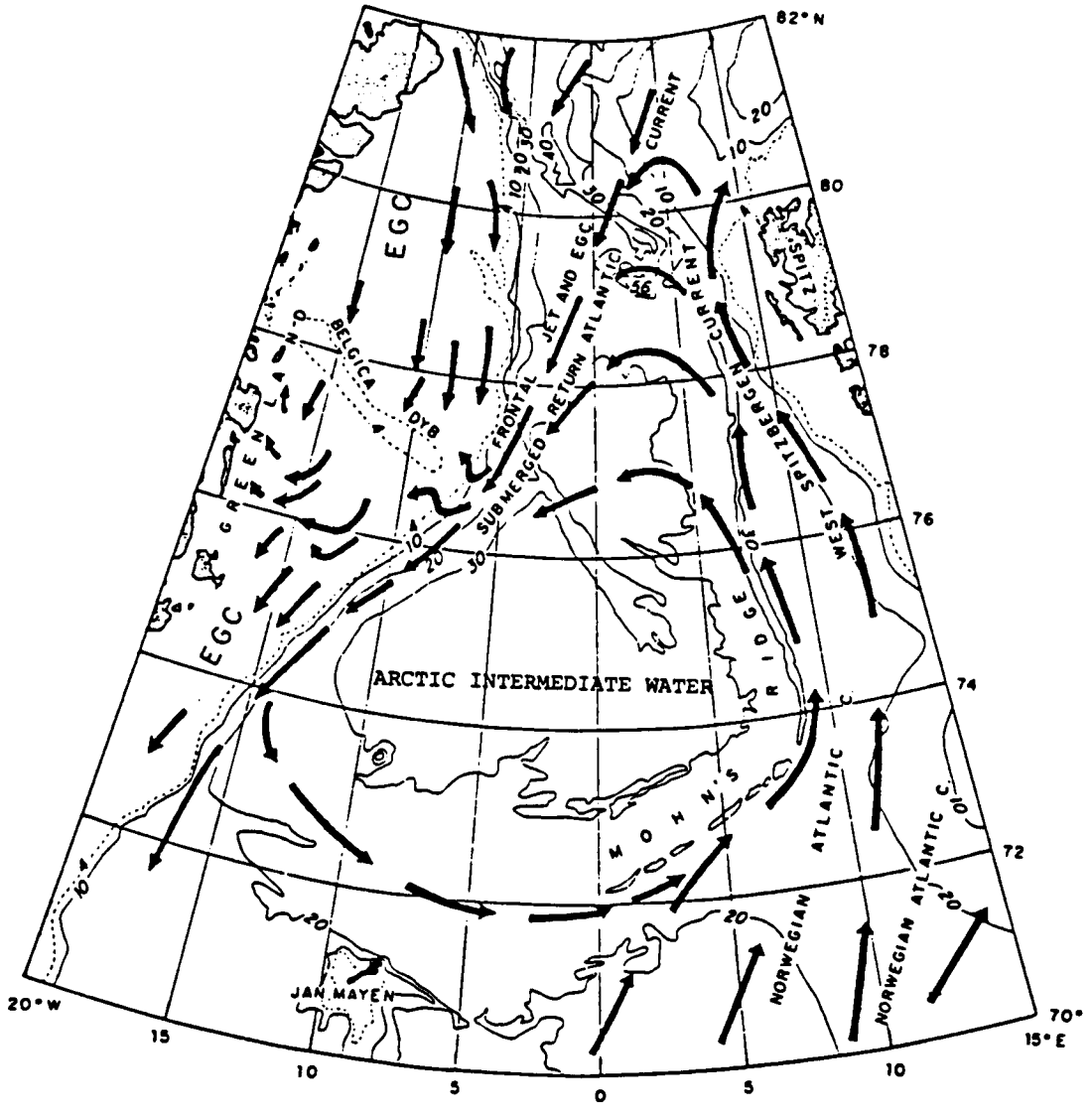


Figure 1. Current patterns in the Greenland-Norwegian Sea (Modified from Paquette et al. 1975).

enhanced primary productivity for polar waters (Smith et al. 1987).

Along with the complex physical features, polar regions such as the Fram Strait exhibit extreme seasonal variations in irradiance, with complete darkness ocurring in winter months and continuous illumination occuring during the summer. Because of the low solar angle at high latitudes, as much as 40% of the surface illumination can be reflected off of the sea surface (Sverdrup et al. 1942). The study area of this research included the ice edge as well as the open ocean, further complicating the light regime imposed on the natural assemblage of phytoplankton present. The marginal ice zone is characterized by having a low salinity meltwater layer at the surface near the receeding ice edge, providing stability in which phytoplankton remain in the euphotic zone and grow. However, the ice edge is a very dynamic feature, and broken ice and snow may be carried and moved by wind alone. Snow and ice greatly reduce the amount of irradiance available to the phytoplankton, reflecting 80-99% of the incoming radiation (Maykut & Grenfell 1975). Hence, the phytoplankton in this area are exposed to a very harsh and limited light regime, where irradiance is a valuable resource and limits productivity for most of the year.

This research attempted to quantify the effect that irradiance had on nitrate and ammonium uptake by natural assemblages of phytoplankton in the Fram Strait. The effect of

nutrient concentration on nutrient uptake was also studied. As a bloom progresses, nutrients are depleted and can be the major factor limiting growth in the phytoplankton assemblege. A third aspect of the nitrogenous nutrition of the phytoplankton in the Fram Strait that was investigated was the effect of ammonium on nitrate uptake. These three types of experiments performed with assemblages of phytoplankton in the Fram Strait should give an idea as to the physiological capabilities of polar phytoplankton relative to other phytoplankton, result in a better understanding of the factors important in limiting their growth, and may in the future aid in characterizing the onset and fate of the phytoplankton bloom in the Fram Strait.

CHAPTER II

MATERIALS AND METHODS

This research was conducted on natural assemblages of phytoplankton in the Fram Strait region of the East Greenland Sea during the April 4 - May 22 leg of the CEAREX (Coordinated Eastern ARctic EXperiment) expedition. All stations were between 78 and 80°N latitude and 4°W and 10°E longitude, including the stations where experiments were conducted (Figure 2). The study area included both open water and the ice edge. During the time of year this study took place, nearly continuous (albeit at a low solar angle) daylight was experienced.

Experimental

Water samples were obtained from 10 l Niskin bottles mounted on a rosette frame. A total of twelve Niskin bottles were attached to the rosette, along with conductivity, temperature, flourescence, and depth (CTD) sensors. Generally, water samples were taken within the euphotic zone which corresponded to 100, 50, 30, 15, 5, 1.0, and 0.1% of surface irradiance levels. The in situ irradiance regime was determined by a MER (Biosperical Instruments) cast immediatly preceeding the CTD cast. Niskin bottles were drained into carboys which were shaken frequently to maintain homogeneity of the seawater, and samples were then taken from the carboys.

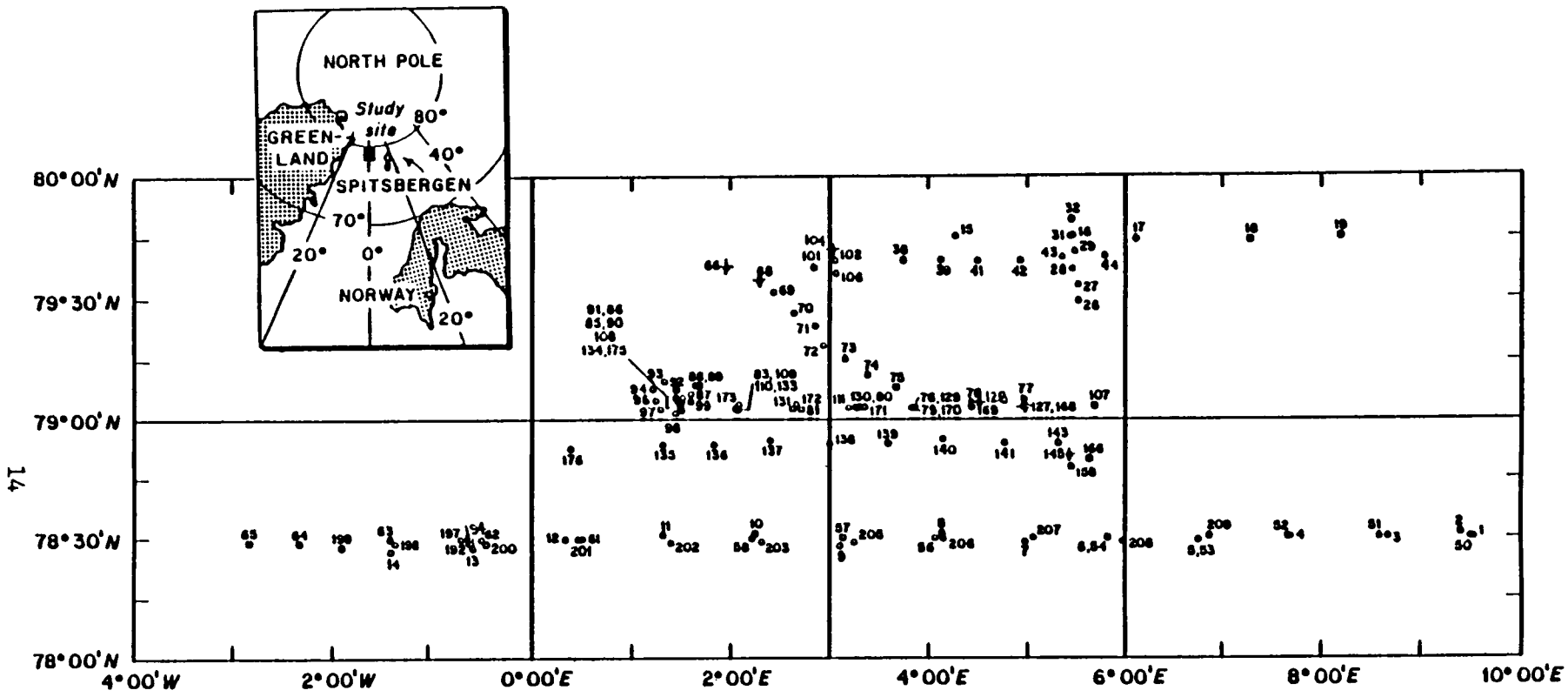


Figure 2. Map of Fram Strait showing all stations sampled during CEAREX, including experimental stations.

The irradiance vs. nitrate or ammonium uptake experiments were all carried out under natural irradiance conditions except at Station 066, where the samples were incubated under artificial irradiance (4.8×10^{16} quanta s^{-1} cm^{-2}). Irradiance levels were determined using a Biospherical Quantum Scalar Irradiance meter, which measured the number of photons arriving at a given point from all directions within the photosynthetically active radiation range (400 - 700 nm). Water samples drawn from the carboys were placed in 1.1 liter polycarbonate bottles, and neutral density screens were used to simulate irradiance levels representing 50, 30, 15, 5, 1, and 0.1% of surface irradiance. The concentration of ambient nutrients in the water samples were obtained shortly after the water was collected by an Alpchem Autoanalyzer.
A 10% addition of ^{15}N-labelled nitrate or ammonium (99.9% carrier free) was made for each water sample, and screened bottles were then incubated for 24 h in an on-deck plexiglas incubator equipped with flowing sea water. A 10% addition of labelled nutrient was considered a tracer experiment, where the nutrient was added in a small enough concentration so as not to significantly effect or alter the rate of uptake by the phytoplankton (Dugdale & Goering 1967). After the 24-h incubation period, water samples were filtered onto precombusted (450°C for 4 h) 25 mm Whatmann GF/F filters and rinsed with filtered sea water. The filters were then placed in precombusted vials and dried and stored at 60°C until analyzed. Separate filtrations for the measurement of chlorophyll

a, particulate carbon, and particulate nitrogen were done at the beginning of all experiments.

A modified version of the model used by Priscu (1989) was used to fit the irradiance vs. nitrogen uptake data. Dark uptake rates were not measured during these experiments, so the dark uptake term used by Priscu (1989) was excluded. The data were fit with the program FitAll (copyright 1985 by MTR software) which used Marquardt's algorithm to determine the best fit. The equation used is as follows:

$$V = V_{max}(1-e^{-a})e^{-b}$$

where:
- $a = \alpha I/V_{max}$
- $b = ßI/V_{max}$
- V = specific nitrogen uptake rate (h^{-1})
- V_{max} = maximum specific nitrogen uptake rate in absence of inhibition (h^{-1})
- I = % surface irradiance
- α = initial slope of curve
- ß = slope of inhibition part of curve

Values of K_{1t} (in units of % surface irradiance, the irradiance level at which the uptake rate is one half that of the maximum uptake rate), were determined graphically.

Unscreened 1.1 liter polycarbonate bottles were used for the nutrient kinetic experiments. For these experiments the ambient concentration of the nutrient in question had to be near zero. This condition was only found to occur in the water column at the very end of the cruise and subsequently, water samples were kept in the on deck incubator until the nutrients were depleted. Additions from 0 to 3 μM (in one case 9 μM) of labelled nitrate or

ammonium were made for each experiment. Nine different substrate concentrations were used, and the bottles were incubated in the on deck incubator for 24 h. Incubation was terminated by filtration and storage as described above.

The nutrient concentration vs. nutrient uptake experiments were fit with the Michaelis-Menton equation (MacIsaac & Dugdale 1969):

$$V = V_{max} \times S/(S+K_t)$$

where: V = specific nutrient uptake (h^{-1})
V_{max} = maximal rate of nutrient uptake (h^{-1})
S = nutrient (NO_3^- or NH_4^+) concentration (μM)
K_t = transport constant; the concentration at which $V=V_{max}/2$ (μM)

This model was fit to the data by using fitAll.

The ammonium inhibition experiments required ambient ammonium levels to be close to zero. Unlabelled ammonium was added to 9 bottles in concentrations ranging from 0 to 3 μM. The ambient nitrate concentration was determined and a 10% addition of labelled nitrate was added to each bottle. The bottles were again incubated for 24 hrs in the on deck incubator and processed as in the other experiments.

There has been no quantitative description as of yet for the relationship between nitrate uptake and ammonium concentration for polar phytoplankton. Models for this relationship have not been developed, and Priscu et al. (1989) fit lines to their data by inspection to indicate the general trends.

Sample Preparation

The percent of ^{15}N atoms incorporated into the particulate matter was determined using a Kamazawa's ^{15}N sampling device system and a Jasco model N-150 emission spectrometer. Sample preparation and preparation of the discharge tubes followed a modified Dumas combustion method (Fiedler & Proksch 1975). Discharge tubes were made of Pyrex with an outer diameter of 7 mm. The tubes were combusted (560°C for 4 hrs) prior to use to eliminate any organics adhering to the surface. Filters were ground with copper oxide (previously combusted at 560°C for 4 hrs) using a mortar and pestle. The amount of CuO was used in excess and served to both aid in the grinding of the filter until a homogeneous mixture was obtained, and to convert all forms of organic nitrogen present on the filter into nitrogen gas upon combustion. Ground samples were transferred into discharge tubes that already had calcium oxide (activated by combusting at 1000°C for 2 hrs) in them. The CaO absorbed any water vapor and other gases released when the sample was combusted, which would interfere with the emission spectrum of nitrogen gas. A few chips of copper were added to the top of the sample to prevent the sample from being drawn up into the vacuum. The discharge tubes were evacuated using a Kamazawa's sampling device. Tubes were evacuated down to 0.003 torr and sealed with a hand torch. All forms of nitrogen present in the sample were then converted to

nitrogen gas by combusting the sealed discharge tubes at 560°C for 6 h.

Correct sample preparation was critical, since too much or too little nitrogen in the tube would not allow the emission spectrometer to excite the sample, and no reading could be obtained. The amount of particulate nitrogen on the filters was determined by using a Perkin-Elmer 240B elemental analyzer on separate filters that were prepared in parallel with those used for the experiments. It was essential to know how much particulate nitrogen was on the sample filters before the discharge tubes were filled and sealed.

N-15 Analysis

The percent of ^{15}N atoms present in the formed nitrogen gas was determined by using a Jasco model 150 emission spectometer. Peaks are given off which represent ^{14}N-^{14}N molecules and ^{14}N-^{15}N/^{15}N-^{15}N molecules, where the height of the peak is proportional to the abundance of that molecule present in the gas. The percentage of ^{15}N atoms in the nitrogen gas were calculated using the following equations (^{15}N analyzer instruction manual 1981):

$$R=I_{28}/(I_{29} \times M) \qquad \text{and} \qquad {}^{15}N \text{ atom } \%=100/(2R+1)$$

where: I_{28} = the height of the ^{14}N-^{14}N peak
I_{29} = the height of the ^{14}N-^{15}N peak
M = multiplier value for $^{29}N^{30}N$

Errors Associated with N-15 Analysis

The error associated with reading a given sample on the emission spectrometer varied with the percentage of ^{15}N atoms present in the gas sample, and ranged from 0.005 to 0.010 ^{15}N atom percent. The error involved in reading a sample never resulted in a variation of more than 2% of the ^{15}N atom percent value for that sample.

The error associated with rerunning a sample in its entirity (i.e., evacuation and reading on the emission spectrometer) ranged from 0.003 to 0.050 ^{15}N atom percent. This again amounts to less than 0.5 to 2.0% error in the final ^{15}N atom percent numbers.

The error involved in the analysis of ^{15}N atom percent after the samples have been taken is very small compared to the errors associated with taking the sample in the first place. Large differences in sample replicates were a result of events occurring during sampling, such as the settling of particulate matter and subsequent filtration of two unequal replicates from the same bottle.

