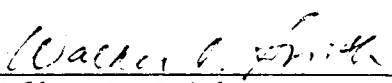
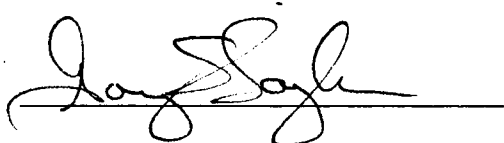
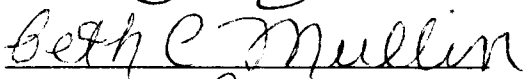
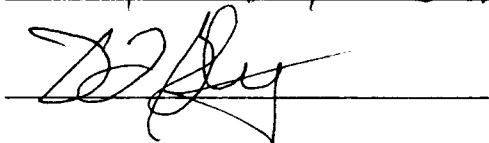


To the Graduate Council:

I am submitting herewith a dissertation written by Nancy K. Keene entitled "Nitrogen Dynamics in the East Greenland Sea." I have examined the final copy of this dissertation for form and content and recommend that it be accepted for the degree of Doctor of Philosophy, with a major in Ecology.


Walker O. Smith
Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:


Vice Provost
and Dean of the Graduate School

NITROGEN DYNAMICS IN THE EAST GREENLAND SEA

A Dissertation

Presented for the

Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Nancy K. Keene

August, 1990

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For all those friends who gave me support, encouragement and wouldn't let me quit, thank you. And thank you Amy Rachel for being Amy Rachel.

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ABSTRACT

This study established ammonium and nitrate uptake rates in the East Greenland Sea at both the Arctic and Polar Fronts in May of 1987 and at the Polar Front in June of 1987 and 1988. In addition, ammonium regeneration rates were measured at the Polar Front in 1987 and 1988. Field experiments carried out at the Polar Front in 1988 examined procaryotic versus eucaryotic uptake and the effects of substrate manipulation on uptake by both eucaryotic and procaryotic organisms. All uptake rates were measured using heavy isotope tracer techniques. The results of this study indicated total nitrogen uptake at the Arctic Front in May of 1987 was nearly one third that of the Polar Front at the same time. In addition, 70% of the nitrogen being assimilated at the Arctic Front was in the form of nitrate as compared to 28% at the Polar Front. Nitrate based or "new" production at the Polar Front was below the levels needed for flux from out of the euphotic zone without detrimental affects on the system. The low percentage of nitrate being assimilated was consistent for the Polar Front during June of 1987 and 1988. Uptake rates of ammonium were higher in June of 1987 than during any other period measured and absolute ammonium uptake rates were as much as 200 times that of nitrate absolute uptake at some stations. The most significant difference in physical parameters between the Arctic and Polar Fronts appeared to be the difference between depth of the pycnocline with relation to the euphotic zone with the Arctic Front having a much deeper mixed layer than the Polar Front. Correlation

analysis of several parameters and nitrogen uptake rates showed a significant negative correlation between ammonium and the depth of the pycnocline. Results from inhibition and substrate manipulation experiments showed that changing substrate C:N ratios affected assimilation of ammonium by procaryotes.

It appears therefore, from this study, that although primary production, as estimated from uptake rates, is consistent with open ocean production at the Arctic Front and that the majority of it is nitrate based. However, at the Polar Front total production is three to four times as high as at the Arctic Front and the majority is ammonium based. In addition bacteria appear to be utilizing ammonium as a source of nitrogen, and therefore may be competing with phytoplankton for this nutrient under certain circumstances.