Other Calculations

Specific uptake rates were calculated using the formula (Dugdale & Wilkerson 1986):

$$V = (1/T)\ln[(^{15}N_{enr}-F)/(^{15}N_{enr}-^{15}N_s)]$$

where: V = specific uptake rate of the nutrient (h^{-1})
$^{15}N_s$ = atom % ^{15}N in the sample (particulate matter)
$^{15}N_{enr}$ = atom % ^{15}N in the initially labelled inorganic fraction
F = natural abundance of ^{15}N
T = incubation time (h)

The transport rate was calculated by multiplying the specific uptake rate with the particulate nitrogen value for that sample:

$$\rho = V \times PN$$

where: ρ = transport rate [μg N l^{-1} h^{-1}]
PN = particulate nitrogen value [μg N l^{-1}]

Relative preference indicies were calculated when possible by using the following equation (McCarthy et al. 1977):

$$RPI_{NH_4^+} = [\rho_{NH_4^+}/(\rho_{NO_3^-} + \rho_{NH_4^+})]/[[NH_4^+]/([NO_3^-] + [NH_4^+])]$$

where: $\rho_{NH_4^+}$ = transport rate of ammonium (μg N l^{-1} h^{-1})
$\rho_{NO_3^-}$ = transport rate of nitrate (μg N l^{-1} h^{-1})
NH_4^+ = ammonium concentration (μM)
NO_3^- = nitrate concentration (μM)

A calculated RPI value of 1 indicates equal affinity for ammonium and nitrate by the phytoplankton. If the $RPI_{NH_4^+}$ is greater than one, it reflects a preference for ammonium. The same applies for the RPI of nitrate.

f-ratios were calculated from the equation (Eppley & Peterson 1979):

$$f = \rho NO_3^-/[\rho NH_4^+ + \rho NO_3^-]$$

An f value represents the fraction of the total production which is new production. A high f value indicates that a large portion of the production is a result of nitrate utilization and may be available for export. Conversely, a small f value is an indicator

of extensive recycling of nitrogenous nutrients within the system, which implies a greater dependency on ammonium.

CHAPTER III

RESULTS

Overall

The timing of the CEAREX expedition was such that we encountered the beginning of the spring bloom and were able to monitor its progression through time. Phaeocystis pouchettii seemed to be the dominant phytoplankter within the bloom from mid-April until we left the region on May 22. Phaeocystis pouchettii blooms have often been recorded as being 'dominated' by this phytoplankter, with minimal co-occurrence of other species (Sieburth 1960, 1979, Smayda 1980, Chang 1983, WeiBe 1983). This species has been encountered before in the Fram Strait, but the timing of its occurance seems to vary. Whereas we encountered large blooms of Phaeocystis pouchettii in April and May of 1989, it has also been found to occur in May (1987) and June (1988) as well (Keene, pers comm). Phaeocystis pouchettii belongs to the class Prymnesiophyceae, and can occur in natural waters as either a single flagellated cell or as a massive colony bound by a gelatenous polysacharride sheath (Guillard & Hellebust 1971, Lancelot 1984). In the flagellated stage the cells are 3-7 um in diameter. However, a colony can be milimeters in length and contain thousands of cells (Verity et al. 1988), with the very large blooms exceeding 10^8 colonies per cubic meter (Kashkin 1963). In polar areas this species forms massive mucilaginous blooms in the spring which can dominate the plankton in terms of biomass and primary productivity

(Joiris et al. 1982).

This study therefore, represents an analysis of the uptake of nitrogenous nutrients by a natural assemblage dominated by Phaeocystis pouchettii. At the beginning of the cruise nutrient concentrations were near their winter maxima (13 μM NO_3, 5-6 μM $Si(OH)_4$, 1 μM PO_4), and were depleted to almost undetectable levels in surface waters by the beginning of May (Codispoti, pers. comm). However, silicic acid concentrations remained fairly uniform as the bloom progressed, and did not decrease in parallel with nitrogen and phosphorous. Transects 1 and 12 are of the same location sampled at different times, and contours of nitrate, silicic acid, and chlorophyll a are included to represent general trends in the area (Figures 3, 4). In the time span between April 10 and May 15, chlorophyll a maximum concentrations increased from 1 mg m^{-3} to greater than 4 mg m^{-3}, and nitrate minimum concentrations decreased from 11 μM to undetectable levels. Silicic acid concentrations generally remained constant at ca. 5 μM, except for occasional patches of depletion. Chlorophyll a concentrations ranged from 0.01 to over 5 mg m^{-3} in the upper 150 m.

Profiles of temperature, fluorescence, and density are shown in Figures 5-8 for stations where irradiance experiments were conducted. Overall, water temperatures ranged from -1.0 to 3.0°C. The pycnocline was generally shallow, occuring within the upper 20 m. The euphotic zone was within the top 50 m for all light experiment stations, and included the pycnocline within it.

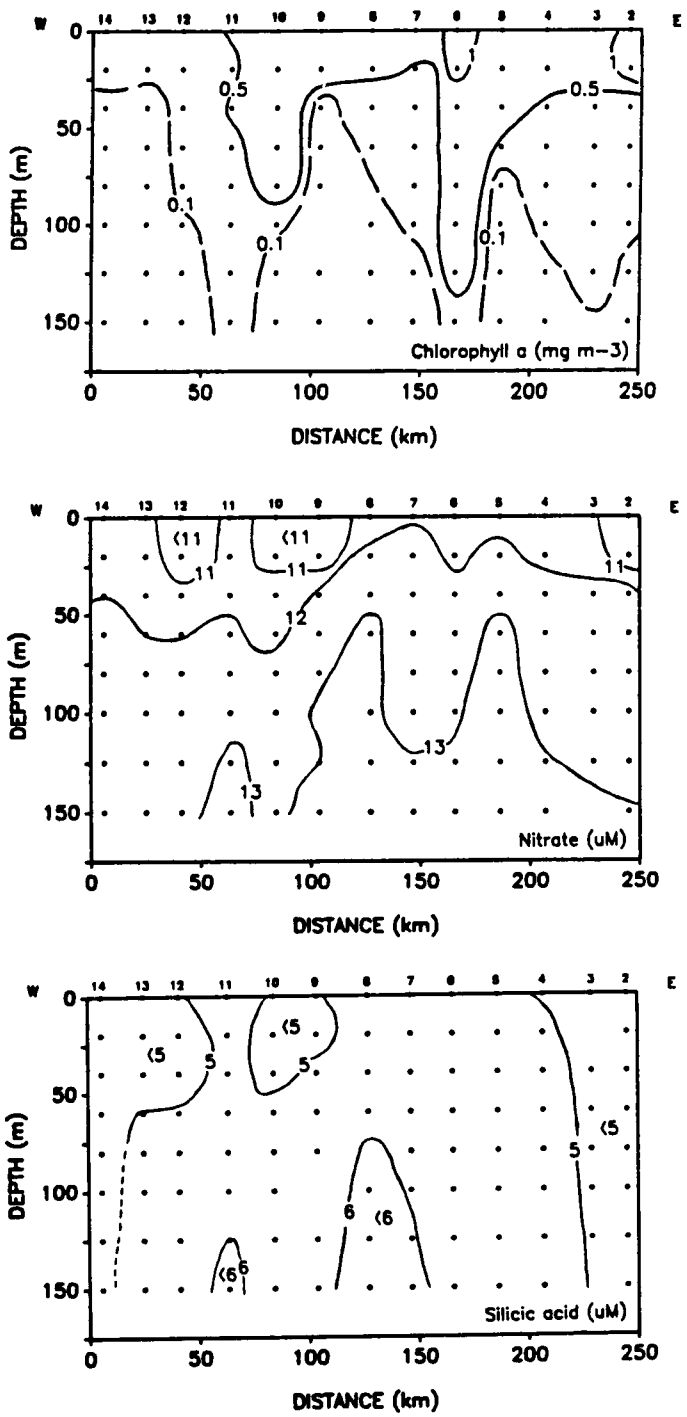


Figure 3. Contour diagrams of chlorophyll a, nitrate, and silicic acid from transect 1 during CEAREX.

CEAREX: TRANSECT 12

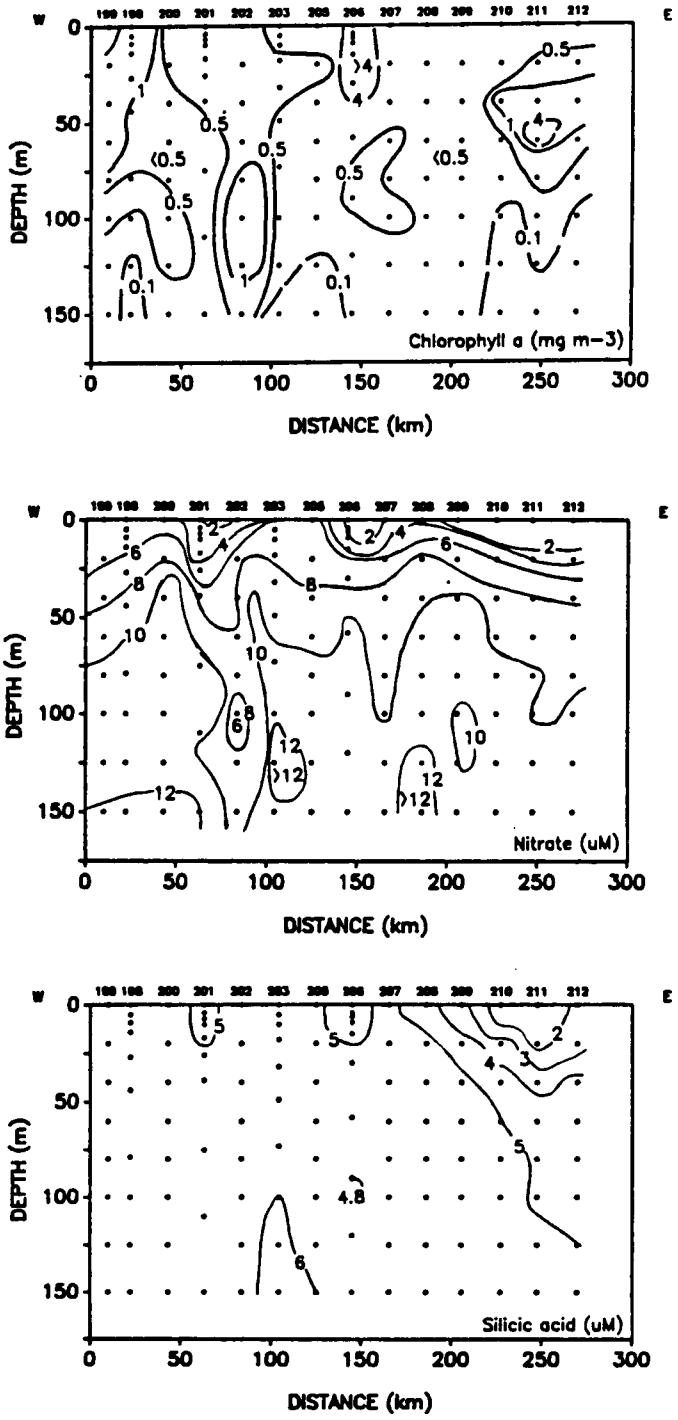


Figure 4. Contour diagrams of chlorophyll a, nitrate, and silicic acid from transect 12 during CEAREX.

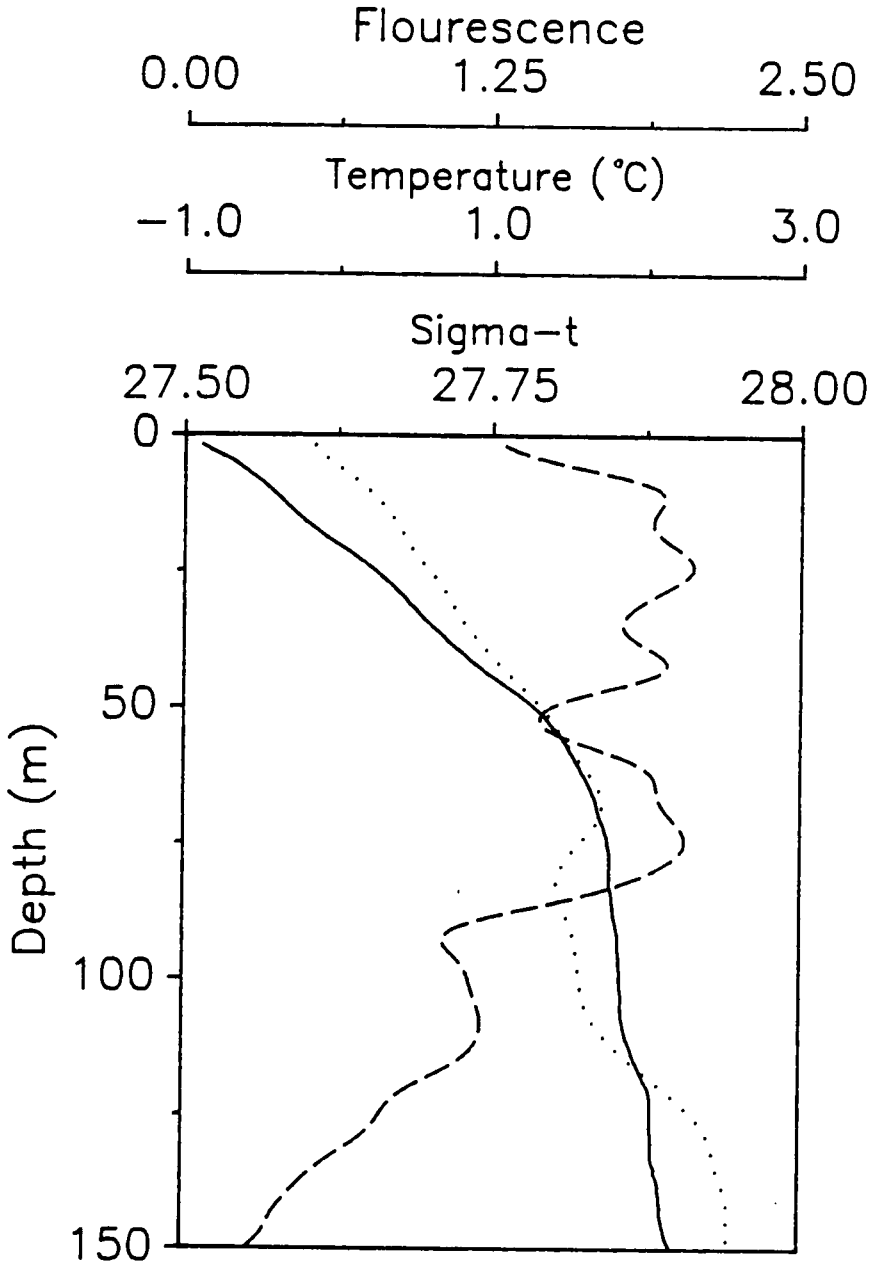


Figure 5. Depth profile for Station 066. Figure shows sigma-t (solid line), temperature (dotted line), and flourescence (dashed line) within the upper 150 m.

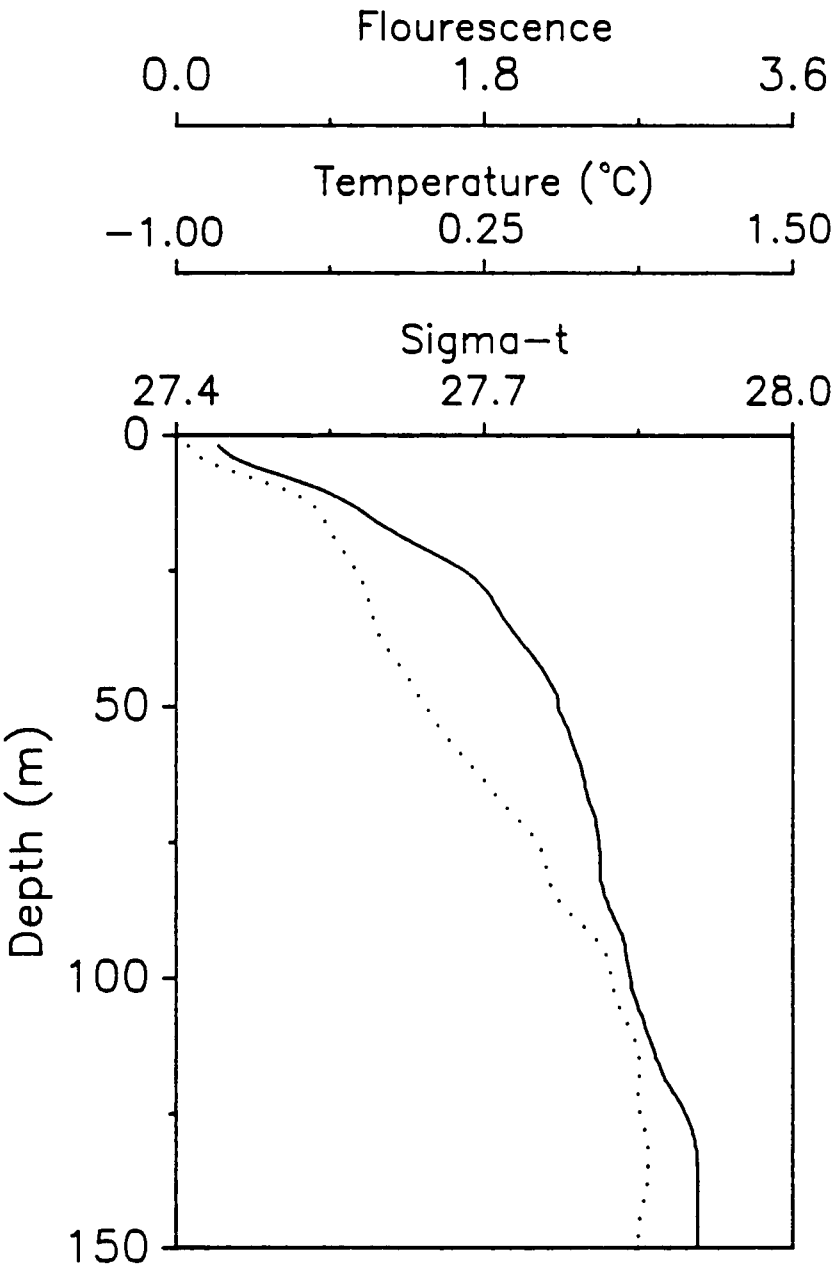


Figure 6. Depth profile for Station 104. Figure shows sigma-t (solid line), temperature (dotted line), and flourescence (dashed line) within the upper 150 m.

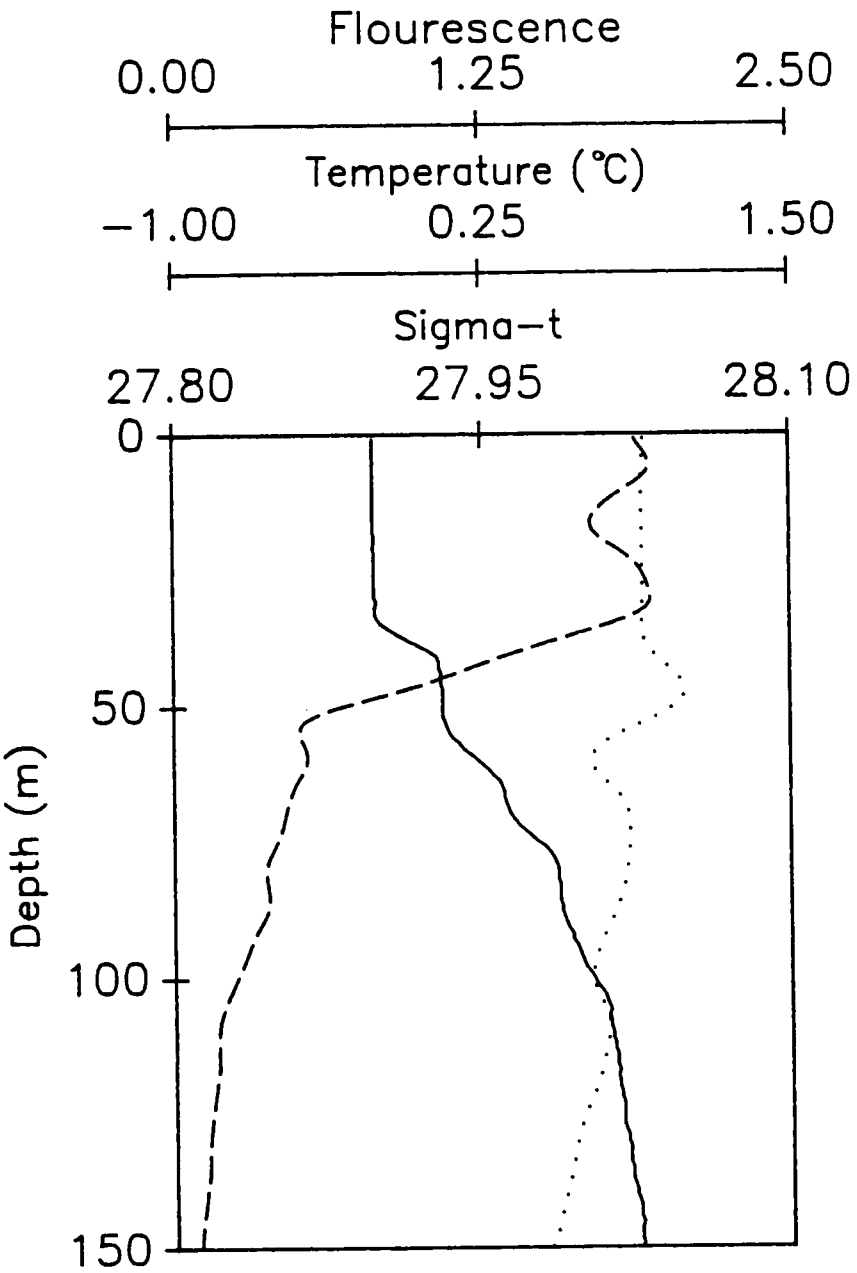


Figure 7. Depth profile for Station 145. Figure shows sigma-t (solid line), temperature (dotted line), and flourescence (dashed line) within the upper 150 m.

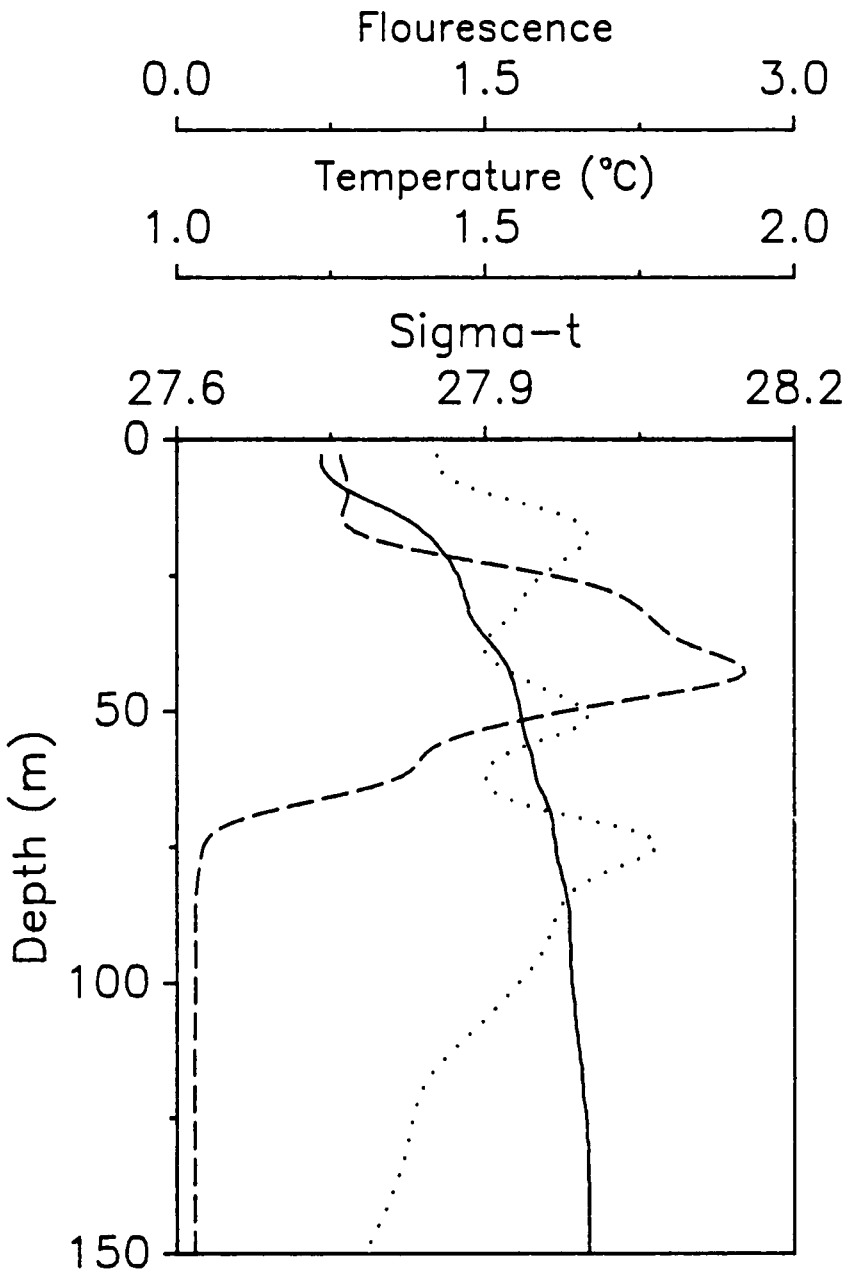


Figure 8. Depth profile for Station 194. Figure shows sigma-t (solid line), temperature (dotted line), and flourescence (dashed line) within the upper 150 m.

Experimental

Effects of Irradiance on Nitrate and Ammonium Uptake

Irradiance vs. nitrate and ammonium uptake experiments were conducted at stations 066, 104, 145 and 194. Irradiance levels on-deck measured on a cloud free day ranged from 3.9×10^{17} at noon to 1.8×10^{16} quanta s^{-1} cm^{-2} at 11:00 pm. CTD profiles for experimental stations are given in Figures 5-8. The uptake of nitrate and ammonium by the assemblages of phytoplankton encountered followed the relationship of the model used (Figures 9-14). Ambient nitrate concentrations for the different experiments ranged from 2.1 to 9.0 μM, and ammonium concentrations ranged from 0.18 to 1.68 μM. In general, the shapes of the nitrate uptake curves were similar to each other and distinguishable from the ammonium uptake curves, which also shared a common shape (Figures 9-14). Differences in nitrate and ammonium uptake were apparrent in all experiments between the 100 and 0.1% surface irradiance assemblages. In some instances the maximal uptake rate achieved was different, while in others the shape of the curve (i.e., % I at V_{max}, extent of inhibition) varied between the surface and deep phytoplankton assemblages. The maximum specific nitrate uptake rate achieved was greater in the 0.1% irradiance assemblages in all cases, with the average V_{max} for the 100% irradiance phytoplankton being 0.0030 h^{-1} and the average V_{max} for 0.1% I being 0.0047 h^{-1} (Table 1). However, greater maximum uptake rates were achieved by the 100% I assemblages for ammonium, with the

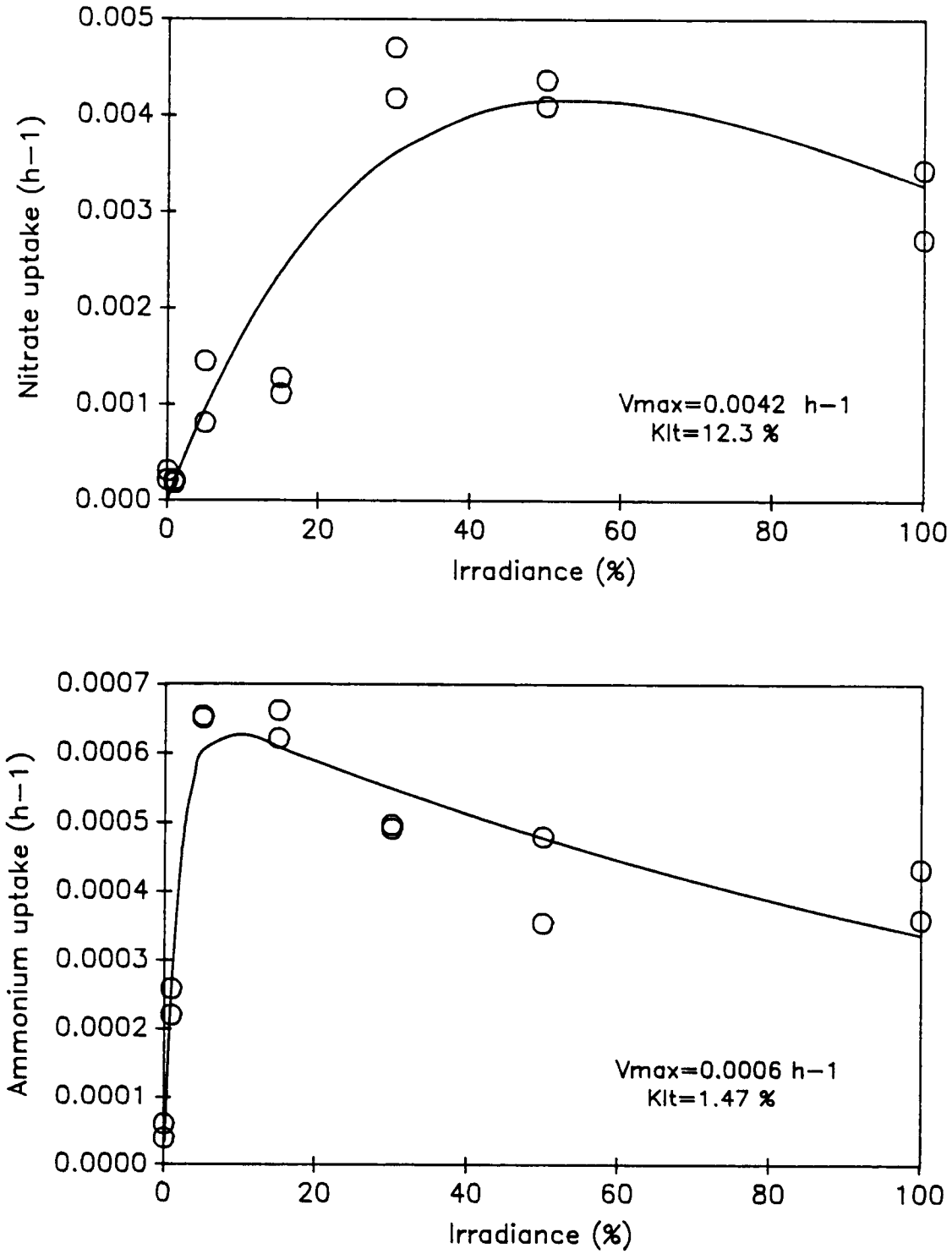


Figure 9. Relationship between specific nitrate and ammonium uptake rates and per cent surface irradiance for the surface sample at Station 104. Top: Specific nitrate uptake rate vs. per cent surface irradiance. Variance of fit = 4.66×10^{-7}. Bottom: Specific ammonium uptake rate vs. per cent surface irradiance. Variance of fit = 3.84×10^{-9}.

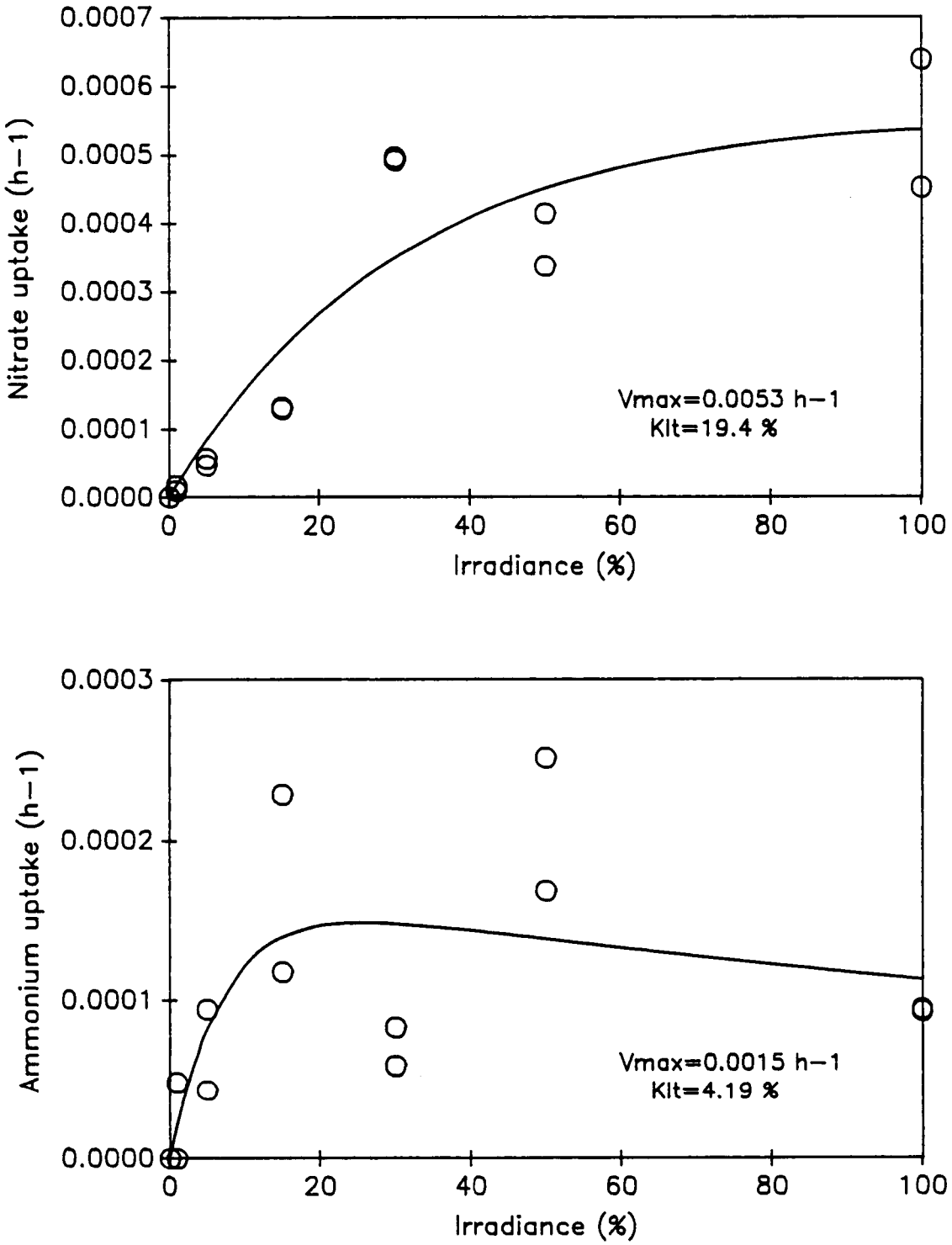


Figure 10. Relationship between specific nitrate and ammonium uptake rates and per cent surface irradiance for the 0.1% irradiance (31 m) sample at Station 104. Top: Specific nitrate uptake rate vs. per cent surface irradiance. Variance of fit = 8.21×10^{-7}. Bottom: Specific ammonium uptake rate vs. per cent surface irradiance. Variance of fit = 3.44×10^{-7}.