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1. INTRODUCTION

NITROGEN

Nitrogen is one of the essential elements needed for growth by phytoplankton in the marine environment, and specifically the euphotic zone, where the other essential nutrients (carbon, phosphorus, etc.) are relatively abundant, and nitrogen availability most often determines phytoplankton dynamics (Dugdale & Goering, 1967; Rhee, 1978; Goldman et al., 1979; McCarthy, 1980; 1981). Some of the forms of nitrogen that are available for use by phytoplankton are nitrate, ammonium, nitrite and urea. Although a few marine algae can fix molecular nitrogen, only one, Oscillatoria (Trichodesmium), reaches locally significant densities (Mague et al., 1974; Carpenter & McCarthy, 1975; McCarthy & Carpenter, 1979). Nitrogen fixation in marine systems is usually considered a quantitatively minor source of nitrogen. Of the forms of nitrogen available to phytoplankton, nitrate and ammonium support most phytoplankton growth, and these two forms arise from different processes and on different time scales.

Nitrate is the end product of a series of bacterial oxidations of soluble and particulate nitrogen compounds from plant and animal excretions and the death of organisms. These processes usually occur at sub-euphotic depths (Stanier et al. 1970; Riley & Chester, 1971); consequently, nitrate must be vertically advected into the surface layer prior to utilization by phytoplankton. Nitrification may occur

at nitracline depths at sufficient rates to supply a variable portion of phytoplankton nitrate (Ward et al., 1989), but further investigation is needed to quantify its effect. The two major sinks for nitrate are denitrification in anoxic environments and assimilation into organic matter in the surface layer.

Ammonium is produced from in situ oxidation of substrates which originate from cell lysis. Ammonium is also produced by multicellular organisms which then actively secrete it into the environment. The cycling of ammonium generally occurs over a short time. Assimilation into organic matter by phytoplankton and oxidation to nitrite (and ultimately nitrate) by heterotrophic bacteria are the major sinks for this form of nitrogen (Stanier et al., 1970; Riley & Chester, 1971). Until recently the major utilizers of ammonium during the production of organic matter were considered to be primary producers, with bacteria acting as a source rather than a sink for ammonium (Riley & Chester, 1971). However, Hasimoto et al. (1983) estimated a half-saturation constant of approximately 0.1 μM for in situ ammonium oxidation rates, which suggests that marine ammonium oxidizers might effectively compete with phytoplankton for substrate (Ward, 1985). Wheeler and Kirchman (1986) hypothesized that under certain conditions a significant amount of ammonium may be assimilated by heterotrophic bacteria, and Goldman et al. (1987) suggested the extent that bacteria compete for ammonium may be affected by the C:N ratio of the dissolved organic substrate. Significant assimilation by heterotrophic bacteria could

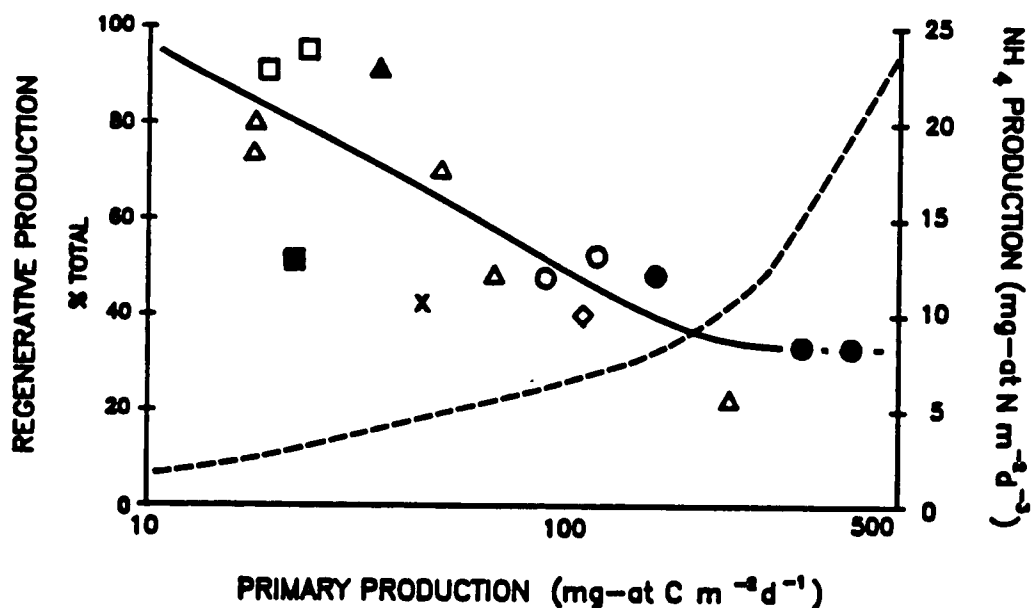
greatly affect ammonium availability and primary production, especially in oligotrophic areas where ammonium is the major source of nitrogen.