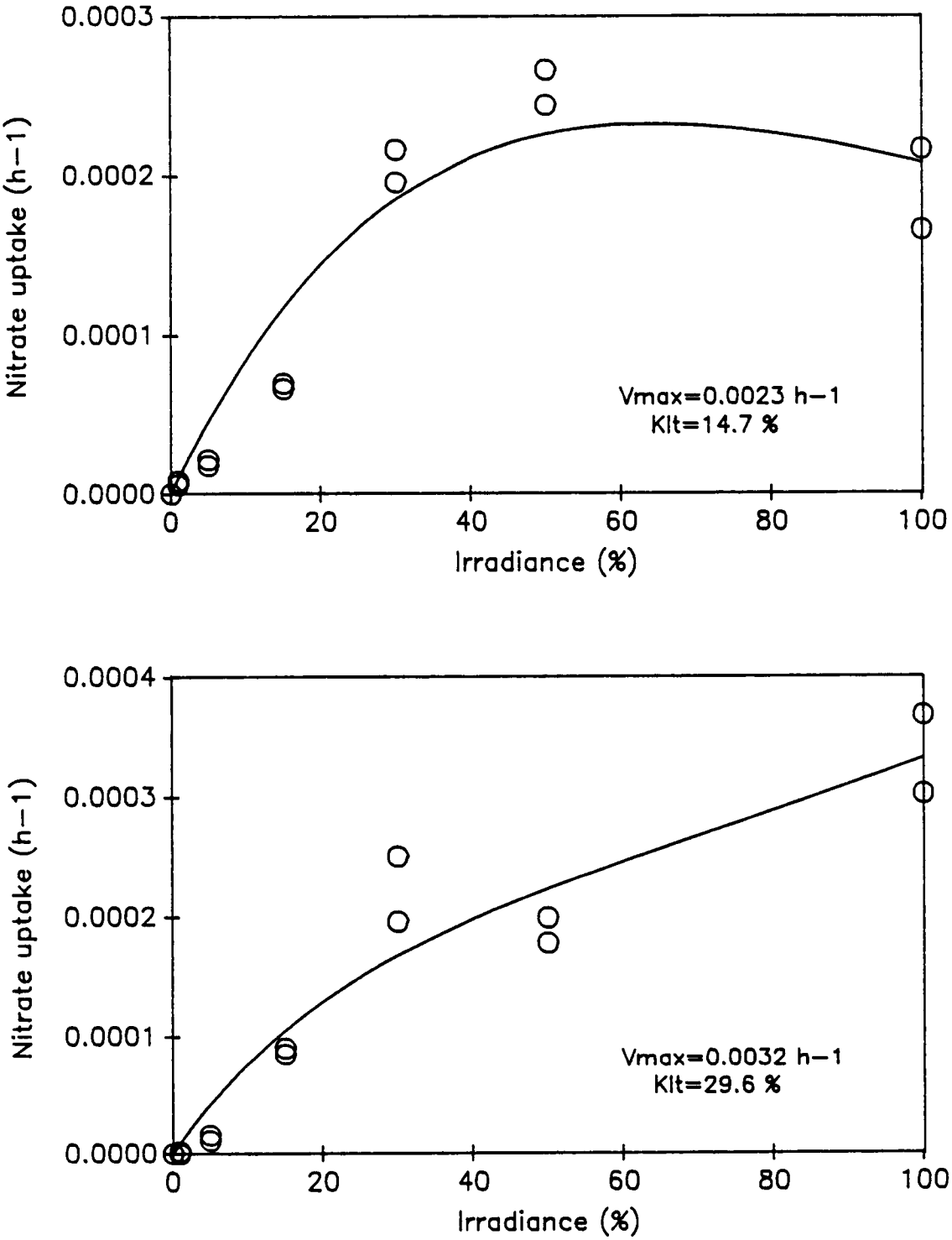


Figure 11. Relationship between specific nitrate uptake rate and per cent surface irradiance for both the surface and 0.1% irradiance (31 m) sample at Station 145. Top: Surface sample. Variance of fit = 1.00×10^{-7}. Bottom: 0.1% irradiance sample. Variance of fit = 1.34×10^{-7}.

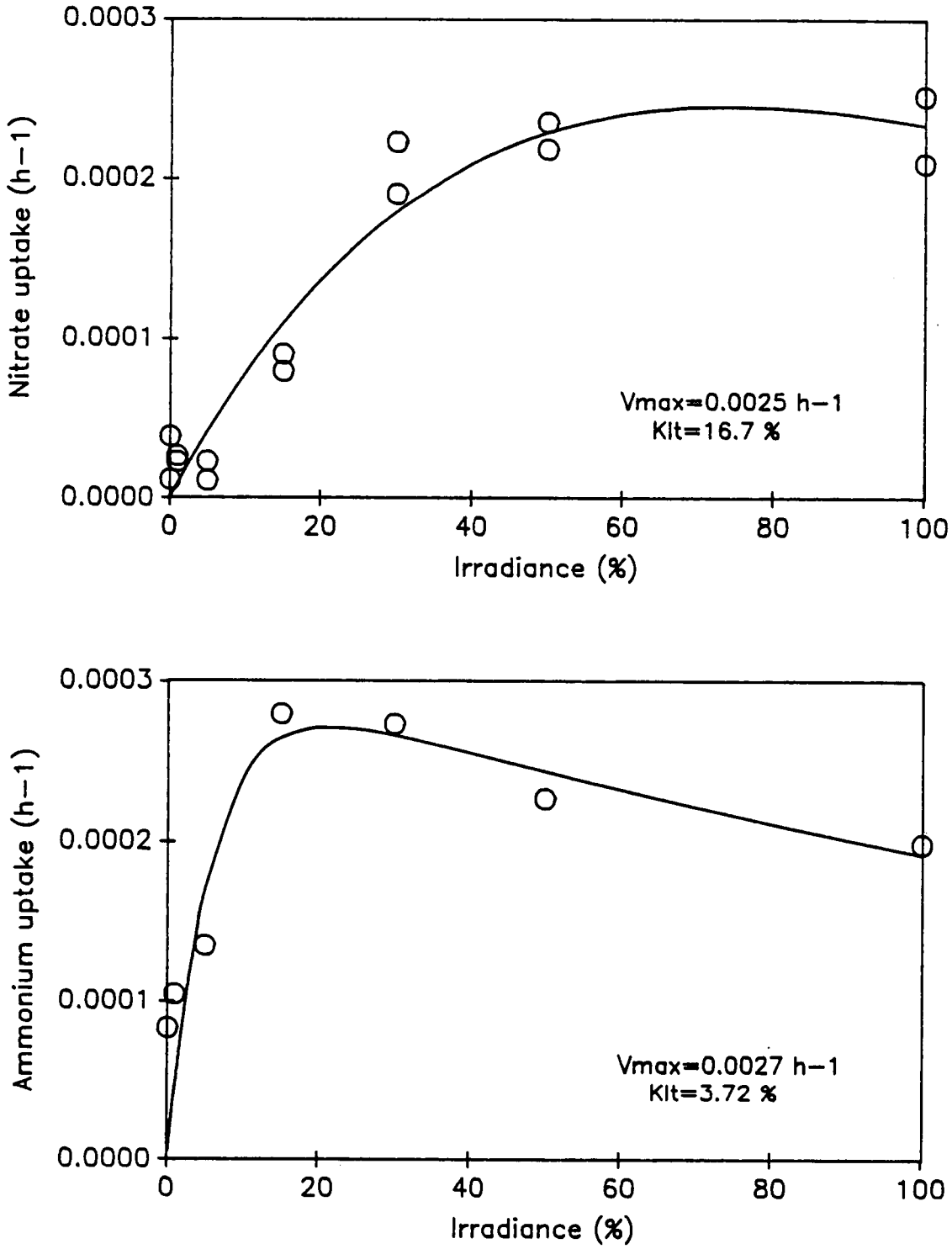
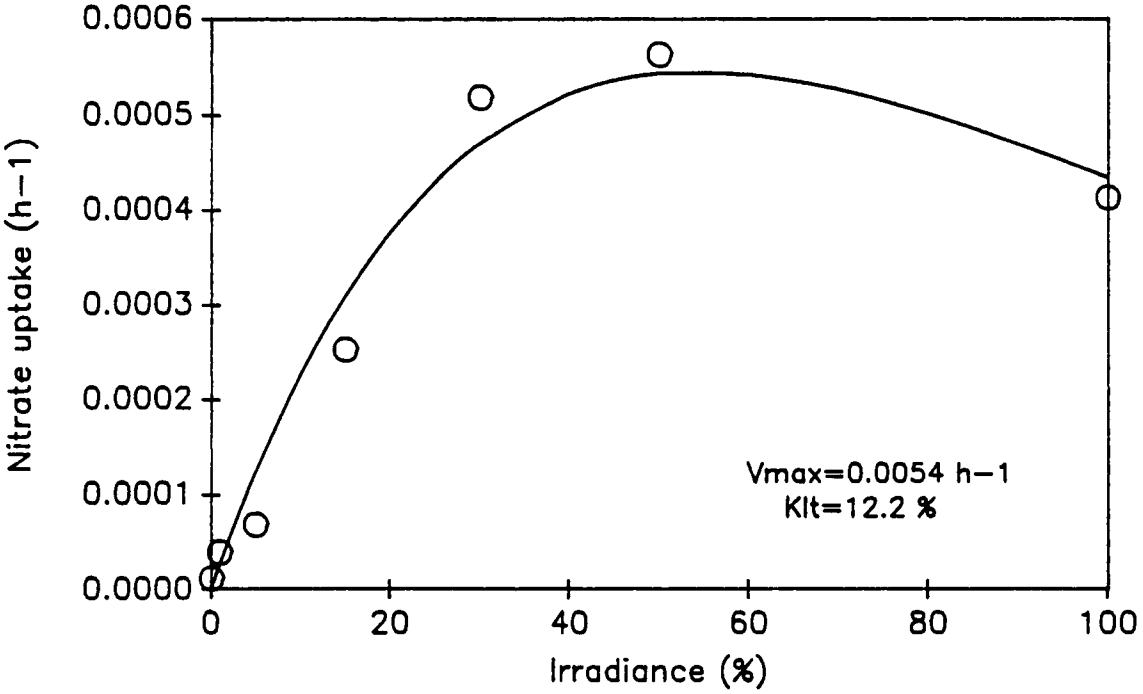


Figure 12. Top: Relationship between specific nitrate and ammonium uptake rates and per cent surface irradiance for the surface sample at Station 194. Top: Specific nitrate uptake rate vs. per cent surface irradiance. Variance of fit = 6.98×10^{-8}. Bottom: Specific ammonium uptake rate vs. per cent surface irradiance. Variance of fit = 2.82×10^{-7}.



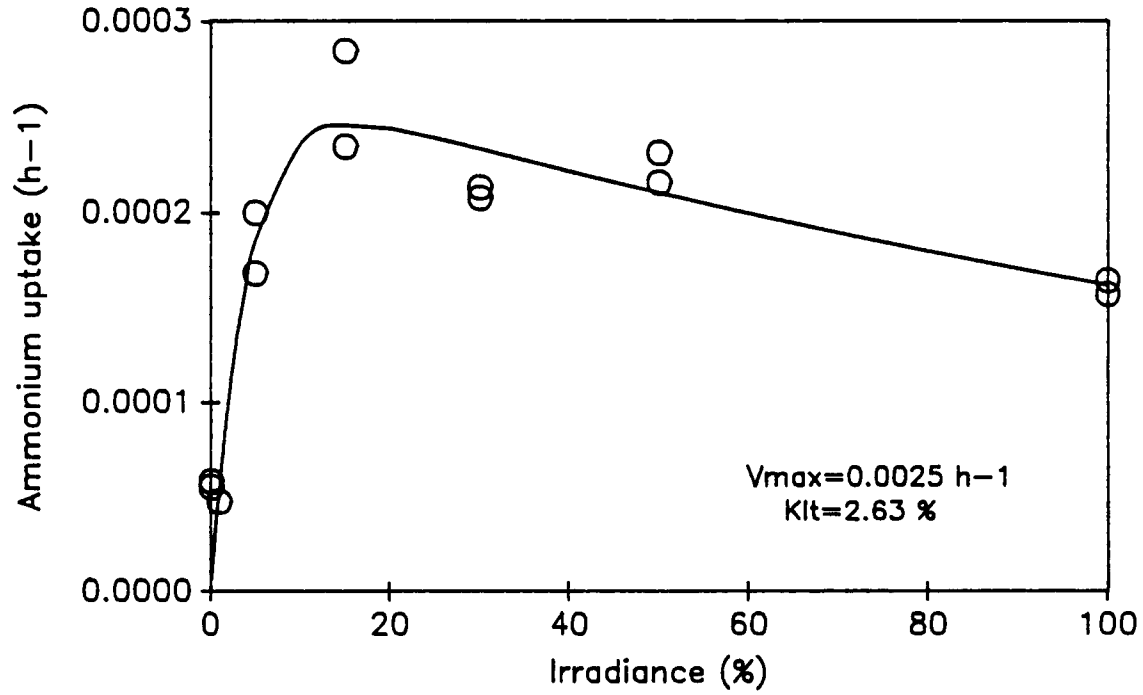


Figure 13. Relationship between specific nitrate and ammonium uptake rates and per cent surface irradiance for the 0.1% irradiance (49 m) sample at Station 194. Top: Specific nitrate uptake rate vs. per cent surface irradiance. Variance of fit = 2.4×10^{-7}. Bottom: Specific ammonium uptake rate vs. per cent surface irradiance. Variance of fit = 8.2×10^{-8}.

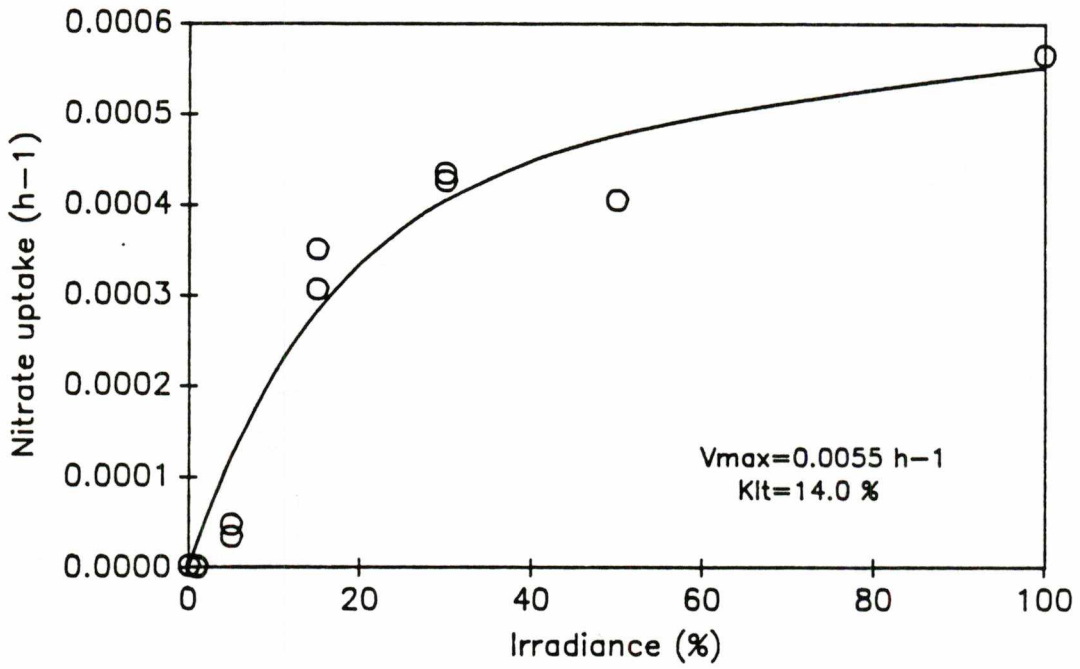


Figure 14. Relationship between specific nitrate uptake rate and per cent irradiance for the surface sample at Station 066. The incubation was conducted under artificial irradiance (ca. 5 x 10^{16} quanta s^{-1} cm^{-2}). Variance of fit = 2.95 x 10^{-7}.

average V_{max} values for the 100% I and 0.1% I samples being 0.0034 h^{-1} and 0.0020 h^{-1}, respectively (Table 1). Specific uptake rates, transport rates, station and nutrient data are given in Tables 2-5.

Differences in the response of nitrate and ammonium uptake to irradiance were apparent in all experiments. The V_{max} values for nitrate and ammonium were in general similar, with V_{max} nitrate values being slightly greater, but the K_{lt} values were very different (Table 1). K_{lt} values for nitrate uptake ranged from 12.2% to 29.6% of surface irradiance, while ammonium uptake K_{lt} values ranged from 1.47% to 4.19% (Table 1). The average K_{lt} value for nitrate uptake was more the 3 times the average K_{lt} value for ammonium uptake. Ammonium uptake was more inhibited by high irradiance levels than nitrate uptake in all cases, where ammonium uptake was always inhibited by high irradiance levels, and in some instances nitrate uptake showed no photoinhibition. The average value for the inhibition of maximal nitrate uptake rates of those assemblages which experienced inhibition was 19.2%, whereas the average inhibition for ammonium uptake rates was 33.3%. The optimal percentage irradiance for maximal uptake rate was greater for nitrate than for ammonium. Nitrate uptake had an average optimal irradiance level of 77.8%, while the average optimal percent irradiance level for ammonium uptake was 18.0%.

The light (100% surface irradiance) vs. dark (no irradiance) nutrient depletion experiment showed a marked difference in nitrate uptake between the light and dark bottles (Figure 15). The

Table 1. Summary of parameters from the irradiance vs. nitrate and ammonium uptake experiments. The per cent surface irradiance at which samples were taken from are indicated in the second column.

Station	% I	Vmax (h-1)	Klt (%I)	Vinhib (h-1)	% Inhib	%I at Vmax
Nitrate Values						
104	surface	0.0042	12.3	0.0033	20.7	51.5
	0.1	0.0053	19.4	0.0053	0.0	100.0
145	surface	0.0023	14.7	0.0021	10.5	63.9
	0.1	0.0032	29.6	0.0032	0.0	100.0
194	surface	0.0025	16.7	0.0023	4.6	74.7
	0.1	0.0054	12.2	0.0043	20.4	54.4
066	surface	0.0055	14.0	0.0055	0.0	100.0
MEAN	overall	0.0038	17.0	0.0037	19.4	77.8
	surface	0.0030			*(n=4)	
	0.1	0.0047				
Ammonium Values						
104	surface	0.0006	1.47	0.0003	45.6	9.6
	0.1	0.0015	4.19	0.0011	25.4	27.4
194	surface	0.0027	3.72	0.0019	29.3	21.6
	0.1	0.0025	2.63	0.0016	33.0	13.4
MEAN	overall	0.0027	3.00	0.0013	33.3	18.0
	surface	0.0034				
	0.1	0.0020				

Table 2. Summary of station data and calculated parameters for irradiance experiments conducted at Station 104.