NITROGEN UPTAKE AND "NEW" VS. "REGENERATED" PRODUCTION

Nitrogen uptake and ammonium regeneration measurements are tools that give information for understanding events within the pelagic ecosystem. In 1967 Dugdale and Goering described experiments that used stable isotope tracer techniques to study nitrogen transformations in the sea. The use of stable isotopes allows direct measurements of nutrient uptake. In this dissertation uptake will refer to the movement of ions through the cellular membrane into the cell, whereas assimilation will refer to the incorporation of ions into organic compounds.

Dugdale and Goering also demonstrated that the form of nitrogen assimilated by phytoplankton was a quantitative and qualitative index of the oceanic source of that nutrient, with ammonium removed by the phytoplankton considered to be "regenerated" productivity. In contrast, nitrate from depth supports "new" productivity that is available for export from the system (Dugdale & Goering, 1967; Eppley & Peterson, 1979; Harrison, 1980). Therefore, "new" and "regenerated" production can be approximated from NO_3^- and NH_4^+ uptake measurements, respectively (Dugdale & Goering, 1967; Eppley & Peterson, 1979; McCarthy, 1980). Eppley and Peterson (1979) suggested a means of estimating how much production is available for

flux from the system by using the assimilation rate of nitrate divided by the sum of the assimilation rates of all forms of nitrogen. A high "f" ratio indicates that a large portion of production is the result of nitrogen brought into the system and therefore could leave the system without a negative impact. This primary production is based primarily on nitrate. Conversely, a low value indicates extensive recycling of nutrients and loss from the system would not be readily replaced. It also indicates production based primarily on regenerated nitrogen (i.e., ammonium). Eppley et al. (1979) also showed that although relative "regenerated" production decreases at the same time that "new" production is stimulated (via the vertical flux of nitrate into the euphotic zone), the absolute "regenerated" production increases with new production (Fig. 1). Although "new" production is important, it is thought that the major fraction of total primary production, especially in oligotrophic environments (i.e., areas of low primary production), is based on regenerated nitrogen. This regenerated nitrogen is usually in the form of ammonium (Dugdale & Goering, 1967; Eppley & Peterson, 1979; McCarthy, 1980), although urea has been shown to be a quantitatively significant component of "regenerated" production at certain times (McCarthy, 1972; McCarthy & Eppley, 1972; Eppley et al., 1979; Kristiansen, 1983; Kaufman et al., 1983).



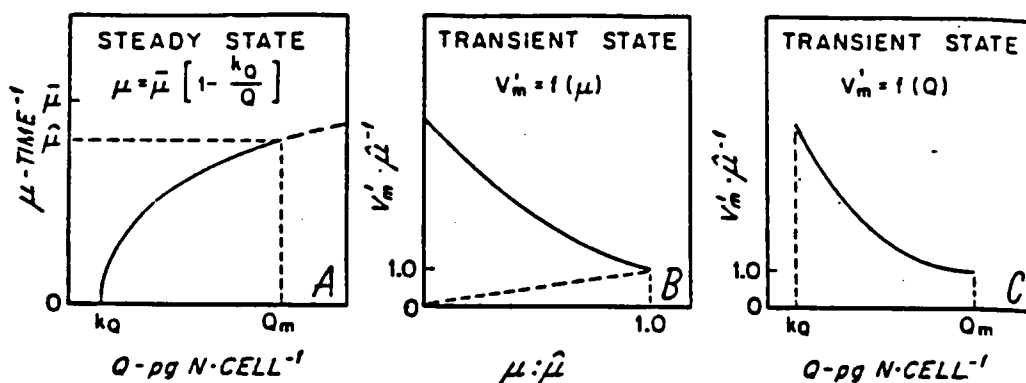
Solid line fit by eye represents relative ammonium production; dashed line represents absolute production. Filled circles are from coastal upwelling; open circles from coastal, non-upwelling; triangles are oceanic; squares are oligotrophic waters; filled squares from Antarctic waters, late winter/spring (Olson, 1980); filled triangle from Antarctic waters, late summer (Ronner et al., 1983); diamond from Antarctic waters, summer (Nelson & Smith, 1986); and cross from Antarctic waters, summer (Glibert et al., 1982a).