Station:	104
Date & Time:	May 3, 1989 14:02
Lat/Long:	79.6860°N 03.0467°E
% ice cover:	9/10
inc started:	15:40 May 3
inc ended:	15:55 - 17:45 May 4

% I	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100	2.09	0.18	0.54	5.12	0.11	3.32	41.6
0.1	4.25	0.76	0.54	5.33	0.08	3.71	51.0

	Specific Uptake Rate (h^{-1})		Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$)		RPI		
% I	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	f-ratio
surface							
100	0.0031	0.00040	0.1282	0.01650	0.963	1.420	0.886
50	0.0042	0.00042	0.1759	0.01735	0.990	1.118	0.910
30	0.0044	0.00049	0.1845	0.02056	0.978	1.249	0.900
15	0.0012	0.00064	0.0495	0.02670	0.706	4.364	0.650
5	0.0011	0.00065	0.0468	0.02715	0.688	4.571	0.633
1	0.0020	0.00023	0.0083	0.00993	0.494	6.802	0.454
0.1	0.0003	0.00005	0.0108	0.00204	0.915	1.975	0.841
MEAN	0.0021	0.00041	0.0863	0.01717	0.819	3.071	0.753
0.1							
100	0.0054	0.00094	0.2776	0.04769	1.006	0.969	0.853
50	0.0038	0.00210	0.1914	0.10698	0.756	2.369	0.641
30	0.0049	0.00071	0.2517	0.03616	1.030	0.830	0.874
15	0.0013	0.00173	0.0662	0.08824	0.505	3.776	0.428
5	0.0005	0.00069	0.0264	0.03513	0.505	3.775	0.429
1	0.0001	0.00012	0.0068	0.00633	0.609	3.191	0.517
0.1	0.0000	0.00000	0.0000	0.00000	--	--	--
MEAN	0.0023	0.00090	0.1171	0.04579	0.735	2.485	0.624

Table 3. Summary of station data and calculated parameters for irradiance experiments conducted at Station 145.

Station:	145
Date & Time:	May 9, 1989 19:00
Lat/Long:	78.5123 °N 05.2614 °E
% ice cover:	0/10
inc started:	22:20 May 9
inc ended:	21:50 May 10

% I	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100	5.03	1.11	0.51	5.40	0.08	1.41	49.6
0.1	6.96	0.95	0.59	5.59	0.07	1.49	35.1

% I	Specific Uptake Rate (h^{-1}) NO_3^-	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NO_3^-
surface		
100	0.0019	0.0945
50	0.0025	0.1264
30	0.0021	0.1020
15	0.0007	0.0336
5	0.0002	0.0097
1	0.0001	0.0034
0.1	0.0000	0.0000
MEAN	0.0011	0.0528
0.1		
100	0.0033	0.1175
50	0.0019	0.0661
30	0.0022	0.0782
15	0.0009	0.0306
5	0.0001	0.0047
1	0.0000	0.0000
0.1	0.0000	0.0000
MEAN	0.0012	0.0425

Table 4. Summary of station data and calculated parameters for irradiance experiments conducted at Station 194.

Station:	194
Date & Time:	May 14, 1989 19:59
Lat/Long:	78.5000 °N 00.6817 °W
% ice cover:	3/10
inc started:	21:00 May 14
inc ended:	20:00 & 21:15 May 15

% I	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100	6.23	1.68	0.58	5.28	0.09	0.70	25.4
0.1	9.00	0.59	0.71	5.70	0.09	2.92	68.4

	Specific Uptake Rate (h^{-1})		Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$)		RPI		
	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	f-ratio
surface							
100	0.0023	0.00199	0.0280	0.05042	0.454	3.026	0.357
50	0.0023	0.00226	0.0575	0.05752	0.635	2.354	0.500
30	0.0021	0.00273	0.0524	0.06936	0.547	2.682	0.430
15	0.0008	0.00280	0.0215	0.07099	0.295	3.614	0.232
5	0.0002	0.00135	0.0349	0.03430	0.640	2.335	0.504
1	0.0002	0.00105	0.0062	0.02656	0.242	3.812	0.190
0.1	0.0002	0.00083	0.0063	0.02116	0.293	3.623	0.231
MEAN	0.0012	0.00186	0.0296	0.04719	0.444	3.064	0.349
0.1							
100	0.0041	0.00160	0.2821	0.10977	0.767	4.546	0.720
50	0.0056	0.00223	0.3846	0.15268	0.763	4.612	0.716
30	0.0052	0.00210	0.3541	0.14384	0.758	4.688	0.711
15	0.0025	0.00259	0.1725	0.17742	0.525	8.228	0.493
5	0.0007	0.00184	0.0464	0.12582	0.287	11.859	0.269
1	0.0004	0.00048	0.0266	0.03293	0.476	8.973	0.447
0.1	0.0001	0.00057	0.0080	0.03910	0.180	13.484	0.169
MEAN	0.0027	0.00163	0.1820	0.11165	0.537	8.056	0.504

Table 5. Summary of station data and calculated parameters for the artificial irradiance experiments conducted at Station 066.

Station:	66
Date & Time:	April 29, 1989 08:27
Lat/Long:	79.6467 °N 01.9625 °E
% ice cover:	7/10
inc started:	10:50 April 29
inc ended:	12:10 April 30

time (days)	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
1	5.58	0.47	0.74	4.99	0.24	2.33	39.01
6	ND	ND	ND	ND	ND	3.55	96.5

% I	Specific Uptake Rate (h^{-1}) NO_3^-	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NO_3^-
time=0		
100	0.0056	0.2203
50	0.0040	0.1580
30	0.0043	0.1678
15	0.0033	0.1281
5	0.0004	0.0159
1	0.0000	0.0000
0.1	0.0000	0.0008
MEAN	0.0025	0.0987
time=5 days later		
100	0.0081	0.7844
50	0.0088	0.8518
30	0.0085	0.8156
15	0.0093	0.8972
5	0.0088	0.8519
1	0.0088	0.8516
0.1	0.0083	0.8057
MEAN	0.0087	0.8369

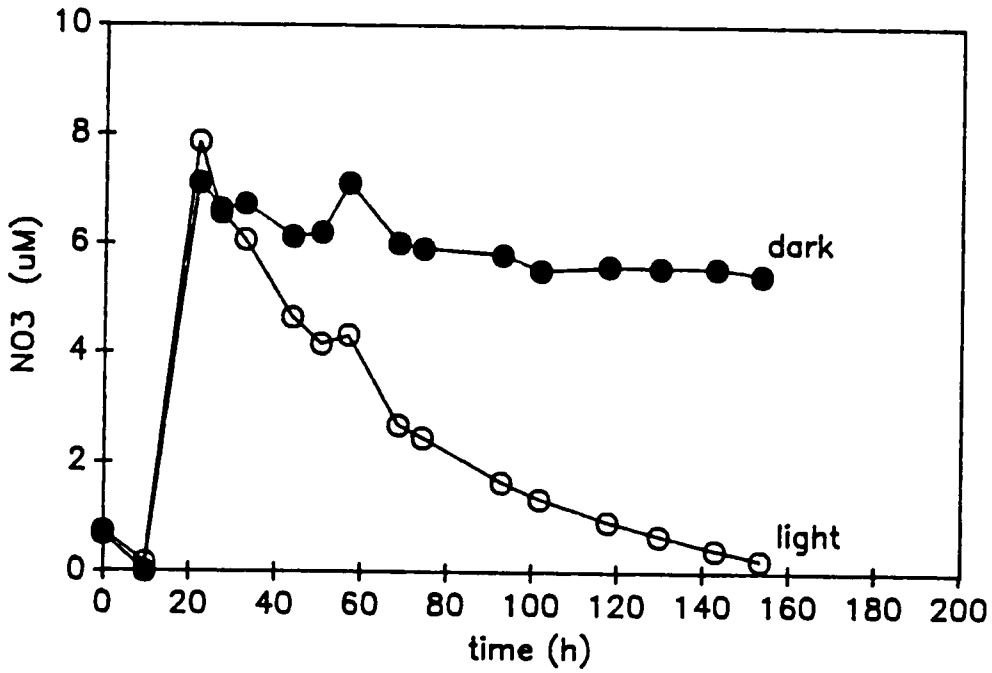


Figure 15. Depletion of nitrate in light (exposed to 100% surface irradiance) and dark bottles. Water sample taken from the surface at Station 028.

assemblage exposed to surface irradiance completely depleted the ambient nitrate, while exposure to no irradiance allowed only a small depletion of the nitrate concentration, if any.

The relative preference index (RPI) for ammonium was higher than the relative preference index for nitrate. The average RPI values over all depths and experiments for ammonium and nitrate were 4.629 and 0.501, respectively (Tables 2, 4). However, in the surface region of an earlier station (stn 104), the RPI values for ammonium and nitrate were very similar (Table 2). Preference for ammonium generally increased with decreasing irradiance levels. The RPI for ammonium also seemed to increase as the bloom progressed. The f-ratios tended to decrease with depth, and decreased for the surface assemblages with time as the bloom progressed (Tables 2, 4). The 0.1% assemblages did not show the same decrease in f-ratios as the surface assemblages.

Simulated in situ nitrate and ammonium uptake rates were taken with depth at all four of the stations in which irradiance experiments were carried out (Figures 16-19). For stations 104 and 145, the maximum nitrate uptake rates were identical to the maximum nitrate uptake rate observed experimentally (Tables 6, 7, 8, 2, 3). However, the simulated in situ ammonium uptake rates for station 104 did not reach the maximal ammonium uptake rate found in the ammonium vs. irradiance experiment (Tables 2, 7). Both the nitrate and ammonium maximum uptake rates for Station 194 were less than those uptake rates achieved in the irradiance experiments (Tables 5, 9).

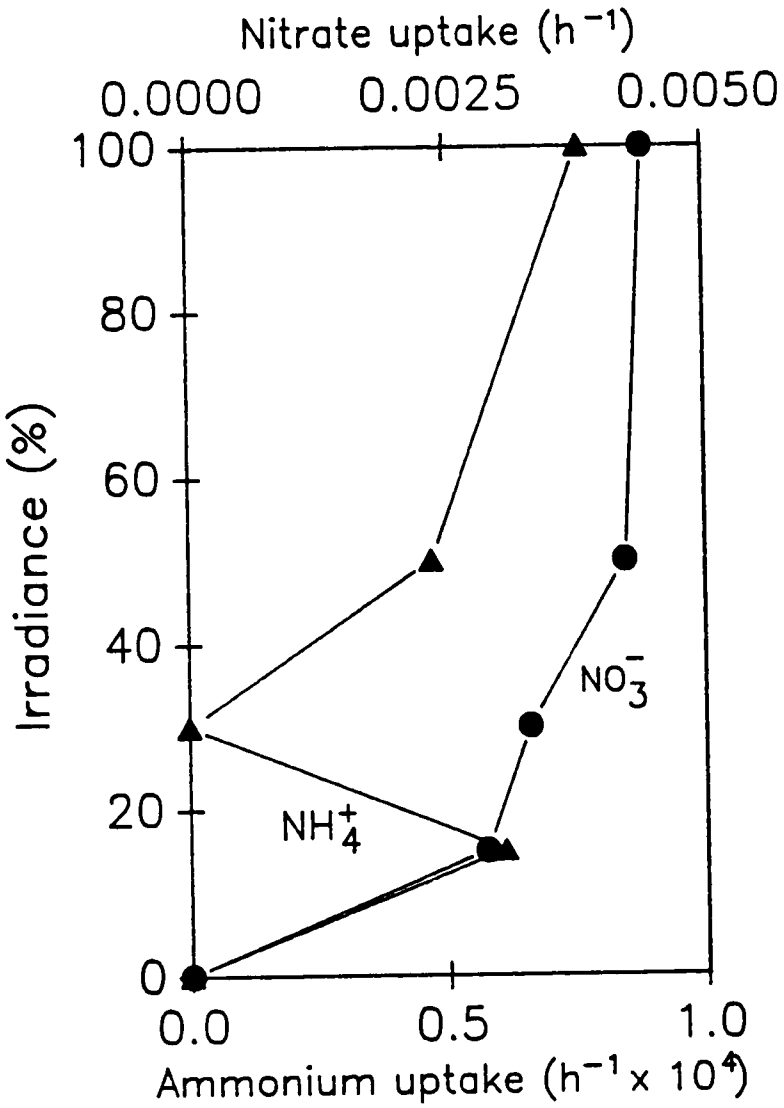


Figure 16. Specific nitrate and ammonium uptake rates vs. depth at Station 066 (depth given as percentage of surface irradiance).

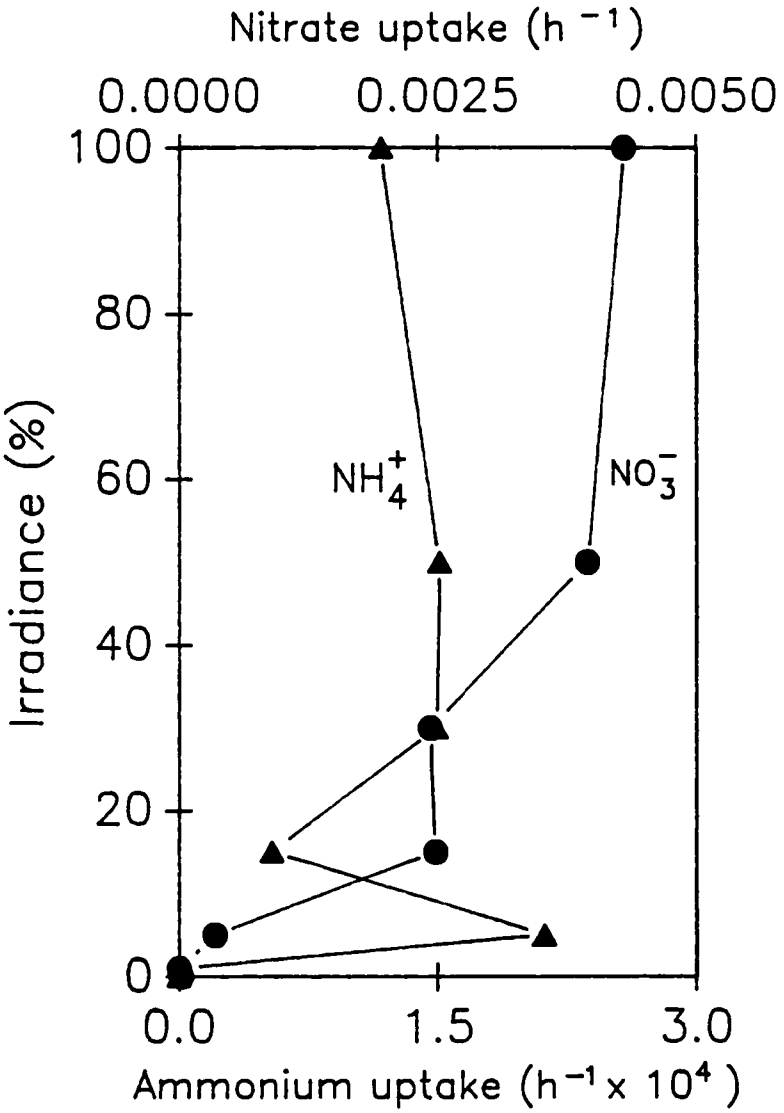


Figure 17. Specific nitrate and ammonium uptake rates vs. depth at Station 102 (depth givien as percentage surface irradiance).

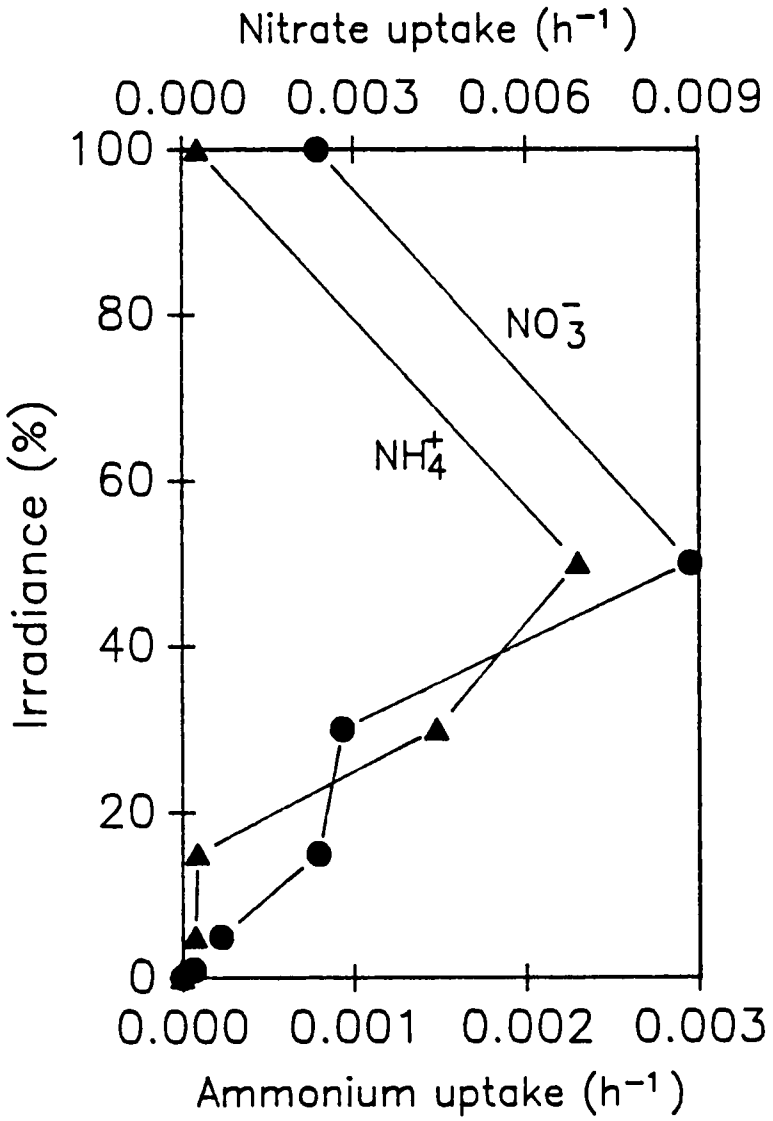


Figure 18. Specific nitrate and ammonium uptake rates vs. depth at Station 145 (depth given as percentage surface irradiance).

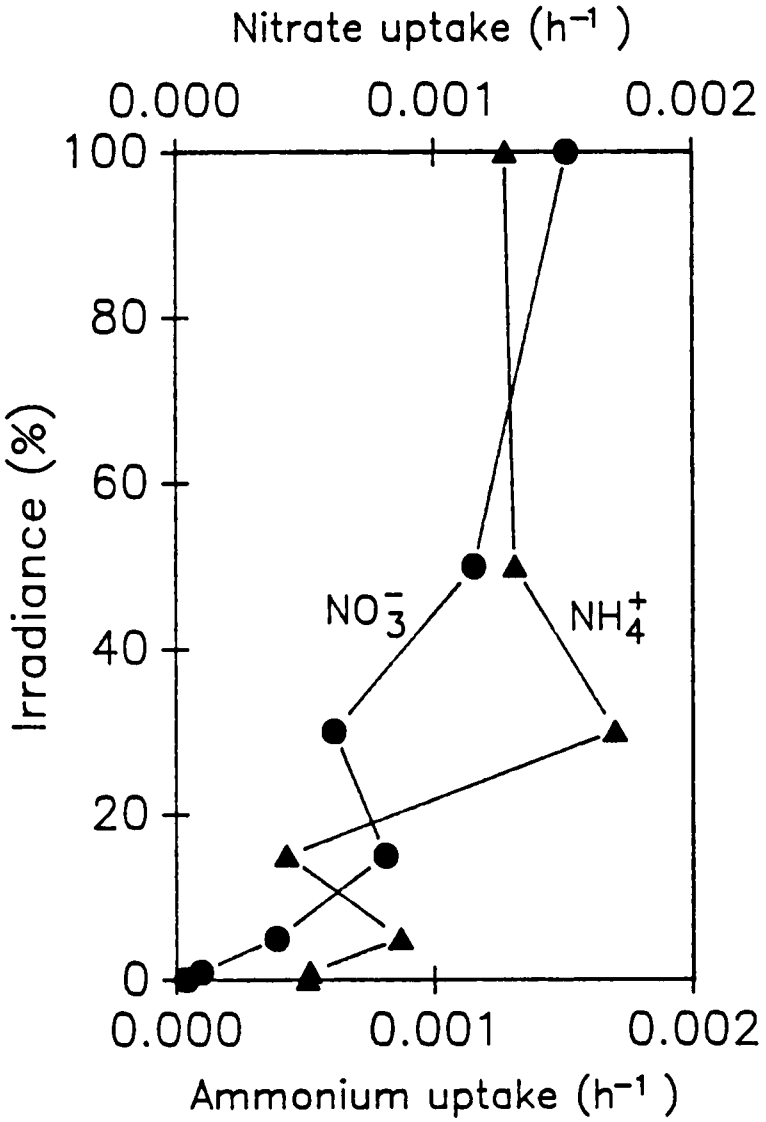


Figure 19. Specific nitrate and ammonium uptake rates vs. depth at Station 192 (depth given as percentage of surface irradiance).

Table 6. Summary of station data and calculated parameters for simulated in situ measurements at Station 066.

Station: 66
Date & Time: April 29, 1989 08:27
Lat/Long: 79.6467°N 1.9625°E
% ice cover: 7/10

%I/ depth(m)	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100/0	5.58	0.47	0.74	4.99	0.24	1.34	33.3
50/3	5.52	0.36	0.71	5.30	0.26	0.53	13.1
30/5	6.14	0.43	0.80	5.34	0.04	0.66	7.4
15/9	5.89	0.58	0.80	5.18	0.05	1.05	1.8
5/15	5.99	0.50	0.82	5.23	0.05	1.90	ND
1/24	6.57	0.53	0.79	5.26	0.05	1.83	ND
0.1/38	7.13	0.56	0.83	5.37	0.04	1.57	29.7

	Specific Uptake Rate (h^{-1})		Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$)		RPI		
% I	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	f-ratio
100	0.0044	0.00008	0.1470	0.00253	1.065	0.219	0.983
50	0.0042	0.00005	0.0555	0.00062	1.053	0.181	0.989
30	0.0033	0.00000	0.0243	0.00000	1.069	0.000	1.000
15	0.0029	0.00006	0.0050	0.00011	1.076	0.231	0.979
5	ND	ND	ND	ND	--	--	--
1	ND	ND	ND	ND	--	--	--
0.1	0.0000	0.00000	0.0002	0.00000	1.079	0.000	1.000

Table 7. Summary of station data and calculated parameters for simulated in situ measurements at Station 102.

Station: 102
Date & Time: May 3, 1989 07:00
Lat/Long: 79.6652°N 3.0615°E
% ice cover: 9/10

%I/ depth(m)	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100/0	3.23	0.37	0.46	5.16	0.09	5.31	60.65
50/3	3.16	0.36	0.45	5.15	0.10	2.62	76.19
30/5	2.99	0.35	0.45	5.14	0.09	2.66	57.14
15/7	2.80	0.40	0.47	5.20	0.09	2.97	53.13
5/11	2.76	0.47	0.45	5.27	0.11	2.99	63.66
1/19	2.75	0.36	0.45	5.23	0.09	1.52	73.69
0.1/31	3.45	0.58	0.49	5.31	0.09	0.30	74.19

% I	Specific Uptake Rate (h^{-1})		Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$)		RPI		f-ratio
	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	
100	0.0043	0.00012	0.2608	0.00710	1.084	0.259	0.974
50	0.0039	0.00015	0.3008	0.01150	1.071	0.365	0.963
30	0.0024	0.00015	0.1386	0.00851	1.052	0.552	0.942
15	0.0025	0.00005	0.1316	0.00287	1.120	0.169	0.979
5	0.0003	0.00021	0.0222	0.01350	0.727	2.610	0.622
1	0.0000	0.00000	0.0002	0.00015	0.677	3.499	0.600
0.1	0.0000	0.00000	0.0018	0.00000	1.169	0.000	1.000

Table 8. Summary of station data and calculated parameters for simulated in situ measurements at Station 145.

Station: 145
Date & Time: May 9, 1989 19:00
Lat/Long: 78.5123°N 5.2614°E
% ice cover: 0/10

%I/ depth(m)	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100/0	5.03	1.15	0.49	5.40	0.08	1.31	42.4
50/4	5.10	1.94	0.49	5.39	0.08	1.32	55.6
30/7	4.98	1.13	0.47	5.45	0.08	1.22	38.7
15/11	5.01	1.41	0.50	5.46	0.08	1.22	51.7
5/18	5.02	1.14	0.52	5.46	0.07	1.40	52.2
1/29	5.19	1.27	0.47	5.49	0.08	1.14	58.6
0.1/41	6.96	1.08	0.57	5.59	0.07	1.49	30.7

	Specific Uptake Rate (h^{-1})		Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$)		RPI		
% I	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	f-ratio
100	0.0024	0.00009	0.1000	0.00382	1.183	0.198	0.963
50	0.0089	0.00230	0.4925	0.12789	1.096	0.748	0.794
30	0.0028	0.00148	0.1081	0.05714	0.803	1.868	0.654
15	0.0024	0.00009	0.1226	0.00460	1.235	0.165	0.964
5	0.0007	0.00008	0.0352	0.00396	1.103	0.548	0.899
1	0.0002	0.00000	0.0120	0.00000	1.245	0.000	1.000
0.1	0.0000	0.00000	0.0000	0.00000	--	--	--

Table 9. Summary of station data and calculated parameters for simulated in situ measurements at Station 192.

Station: 192
Date & Time: May 14, 1989 14:02
Lat/Long: 78.4985°N 0.5840°W
% ice cover: 3/10

%I/ depth(m)	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100/0	7.73	1.09	0.49	5.45	0.08	0.61	16.95
50/5	7.92	0.87	0.64	5.26	0.09	0.52	14.39
30/8	7.81	0.84	0.48	5.40	0.08	0.59	17.17
15/12	7.23	0.93	0.53	5.53	0.08	1.14	25.75
5/20	6.56	0.98	0.53	5.52	0.09	1.49	31.55
1/32	6.33	0.78	0.48	5.57	0.08	2.10	34.33
0.1/49	8.05	0.91	0.56	5.69	0.07	1.66	27.51

% I	Specific Uptake Rate (h^{-1})		Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$)		RPI		f-ratio
	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	
100	0.0015	0.00128	0.0257	0.02163	0.619	3.714	0.543
50	0.0012	0.00131	0.0166	0.01889	0.519	5.389	0.468
30	0.0006	0.00170	0.0105	0.02919	0.293	7.536	0.265
15	0.0008	0.00043	0.0209	0.01102	0.738	3.038	0.655
5	0.0004	0.00087	0.0123	0.02742	0.359	5.295	0.309
1	0.0001	0.00052	0.0033	0.01775	0.177	7.675	0.158
0.1	0.0000	0.00051	0.0011	0.01400	0.081	9.117	0.073

Specific uptake rates, transport rates, RPIs, and f-ratios for the simulated in situ uptake measurements with depth are given in Tables 6-9. The RPI values for nitrate were greater than ammonium for the two earlier stations, with the RPI ammonium values increasing with depth and time. By station 192, the average RPI ammonium value was 15 times greater than the average nitrate RPI value. The RPI ammonium values from station 104 were lower than the RPI ammonium values reached in the irradiance experiment (Tables 2, 7). Station 192 RPI values were slightly less than those of the irradiance experiment, but were generally in the same ratio (Table 5, 9). f-ratios were higher in the water column than those found in the irradiance experiment for station 104, with the f-ratio from the water column ranging from 0.6-1.0 (Table 7). The f-ratios were more similar between the water column measurements and the irradiance experiment data for station 194 (Tables 4, 9).

Effects of Nutrient (Nitrate, Ammonium) Concentration on Nutrient (Nitrate, Ammonium) Uptake

The nitrate concentrations to which the phytoplankton were exposed ranged from 0.3 - 7.9 μM in one experiment and 0.02 - 2.8 μM in another, and ammonium concentrations varied between 0.0 - 2.2 μM in the ammonium uptake experiment. The uptake of nitrate and ammonium by the phytoplankton assemblage as a function of nitrate and ammonium concentration could be characterized by the Michaelis-Menton model (figures 20-22). However, saturation was not reached in two cases, and hence an empirical V_{max} value was not obtained. The data fit the model very well in these cases, but represent the initial slope of the curve only (Figures 21, 22).

The maximum uptake rate achieved by the different assemblages were all similar and around 0.006 h^{-1}. However, the V_{max} value predicted by the model for two of the experiments was much greater because saturation was not reached. V_{max} values predicted by the model ranged from 0.006 to 0.010 μM (Table 10). Actual uptake rates, station and nutrient data are listed in Tables 11-13. The K_t values were similar for the 0.0 to 2.8 μM nitrate experiment and the 0.0 to 2.2 μM ammonium experiment. K_t values ranged from 0.3 to 2.7 μM (Table 10).

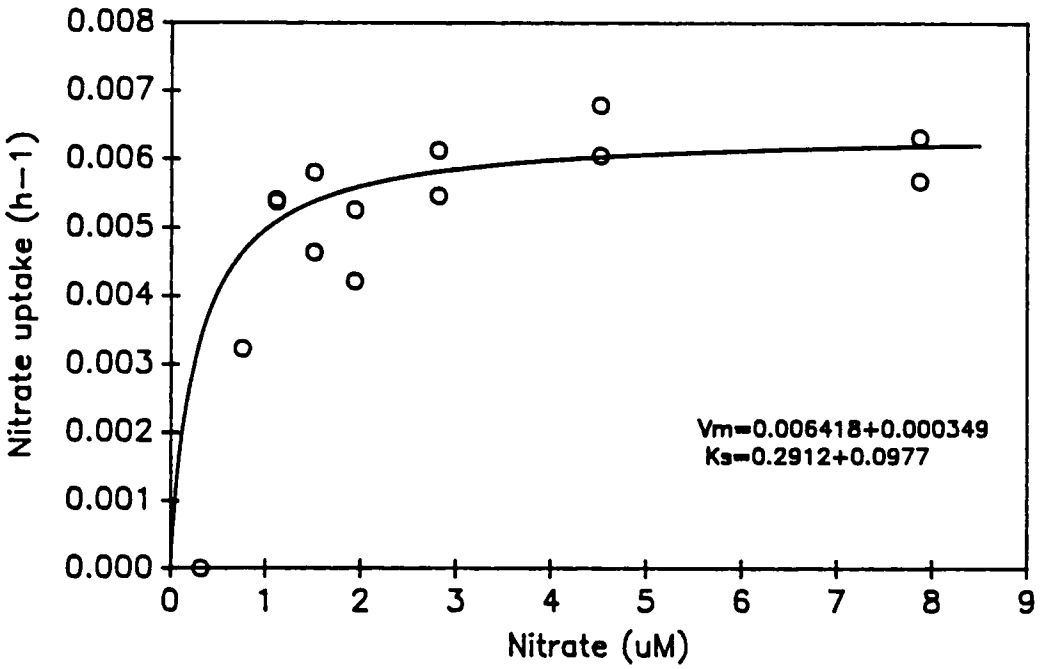


Figure 20. Relationship between specific nitrate uptake rate and nitrate concentration. Water sample taken from the surface at Station 128. Variance of fit = 3.61×10^{-7}.

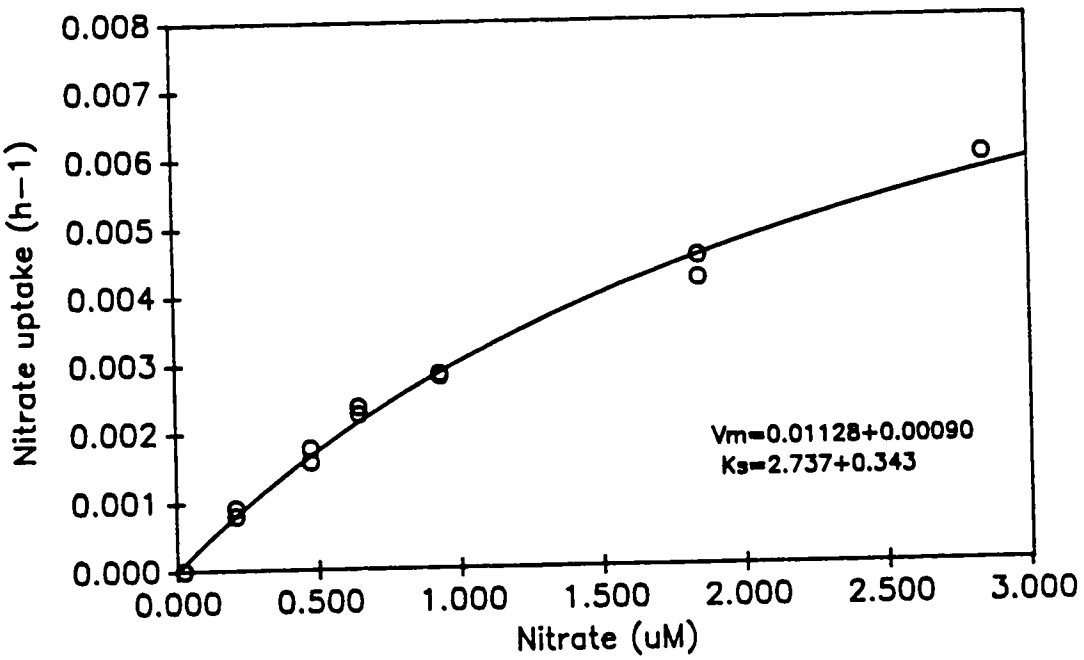


Figure 21. Relationship between specific nitrate uptake rate and nitrate concentration. Water sample taken from the 0.1% irradiance level at Station 104. Variance of fit = 2.51×10^{-8}.

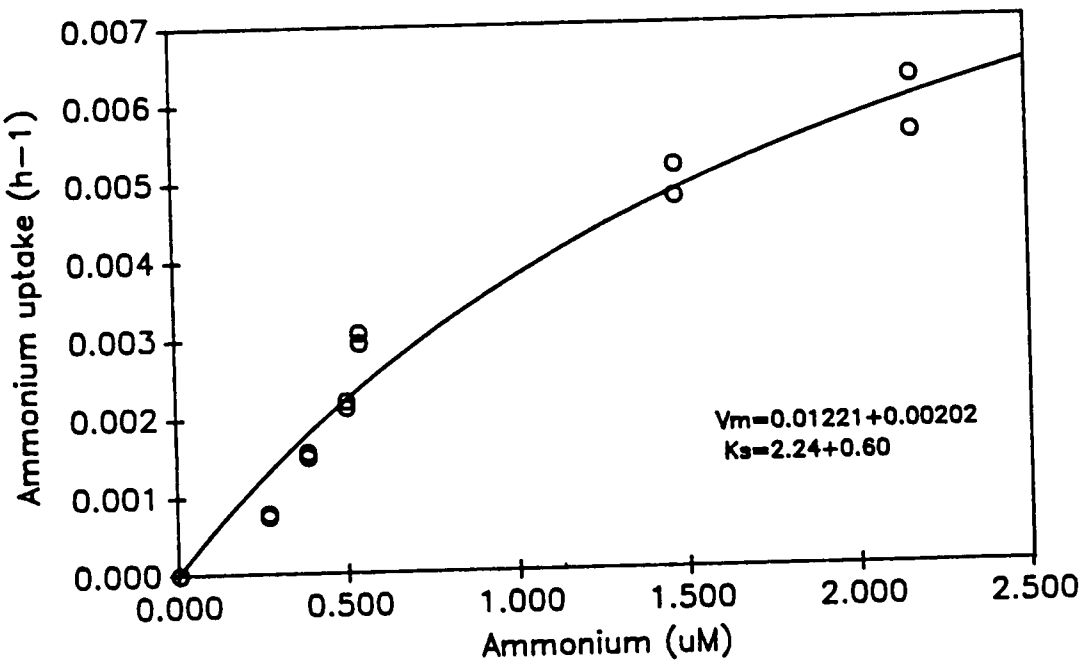


Figure 22. Relationship between specific ammonium uptake rate and ammonium concentration. Water sample taken from the surface at Station 068. Variance of fit = 1.62×10^{-7}.