FIGURE 1. Relationship between regenerative and total production.

FACTORS AFFECTING NITROGEN UPTAKE

Eppley and Coatsworth (1968) used laboratory cultures to demonstrate that rates of nitrogen assimilation could be approximated by hyperbolic functions of either the ambient nutrient concentration or the cellular nitrogenous nutrient concentration. MacIsaac and Dugdale (1969) found in experiments in Alaskan coastal waters and the northeastern tropical Pacific Ocean that the uptake of both nitrate and ammonium was best described in the manner of the Michaelis-Menten expression for enzyme kinetics. Therefore, with natural populations a hyperbolic function also describes the relationship between the concentration of these nutrients and the uptake of the nutrient. Droop (1974) showed that growth is dependent on cell quota (cellular nutrient mass $\times$ total cellular mass⁻¹; Goldman & Glibert, 1983; Fig. 2). Dugdale (1967), in a mass balance model of phytoplankton nitrogenous-nutrient dynamics, connected the summed events of uptake and growth with the available external source of limiting nutrient.

Nutrient uptake in natural phytoplankton populations can also be affected by changes in irradiance (Caperon & Ziemann, 1976; Eppley et al., 1979). MacIsaac and Dugdale (1972) studied uptake rates as a function of irradiance and found half-saturation constants at low irradiances for nitrate uptake and even lower constants for ammonium uptake (1-14% of surface irradiance). In Antarctic waters (austral late winter/early spring), Olson (1980) found that nitrate uptake ceased in the dark while ammonium uptake, in the dark, was



A. Graphical depiction of the Droop equation when used to describe the relationship between steady-state growth rate (μ) and cell quota (Q); B. conceptual relationship between transient uptake represented by relative maximum uptake rate $V_m' : \mu$ and steady state growth rate defined as relative growth rate $\mu : \hat{\mu}$. Dashed line between origin and datum point $V_m' : \mu = \mu : \hat{\mu} = 1$ represents balanced rates of nutrient uptake and growth, whereas curvilinear increase in $V_m' : \mu$ with decreasing $\mu : \hat{\mu}$ represents enhanced nutrient uptake relative to growth for a given duration of exposure to saturating nutrient; C. alternative depiction of curve in panel B in which cell quota (Q) derived as a function of growth rate μ is used in place of $\mu : \hat{\mu}$.

FIGURE 2. The effect of phytoplankton cell physiological state on growth and NH_4 uptake (Goldman & Glibert, 1983).

approximately one half that which occurred in the light. Energetic considerations both in membrane transport and assimilation could account for these rate changes.