Table 10. Summary of maximum specific uptake rates and transport constants as predicted by the Michaelis-Menton model for nutrient kinetic experiments.

Station	V_{max} (h^{-1})	Kt (μM)	nutrient range (μM)
(NO_3^-) vs. nitrate uptake			
128	0.0064	0.29	0 - 7.9
104	0.0113	2.74	0 - 2.8
(NH_4^+) vs. ammonium uptake			
68	0.0122	2.24	0 - 2.2

Table 11. Summary of station data and calculated parameters for kinetic experiment conducted at Station 128.

Station:	128
Date & Time:	May 6, 1989 21:28
Lat/Long:	79.0401°N 04.2657°E
% ice cover:	0/10
inc started:	22:35 May 6
inc ended:	22:30 May 7

% I	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
100	0.32	0.64	0.35	5.15	0.05	0.17	145.4

NO_3^- (μM)	Specific Uptake Rate (h^{-1}) NO_3^-	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NO_3^-
0.32	0.0000	0.0000
0.75	ND	ND
1.11	0.0054	0.7805
1.51	0.0058	0.8429
1.94	0.0042	0.6117
2.81	0.0061	0.8894
4.51	0.0068	0.9855
7.87	0.0057	0.8251
0.32	0.0000	0.0000
0.75	0.0032	0.4684
1.11	0.0054	0.7849
1.51	0.0046	0.6729
1.94	0.0053	0.7633
2.81	0.0055	0.7928
4.51	0.0060	0.8785
7.87	0.0063	0.9170
MEAN	0.0047	0.6809
range	0 - 0.0068	0 - 0.9855

Table 12. Summary of station data and calculated parameters for kinetic experiment conducted at Station 104.

Station:	104
Date & Time:	May 3, 1989 14:02
Lat/Long:	79.4116°N 03.0280°E
% ice cover:	9/10
inc started:	15:50 May 10
inc ended:	16:30 May 11

% I	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
0.1							
May 3	4.25	0.76	0.54	5.33	0.08	3.71	51.0
May 10	0.02	0.02	0.19	5.25	0.02	ND	64.6

NO_3^- (μM)	Specific Uptake Rate (h^{-1}) NO_3^-	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NO_3^-
0.02	0.0000	0.0000
0.21	0.0009	0.0587
0.47	0.0018	0.1141
0.65	0.0024	0.1529
0.93	0.0028	0.1831
1.84	0.0042	0.2709
2.84	ND	ND
0.02	0.0000	0.0000
0.21	0.0008	0.0514
0.47	0.0016	0.1016
0.65	0.0023	0.1458
0.93	0.0028	0.1811
1.84	0.0045	0.2919
2.84	0.0060	0.3849
MEAN	0.0023	0.1490
range	0 - 0.0060	0 - 0.3849

Table 13. Summary of station data and calculated parameters for kinetic experiment conducted at Station 068.

Station:	068
Date & Time:	April 29, 1989 15:05
Lat/Long:	79.5972°N 02.2893°E
% ice cover:	5/10
inc started:	20:54 May 11
inc ended:	20:54 May 12

% I	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
surface							
April 29	5.77	0.64	0.33	5.26	ND	1.92	60.4
May 11	0.00	0.01	0.12	0.40	0.06	ND	116.3

NH_4^+ (μM)	Specific Uptake Rate (h^{-1}) NH_4^+	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NH_4^+
0.01	0.0000	0.0000
0.27	0.0007	0.0864
0.39	0.0016	0.1810
0.50	0.0022	0.2561
0.54	0.0031	0.3566
1.47	0.0052	0.5992
2.17	0.0055	0.6436
0.01	0.0000	0.0000
0.27	0.0008	0.0906
0.39	0.0015	0.1740
0.50	0.0021	0.2466
0.54	0.0029	0.3415
1.47	0.0047	0.5523
2.17	0.0063	0.7273
MEAN	0.0026	0.3039
range	0 - 0.0063	0 - 0.7273

Effect of Ammonium on Nitrate Uptake

Curves for the ammonium inhibition of nitrate uptake experiments were drawn by inspection (Figures 23, 24). Ammonium concentrations ranged from ca. 0.0 to 3.0 μM in both experiments. The ambient nitrate concentration at station 168 was ten times lower than the ambient nitrate concentration at station 104 (Tables 14, 15). The general shape of the inhibition curves were the same, but the absolute values were different (Figures 23, 24). The average nitrate specific uptake for stations 168 and 104 were 0.0025 h^{-1} and 0.0072 h^{-1}, respectively (Tables 14, 15). The maximum nitrate uptake rate achieved when no ammonium was present, V(initial), was 0.0035 h^{-1} for station 168 and 0.0091 h^{-1} for station 104 (table 16). However, the extent of inhibition was very similar for both assemblages. K_i (for K inhibition) values representing the ammonium concentration when nitrate uptake equals (V(initial)-V(inhibition)/2) were 0.66 and 0.54 μM for stations 168 and 104, respectively. The maximal extent of inhibition given as a percentage of V(initial) was also similar for the two different experiments: 45.1% for station 168, and 34.7% for station 104 (Table 16).

In the irradiance vs. nitrate uptake experiments, maximal nitrate uptake rates achieved over all experiments generally increased with decreasing ambient ammonium concentrations (Figure 25). The maximal nitrate uptake values achieved in the irradiance experiments (0.0023 - 0.0056 h^{-1}) with the natural ambient

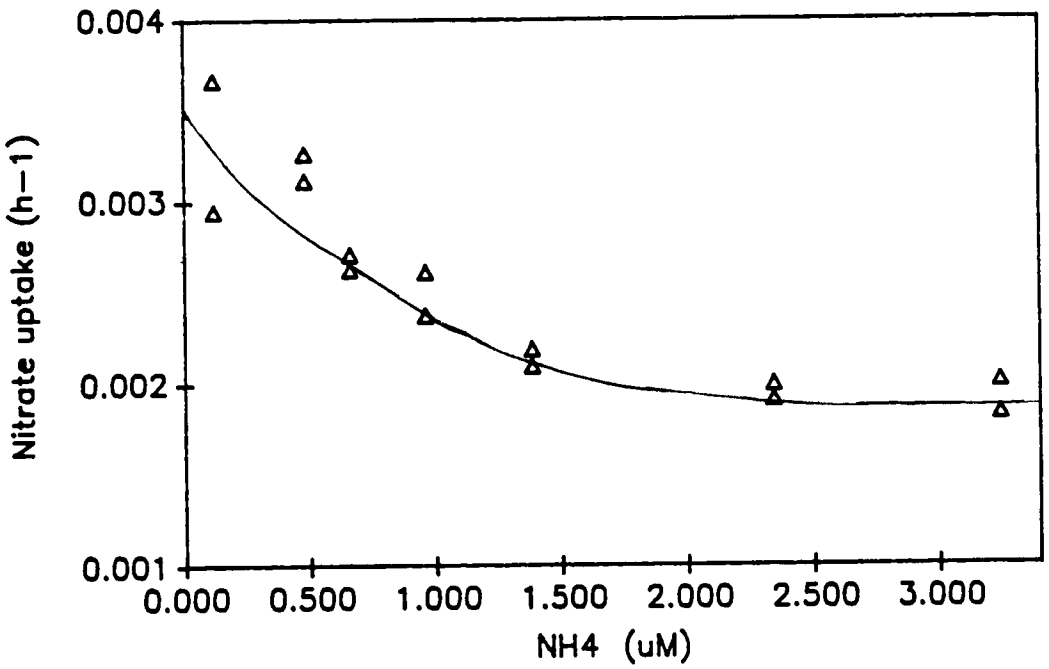


Figure 23. Relationship between specific nitrate uptake rate and ammonium concentration. Water sample taken from the surface at Station 168.

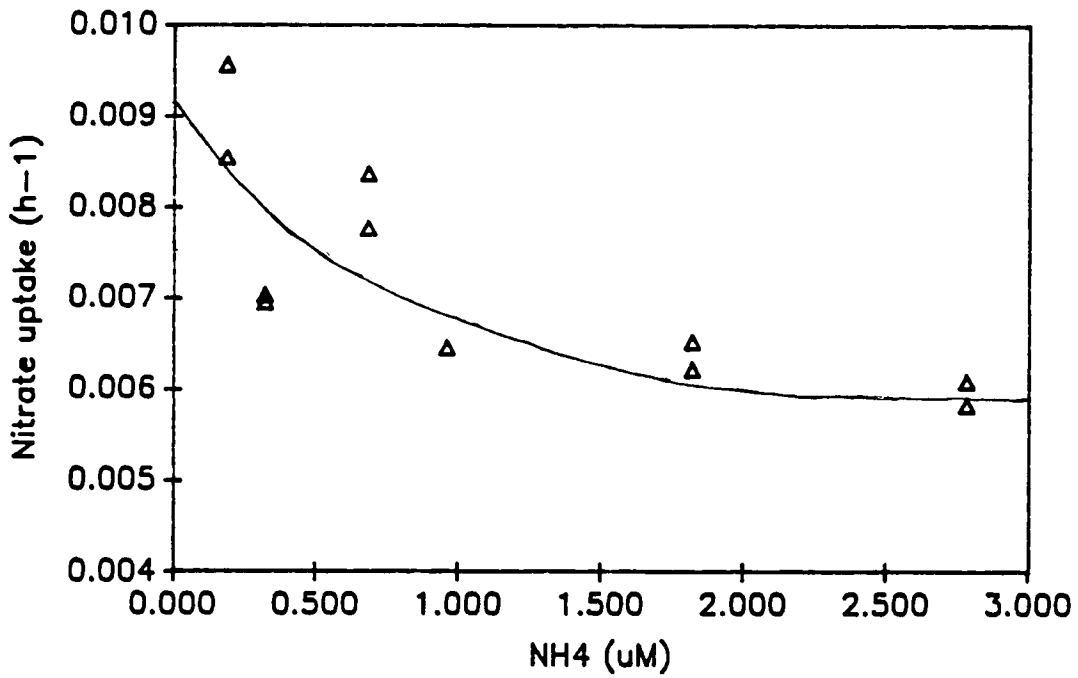


Figure 24. Relationship between specific nitrate uptake rate and ammonium concentration. Water sample taken from 18 m at Station 104.

Table 14. Summary of station data and calculated parameters for the ammonium inhibition experiment conducted at Station 168.

Station:	168
Date & Time:	May 13, 1989 16:47
Lat/Long:	79.0309°N 04.5970°E
% ice cover:	0/10
inc started:	12:27 May 13
inc ended:	11:57 May 14

Depth	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
surface	0.33	0.12	0.15	3.77	0.04	1.82	24.4

NH_4^+ (μM)	Specific Uptake Rate (h^{-1}) NO_3^-	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NO_3^-
0.12	0.0029	0.0719
0.48	0.0033	0.0796
0.66	0.0026	0.0641
0.96	0.0026	0.0637
1.38	0.0022	0.0534
2.34	0.0020	0.0486
3.24	0.0020	0.0490
0.12	0.0037	0.0895
0.48	0.0031	0.0760
0.66	0.0027	0.0661
0.96	0.0024	0.0579
1.38	0.0021	0.0511
2.34	0.0019	0.0466
3.24	0.0018	0.0446
MEAN	0.0025	0.0616
range	0 - 0.0037	0 - 0.0895

Table 15. Summary of station data and calculated parameters for the ammonium inhibition experiment conducted at Station 104.

Station:	104
Date & Time:	May 3, 1989 14:02
Lat/Long:	79.4116 °N 03.0280 °E
% ice cover:	8/10
inc started:	15:40 May 3
inc ended:	16:45 May 4

Depth	NO_3^- (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)	$Si(OH)_4$ (μM)	NO_2^- (μM)	chl a ($\mu g\ l^{-1}$)	PN ($\mu g\ l^{-1}$)
18m	3.95	0.19	0.39	5.16	3.95	3.78	62.2

NH_4^+ (μM)	Specific Uptake Rate (h^{-1}) NO_3^-	Transport Rate ($\mu g\ N\ l^{-1}\ h^{-1}$) NO_3^-
0.19	0.0096	0.5941
0.32	0.0070	0.4370
0.69	0.0084	0.5199
0.96	ND	ND
1.82	0.0062	0.3862
2.78	0.0061	0.3782
0.19	0.0085	0.5313
0.32	0.0069	0.4319
0.69	0.0078	0.4827
0.96	0.0064	0.4009
1.82	0.0065	0.4052
2.78	0.0058	0.3620
MEAN	0.0072	0.4481
range	0 - 0.0096	0 - 0.5941

Table 16. Summary of calculated parameters for ammonium inhibition experiments.

Station	$V_{(initial)}$ (h^{-1})	$V_{(inhibition)}$ (h^{-1})	Ki (μM)	% inhibition of $V_{(initial)}$
168	0.0035	0.0019	0.658	45.1
104	0.0091	0.0060	0.541	34.7

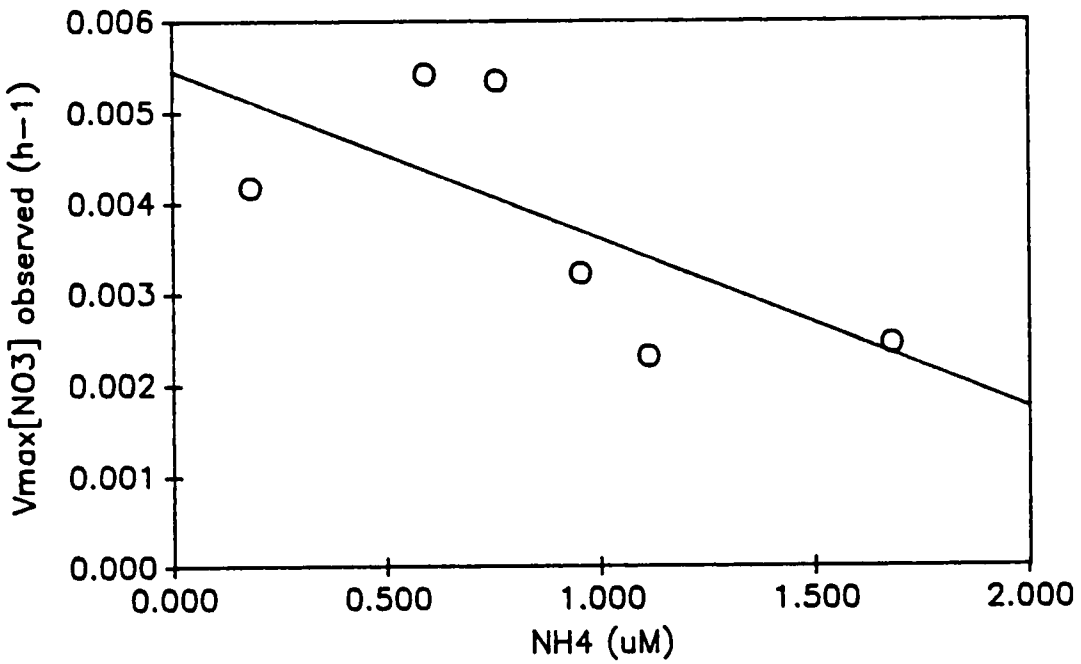


Figure 25. Maximum specific nitrate uptake rates observed from simulated in situ measurements (stations where experiments were also conducted), plotted against ambient ammonium concentrations. The regression equation is y = -0.001853x + 0.005446.

concentration of nutrients present was near the minimal uptake values obtained in the ammonium inhibition experiments. For example, in the irradiance experiment carried out at station 104, the maximum nitrate uptake rate achieved was 0.0054 h^{-1}, with the ambient ammonium concentration being 0.76 μM (refer to Figures 9, 24). Also, the maximum nitrate uptake rate achieved in the substrate experiment conducted at station 104 (Figure 21) was 0.006 h^{-1} (again close to the minimum nitrate uptake value from the ammonium inhibition experiment at station 104), with the ambient ammonium concentration present in the substrate experiment being 0.64 μM. The ammonium inhibition experiment conducted at station 104 was a better representation of the nutrient regime present at the irradiance experiment stations than was the inhibition experiment conducted at station 168. Ambient nitrate and ammonium concentrations at station 104 were 3.95 and 0.187 μM, respectively, while the ambient nitrate concentration at station 168 was 0.32 μM (see Tables 2-5, 15, 16). Hence, the ambient nitrate concentration found at station 168 was much lower than the ambient nitrate concentration found at any of the stations where irradiance experiments were conducted.

CHAPTER IV

DISCUSSION

Effects of Irradiance on Nitrate and Ammonium Uptake

Nitrate and ammonium uptake rates were measured in the Fram Strait during the summer of 1984 (Smith & Kattner 1989) in a similar manner to those reported for this study. Ambient nutrients were lower in the summer of 1984 than those found in the same area during the spring of 1989, with average surface concentrations of nitrate and ammonium being 1.6 and 0.2 μM, respectively (Smith & Kattner 1989). Smith & Kattner (1989) reported that specific nitrate uptake values were slightly higher than specific ammonium uptake values, and found the average surface nitrate uptake rate to be 0.0039 h^{-1} and the average surface ammonium uptake rate to be 0.0028 h^{-1}. These values are similar to the uptake rates reported here. The average nitrate uptake rate from surface samples exposed to surface irradiance from the irradiance experiments is almost identical to that reported by Smith and Kattner (1989), 0.0032 h^{-1}, with the average ammonium uptake rate being slightly less at 0.0012 h^{-1} (Tables 2, 3, 4). The average surface nitrate uptake rate obtained from the simulated in situ measurements carried out at irradiance experiment stations was also similar to that measured in the irradiance experiments and by Smith & Kattner (1989) at 0.0032 h^{-1}. However, the average ammonium uptake value achieved in the simulated in situ measurements during the spring of 1989 was seven times less

than the rate achieved in the Fram Strait during the summer of 1984. The average surface ammonium uptake rate calculated from those stations where irradiance experiments were carried out was 0.0004 h^{-1}. Because of the severe inhibition of ammonium uptake by surface irradiance levels found to occur in the irradiance experiments, ammonium uptake rates in the surface layers of the water column were probably supressed by high irradiance levels. In this study, surface irradiance levels were found to inhibit surface ammonium uptake rates on the average of 33%. Phytoplankton assemblages present in the spring during the early stages of the seasonal bloom have adequate amounts of nutrients available to them initially, and the light regime is probably the most important factor affecting nitrogen uptake.

Studies conducted in the summer have found that nitrate and ammonium uptake exhibit only a weak dependence on irradiance for polar phytoplankton assemblages (Kristiansen & Lund 1989, Smith & Kattner 1989). However, these studies were conducted after the spring bloom. Also, Smith & Kattner (1989) found no photoinhibition of nitrate or ammonium uptake in the Fram Strait during the summer of 1984, whereas ammonium uptake was always inhibited by surface irradiances in the irradiance experiments conducted in the Fram Strait during the spring of 1989. Nitrate uptake was inhibited in some, but not all, cases during the spring of 1989. This confirms the greater irradiance dependence and hence regulation by irradiance levels of nitrate and ammonium uptake during the early stages of the

phytoplankton bloom in the Fram Strait.

Differences in the responses of nitrate and ammonium uptake to irradiance have been observed by a number of researchers. One of the major differences between the uptake of nitrate and ammonium found to occur in the natural assemblage of phytoplankton in the Fram Strait during the spring of 1989 was the irradiance level at which the uptake of the respective nutrient was optimal. The average optimal per cent surface irradiance (the irradiance at which V_{max} is reached) for nitrate uptake by the phytoplankton in the Fram Strait was 77.8%, while the optimal percentage of surface irradiance level for ammonium uptake was 18.0%. This phenomenon is also reflected in the K_{1t} values; the average K_{1t} for nitrate uptake was 17% of surface irradiance and the average K_{1t} value for ammonium uptake was 3%. The ratio of the optimal percentage of irradiance of nitrate and ammonium uptake is similar to the ratio found for the percentage of irradiance at which saturation uptake occurs for nitrate and ammonium by the phytoplankton assemblage in the Fram Strait during the summer of 1984, where nitrate uptake was found to be saturated at 15% of surface irradiance and ammonium uptake at 5%. Even though the summer assemblage was capable of utilizing nitrate and ammonium at low irradiance levels, no inhibition was detected and high irradiance levels did not decrease uptake rates.

Differences in K_{1t} values for nitrate and ammonium uptake have been found in other natural phytoplankton assemblages as well. The K_{1t}-nitrate value measured for the Fram Strait phytoplankton during

the spring of 1989 was about five times that of the K_{lt}-ammonium value. Slawyk (1979) reported K_{lt} nitrate values about twice those of K_{lt} ammonium values for phytoplankton in the Indian sector of the Southern Ocean, and MacIsaac and Dugdale (1972) found that the K_{lt} values for nitrate uptake were twice as great as those of ammonium for natural assemblages in the eastern tropical Pacific. Similarly, MacIsaac (1978) reported that for a dinoflagellate-dominated assemblage off Baja, California, K_{lt}-nitrate values that were twice those of ammonium. It seems then, that the Arctic assemblages present during the spring in the Fram Strait are unique in that they exhibit a greater difference in the K_{lt}-nitrate:K_{lt}-ammonium ratio than phytoplankton from other regions. This could mean that nitrate uptake by this arctic assemblage requires higher irradiance levels than other assemblages do, that this assemblage is capable of utilizing ammonium at lower irradiance levels relative to phytoplankton in other regions, or a combination of the two.

Even though the phytoplankton assemblage of the Fram Strait during the spring is similar to other phytoplankton assemblages in that they have the ability to utilize ammonium at lower irradiance levels than nitrate, the photoinhibition of nitrate and ammonium uptake observed for the Fram Strait phytoplankton does not seem to be a general feature of phytoplankton. Ammonium uptake by the assemblage in the Fram Strait during the spring was much more inhibited by high irradiance levels than was nitrate uptake. Photoinhibition always occured for ammonium uptake, whereas nitrate

uptake was not always inhibited and had a lower average percentage of inhibition than ammonium uptake by a factor of two. The assemblage was capable of utilizing ammonium at lower irradiance levels than nitrate, but ammonium uptake was also more sensitive to inhibition by high irradiance levels than was nitrate uptake. Natural phytoplankton assemblages in Ungava Bay, Canada, showed greater sensitivity to photoinhibition of nitrate uptake rather than ammonium uptake (Smith & Harrision, pers comm). On the other hand, Nelson and Conway (1979) reported that no photoinhibiton of nitrate uptake occured in phytoplankton off Baja, California, but inhibition of ammonium uptake may have occured. In Antarctic freshwater assemblages, Priscu (1989) found that nitrate uptake was more strongly inhibited by high irradiance levels than was ammonium uptake, and Dodds and Priscu (1989) reported photoinhibition of both nitrate and ammonium uptake of about the same magnitude for freshwater phytoplankton in Flathead Lake, Montana. Because irradiance levels can be a factor controlling nutrient uptake, it should be noted that phytoplankton from these different regions experience very different light regimes. The difference in the irradiance level at the surface relative to that present where the assemblages were sampled from must invariably be different, in addition to mixing/stratification effects. The change in irradiance levels that some of the phytoplankton may have been exposed to in irradiance vs. uptake experiments could possibly not have been great enough to induce a photoinhibition response.

Another possible explanation for the discrepancies found between the irradiance sensitivities of nitrate and ammonium uptake could entail the actual mechanism of transport across the membrane, which could be species-specific. Falkowski and Stone (1975) reported that for natural assemblages from Knight Inlet, B. C., Canada, the source of ATP for nitrate uptake was primarily from cyclic photophosphorylation (PSI), which is dependent on light. The actual mechanism of ammonium transport is even less well understood than the mechanism for nitrate transport. If the nitrate uptake mechanism is tightly coupled to photosynthetically derived ATP, high irradiance levels should have a negative effect on nitrate uptake if the irradiance is strong enough to damage the photosynthetic apparatus. This is what is hypothesized to occur for those assemblages showing greater photoinhibition of nitrate uptake over ammonium uptake. If the energy source for ammonium uptake is not light dependent, the greater photoinhibition of ammonium uptake rather than nitrate uptake seems paradoxal. One possibility is that the energy source required for ammonium uptake is needed for other neccessary cell functions when stressed cells are unable to produce light-derived energy sources due to damage of the photosynthetic apparatus. Other metabolic processes may compete for the energy source normally used for ammonium uptake, with the allocation patterns changing and reducing the amount of that energy source available for ammonium transport. The needs of cells from different regions would vary and depend on the nutrient regime, light regime, and recent history of

the cells involved. As mentioned earlier, the actual role that irradiance plays in the transport mechanisms of ammonium and nitrate is poorly understood (Falkowski 1983), and hence only speculations can be made at this time.

The irradiance experiments carried out between the 100% and 0.1% surface irradiance phytoplankton from the Fram Strait add to the differences between the effects of irradiance on nitrate and ammonium uptake. For the irradiance vs. nitrate uptake experiments, the average maximum nitrate uptake rate was greater for the 0.1% irradiance sample than for the surface sample. Aside from the photoinhibition of nitrate uptake that occured in the surface samples, another phenomenon may have contributed to the observed difference in uptake rates between the 100% and 0.1% surface irradiance assemblages. Phytoplankton present in low irradiance environments can become shade adapted, thereby increasing their chlorophyll a levels to maximize photosynthesis. The relationship between shade adaptation and nitrogen metabolism was studied by Falkowski and Stone (1975) and Falkowski (1980), who found that organisms living in low-irradiance environments can maximize their chlorophyll a concentrations and the production of cellular ATP, supporting the transport of nitrate across the cell membrane. Three of the four stations where light experiments were conducted during CEAREX were stratified, with the 0.1 % irradiance level occuring deeper than the pycnocline. This would prevent mixing and allow the 0.1% irradiance sample to become shade adapted with time.

In contrast to the results found for nitrate uptake, the surface irradiance assemblages had a greater average ammonium maximum uptake rate than that of the 0.1% irradiance assemblage. When the 0.1% surface irradiance samples were exposed to irradiance levels ranging from 0.1 to 100% I, the uptake rates acheived were less than the uptake rates that the 100% I sample attained. The higher irradiacane levels were a drastic change for the shade adapted 0.1% irradiance sample and inhibited ammonium uptake, whereas the 100% irradiance sample was exposed to lower irradiance levels and was subsequently able to achieve greater ammonium uptake rates. The exposure of the shade adapted phytoplankton to high irradiance levels resulted in the greater inhibition of ammonium uptake relative to nitrate uptake. These data are in agreement with other data in that the energy source required for ammonium uptake is derived from a different source than that utilized in nitrate uptake, and the energy needed for ammonium transport is not obtained directly from photosynthesis (Falkowski & Stone 1975, Nelson & Conway 1979). The remaining mechanisms possible for the origin of the energy source utilized in ammonium uptake include substrate phosphorylation and oxidative phosphorylation (Falkowski & Stone 1975, Nelson & Conway 1979), but more research at the physiological level is needed before differences in nitrate and ammonium uptake mechanisms can be quantified.

Effects of Nutrient (Nitrate, Ammonium) Concentration on Nutrient (Nitrate, Ammonium) Uptake

The maximal uptake rates actually achieved in the substrate

experiments were 0.0068 and 0.0060 h^{-1} for nitrate and 0.0063 h^{-1} for ammonium. A nitrate concentration of 3.0 μM was high enough to saturate nitrate uptake by the phytoplankton assemblage at Station 128. Because higher nitrate levels were not used in the nitrate uptake experiment at station 104, it is difficult to say whether the uptake rate would have increased much over 0.006 h^{-1}. The maximum uptake rate predicted by the model (0.0113) is much greater than the maximum uptake rate observed for the in situ measurements, irradiance experiments and nutrient concentration experiments. The high V_{max} value predicted for Stations 104 and 068 is probably due to the sluggish nature with which the assemblages removed nitrate and ammonium. The water samples used for these experiments were kept in unscreened bottles in an on-deck incubator for a week prior to the experiments to allow for ambient nutrient depletion. In contrast, the uptake experiment at station 128 was conducted immediately with the nutrient-depleted surface water, and hence represents the more natural in situ characteristics of the phytoplankton. The V_{max}-nitrate values obtained from the irradiance experiment and in situ measurements at station 104 were 0.0054 and 0.0039 h^{-1}, respectively. Ambient nitrate and ammonium concentrations at station 104 were ca. 3.0 and 0.37 μM, respectively, whereas ambient nitrate and ammonium concentrations present when the irradiance experiment was conducted were 4.2 and 0.76 μM. The ambient ammonium concentrations were probably responsible for supressing the maximum nitrate uptake rates in situ and in the irradiance experiment, and while the ammonium

level was almost undetectable for the nitrate concentration versus nitrate uptake experiment, irradiance may have caused a slight inhibition of the maximal nitrate uptake rate. MacIsaac and Dugdale (1972) reported identical V_{max} values for irradiance experiments and nutrient experiments in phytoplankton assemblages from the eastern tropical Pacific Ocean and Peru. The V_{max} nitrate values achieved at station 104 are similar, and all V_{max} values lie within the range of specific uptake rates found for oligotrophic regions. MacIsaac and Dugdale (1969) reported V_{max} nitrate values between 0.001 and 0.007 h^{-1} for oligotrophic waters in the north east tropical Pacific ocean. V_{max} ammonium values for this same area ranged from 0.0057 to 0.0088 h^{-1}. Nitrate uptake values reported for the Sargasso Sea by Glibert and McCarthy (1984) range from 0.0007 to 0.0041 h^{-1}. In polar waters, the nitrate uptake rates acheived by the spring phytoplankton assemblage in the Fram Strait were slightly higher but within the range of uptake rates by phytoplankton from other polar regions. Kristiansen and Lund (1989) found nitrate uptake rates to be between 0.000 to 0.0093 h^{-1} for phytoplanton in the Barents Sea, with the nutrient regime present at the time of study almost identical to that found during the spring in the Fram Strait. Ammonium uptake rates were found to be slightly less, ranging from 0.0002 to 0.0076 h^{-1}. In the Eastern Canadian Arctic, Smith & Harrision (pers comm) reported the maximum nitrate uptake rate to be 0.00185 h^{-1} as determined by nutrient kinetic experiments. The low uptake rates were attributed to low temperatures.

Because the nutrient concentration versus nutrient uptake curves did not level off and were somewhat sluggish for the experiments conducted at stations 104 and 068, the actual Kt value for phytoplankton in the Fram Strait during spring is probably more similar to the Kt value obtained from the experiment conducted at staion 128. Transport constants for oligotrophic waters have been reported to be less than or equal to 0.2 μM by MacIsaac and Dugdale (1969). In polar regions, Kristiansen and Lund (1989) report nitrate Kt values between 0.1 and 2.2 μM and ammonium Kt values of 0.1 and 0.2 for phytoplankton in the Barents Sea. The estimate of the Kt value for ammonium from the Fram Strait assemblage is probably an overestimate. Transport constants for the Eastern Canadian Arctic were found to be 0.87 μM for nitrate and 0.17 μM for ammonium by Smith & Harrison (pers comm). The lower Kt ammonium values would again indicate that the estimated Kt ammonium value from the Fram Strait is probably not representative of in situ ammonium uptake characteristics. Additional experiments conducted by Dr. David Nelson (Oregon State University) in the Fram Strait during CEAREX may give further insight as to realistic Kt values of nitrate and ammonium for the assemblage present during the spring bloom.

Effect of Ammonium on Nitrate Uptake

Ammonium concentrations have been demonstrated to significantly reduce nitrate uptake in temperate water, but this phenomenon has not

been shown to occur in polar phytoplankton until recently (Kristiansen & Lund 1989). In the Fram Strait during the spring of 1989, nitrate uptake was inhibited by ammonium concentrations ranging from 0.3 to 2.2 μM by ammonium inhibition experiments. The onset of inhibition required very low concentrations of ammonium, where ammonium concentrations of less than 0.5 μM decreased the uptake rate of nitrate ca. 18%. Kristiansen and Lund (1989) reported that nitrate uptake was inhibited by ammonium concentrations of 0.8 μM and greater in the Barents Sea. Ambient ammonium concentrations present in the Fram Strait during the spring of 1989 ranged from ca. 0.3 to 1.5 μM, and were capable of supressing in situ nitrate uptake rates during this study. Maximum nitrate uptake rates measured by simulated in situ methods did indeed decrease with increasing ambient ammonium levels. Ammonium concentrations were not the only factor responsible for limiting nitrate uptake (light and possibly nitrate concentration also had an effect), but the ammonium inhibition experiments indicate that ammonium concentrations encountered could have been an important factor in decreasing nitrate uptake rates within the Fram Strait during the spring of 1989.

CHAPTER V

CONCLUSIONS

1. Both nitrate and ammonium uptake were strongly dependent on irradiance in the Fram Strait during the spring of 1989, and the relationship appears to be described by the equation used by Priscu (1989).

2. The phytoplankton assemblages present during this study were able to utilize ammonium at lower irradiance levels than nitrate; with the average optimal percent irradiance for ammonium and nitrate uptake being 18.0% and 77.8%, respectively.

3. Photoinhibition was found to occur for both ammonium and nitrate uptake.

4. Ammonium uptake was more sensitive to photoinhibition than was nitrate uptake: ammonium uptake was always inhibited by surface irradiance levels whereas nitrate uptake was not.

5. Surface irradiance levels caused an average of 33.3% reduction of ammonium uptake rates, whereas surface irradiance levels caused an average of 19.4% reduction of nitrate uptake rates out of those samples that exhibited photoinhibition.

6. The relationship between nutrient (NO_3^-, NH_4^+) uptake and nutrient (NO_3^-, NH_4^+) concentration appears to be characterized by the Michaelis-Menton equation.

7. The best estimates for the maximal nitrate uptake rate and nitrate transport constant values for the Fram Strait during the spring are 0.0064 h^{-1} and 0.29 μM, respectively. A maximum nitrate uptake rate of 0.0090 h^{-1} was obtained during an ammonium inhibition

experiment, but the ammonium concentration present was lower than that found in the water column. The maximum nitrate uptake rates found are comparable to higher values found for oligotrophic waters, and of the same range for uptake rates reported for polar waters.

8. Nitrate uptake rates were found to be dependent on ammonium concentrations.

9. Ammonium concentrations of less than 0.5 μM were able to decrease nitrate uptake rates ca. 18%.

10. The average maximum extent of the inhibition of nitrate uptake by ammonium was 40%, and occurred at ammonium concentrations equal to or greater than ca. 2.5 μM.

11. Overall, nitrate uptake rates in the Fram Strait during the spring were predominantly controlled by irradiance and ammonium concentrations, with ammonium concentrations having the potential to supress nitrate uptake rates by ca. 40%.

12. Overall, ammonium uptake rates in the Fram Strait during the spring were predominantly controlled by irradiance, where surface irradiance levels were capable of supressing ammonium uptake rates by 33.3%. Ambient ammonium concentrations may have had an effect on ammonium uptake, but insufficient data were collected to examine this possibility.

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VITA

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