Nitrate uptake rates are affected by the apparent preference of ammonium over nitrate by natural phytoplankton populations (Dugdale & Goering, 1967; Eppley et al., 1969; McCarthy, 1972; McCarthy et al. 1977; 1982; Eppley & Peterson, 1979; Glibert et al., 1982a). If there is enough ammonium to meet the entire nitrogen requirement, complete inhibition of nitrate uptake occurs (Syrette & Morris, 1963; Eppley et al., 1969; MacIssac & Dugdale, 1972; McCarthy et al., 1977). If there is not enough ammonium to meet the entire nitrogen requirement, there is a simultaneous utilization of ammonium and nitrate (Glibert & McCarthy, 1984). Although the mechanism for NH_4^+ inhibition of NO_3^- uptake is not well understood (Collos & Slawyk, 1980), there is evidence for regulation at the level of nitrate transport (Eppley & Rogers, 1970; Serra et al., 1978; Tischner & Lorenzen, 1979) and nitrate reduction (Syrett & Morris, 1963; DeManche et al., 1979). McCarthy et al. (1977) suggested the use of a Relative Preference Index (RPI) to determine which nitrogen form was preferred by phytoplankton. For example, the RPI for ammonium would be the ratio of the uptake rate of ammonium divided by the total nitrogen uptake rate in the numerator and the denominator would be the ambient concentration of ammonium divided by total ambient nitrogen concentration; or $\text{RPI}_{\text{NH}_4} = [\rho/(\rho\text{NO}_3^- + \rho\text{NH}_4^+)]/[\text{total } [\text{N}]/([\text{NH}_4^+] + [\text{NO}_3^-])]$. A value less than one indicates relative

rejection of the nitrogen form being examined, a value greater than one indicates preference and a value of one indicates uptake equitable with availability.

REGENERATION

The amount of primary productivity in areas where there is no significant input from external sources (i.e., NH_4^+ from atmosphere, NO_3^- from sub-euphotic zone) is usually limited by regenerative fluxes. Rates of ammonium regeneration determine how rapidly ammonium is made available for primary producers. In areas of negligible sources of other forms of nitrogen, primary production proceeds at a rate limited by the rate of regeneration (Glibert, 1982). Phytoplankton are capable of high assimilation and high growth rates in oligotrophic waters (Goldman et al., 1979; McCarthy & Goldman, 1979). Therefore, in environments where ammonium concentrations are often below the limits of detection, absolute ammonium concentrations are not a good indication of assimilation rate (Glibert, 1982; Ward, 1985).

Ammonium regeneration rates are necessary for a quantitative description of the nitrogen cycle and phytoplankton growth. These rates are affected by grazing and oxidative rates of heterotrophs, which in turn are affected by the availability of primary production. It now appears that most ammonium regeneration is done by microheterotrophs (protozoans and bacteria) (Harrison, 1978; Caperon et al., 1979; Harrison, 1980; Glibert, 1982; Probyn & Painting,

1985). Bacteria contribute to ammonium regeneration as decomposers of organic matter, using inorganic forms of nitrogen when organic forms are unavailable (Riley & Chester, 1971). The use of inorganic nitrogen by bacteria is being more closely examined in the open ocean where dissolved amino acids and proteinaceous material may not provide sufficient nitrogenous nutrients for bacterial growth (Azam et al., 1983; Harder & Dijkhuizen, 1983; Goldman et al., 1987).

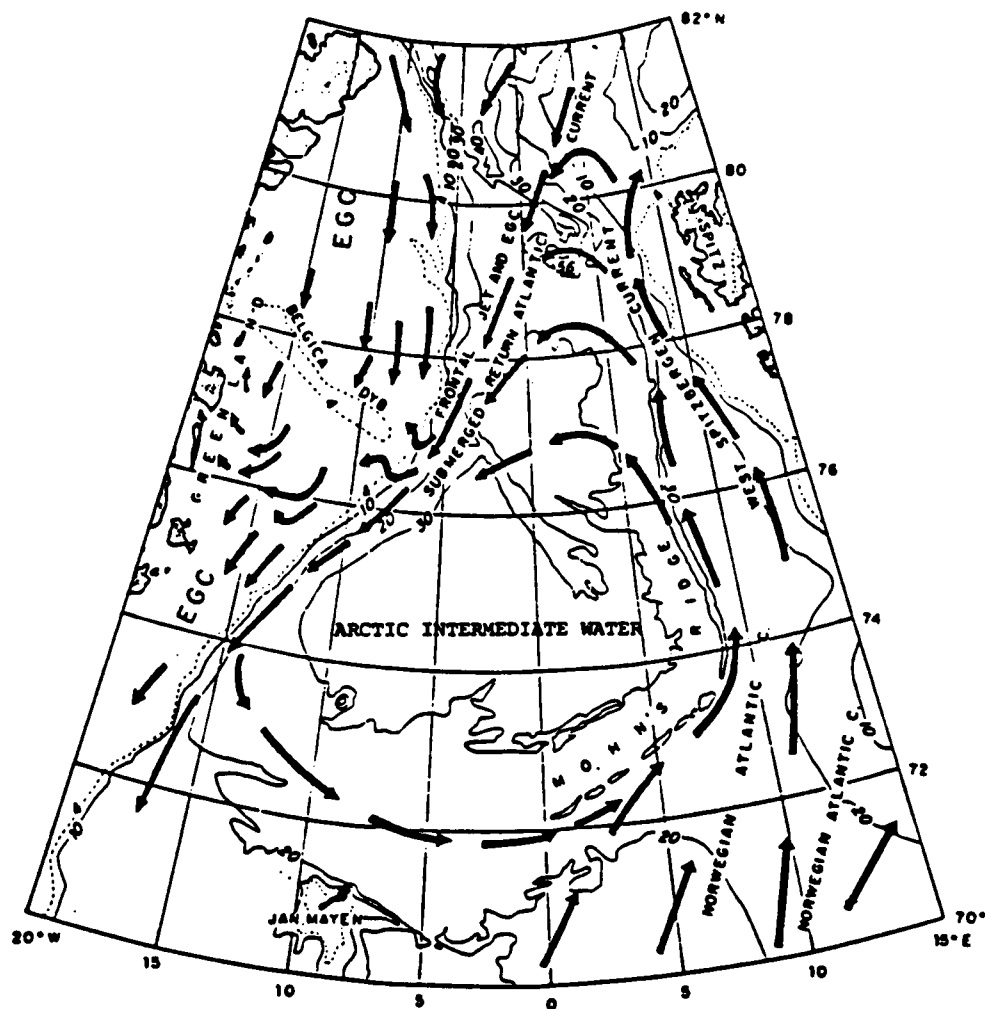
EAST GREENLAND SEA

The East Greenland Sea is a high latitude system characterized by seasonal and environmental extremes. Seawater temperatures are low (generally -2 to 1°C), and a long period of darkness is followed by a rapid change to continuous irradiance. Pack ice forms in the winter and melts in the spring and summer, resulting in a dynamic ice edge and heightened biological activity (Smith, 1987). The spring melt forms a low density, low salinity, stable lens that enhances phytoplankton growth (Alexander & Niebauer, 1981; Smith et al., 1985; Smith & Nelson, 1986; Wilson et al., 1986). Ice also affects rates of primary production by modifying both the quantity of irradiance that reaches the water column and the air-sea interaction (Smith, 1987). Surface nitrate values in the winter are close to those of the deep Atlantic (ca. 12 μM), and nutrient depletion can occur after a spring bloom in some regions (Sakshaug & Holm-Hansen, 1984).

The Greenland Sea is characterized by frontal zones whose positions vary both spatially and temporally. These zones are

important because they are areas of either accumulation or dispersion of biomass and nutrients (Alexander & Niebauer, 1981; Owen, 1981; Fedorov, 1983). The two major frontal regions in the Greenland Sea are the Polar Front and the Arctic Front, which are delineated by their marked changes in temperature and salinity over short distances. The Arctic Front forms where the cold, Arctic Intermediate Water meets the warmer North Atlantic Water; it is dynamic in nature with deep mixing and eddy generation consistently occurring in the area of the front. The Polar Front forms where the Arctic Intermediate Water meets the Polar water (Paquette et al., 1985; Fig. 3). In addition, the Polar Front is usually associated with the marginal ice zone and the ice melts in summer and spring, resulting in an area of water column stability with a shallow mixed layer usually above the base of the euphotic zone.

The East Greenland Sea is recognized as a critical area for the ventilation of the Atlantic deep ocean (Broecker & Peng, 1982; Peng et al., 1987). It is a link between the Arctic Ocean and the North Atlantic where deep water formation occurs. This deep water has a residence time on the scale of thousands of years (Pickard, 1975; Dobson, 1983). The process of deep water formation is of global importance for its role in carbon dioxide flux (Sarmiento & Toggweiler, 1984). Primary production removes carbon dioxide from the surface layers by sequestering carbon in the form of particulate organic matter, and the surface layers become a carbon dioxide sink. However, for organic matter to act as a carbon sink on a more



Arctic Front forms at convergence of W. Spitzbergen Current and Arctic Intermediate Water; Polar Front forms at convergence of Arctic Intermediate Water and East Greenland Current (Frontal Jet & EGC).

FIGURE 3. Water masses in the East Greenland Sea (modified from Paquette et al., 1985).

permanent basis, production must be removed from the short-term biological cycle in the ocean's upper layer. Organic carbon which sinks to depth can no longer participate in oxidative cycles on biologically relevant time scales, and therefore, cannot exchange with the atmosphere. Flux of particulate matter into the deep waters of the Atlantic via the Greenland Sea could contribute substantially to this carbon sink.

OBJECTIVES

The oceans are widely recognized as a major sink for anthropogenic CO₂ released into the atmosphere (Liss, 1983; Peng et al., 1987). Nitrogen is the limiting nutrient for photosynthesis and consequently the rate of nitrogen uptake has an effect on the rate of flux of organic carbon from the surface layer of the sea. Spatial and temporal variability of nitrogen uptake as well as the predominant form being utilized affects our ability to determine how much carbon is available for export.

The East Greenland Sea may have a major impact on carbon flux. Uptake measurements of nitrate and ammonium are useful in describing organic carbon flux, but uptake measurements from the Greenland Sea have only been available from the Fram Strait (Smith & Kattner, 1989) and at a few stations in the vicinity of the Polar and Arctic Fronts in the Barents Sea (Kristiansen & Lund, 1989).

In this study, the major objective was to measure the nitrate and ammonium uptake in the the East Greenland Sea and to determine

by the means of f-ratios what percentage of total production is available for export from this area. In addition, other specific objectives include:

1. To look for spatial and temporal variability in nitrate and/or ammonium uptake in the East Greenland Sea.
2. To test the hypothesis that the Polar Front contributes more to "new" production than does the Arctic Front;
3. And to perform a preliminary set of experiments to test the hypothesis that bacteria are a sink rather than a source of ammonium in the East Greenland Sea.

2. METHODOLOGY

SAMPLE COLLECTION

Samples were collected on transects in the Greenland Sea (Fig. 4) in May and June of 1987 and May of 1988 from the research vessel F.S. Polarstern during research cruises ARK IV-1, ARK IV-2 and ARK V-2, respectively. During ARK IV-1, samples were collected at stations along transects that repeatedly crossed both the Arctic Front and the Polar Front, forming two distinct grids. Samples collected during ARK IV-2 and ARK V-2 were collected at stations on transects that ran approximately east to west and extended from 72 to 80°N. Samples for determination of salinity, temperature and chemical and biological properties were taken at light depths corresponding to the 100, 50, 30, 15, 5, and 1‰ isolume on ARK IV-1 and ARK IV-2 and the 100, 50, and 1‰ isolume on ARK V-2. Attenuation was determined using a Secchi disc. Samples were obtained using a rosette sampler mounted with either 24 10-liter Niskin bottles or 6 20-liter Niskin bottles. All were then prefiltered through a 325 μ M mesh prior to measurement of nitrogen uptake. Prefiltration was performed in order to remove larger zooplankton.

PARTICULATE NITROGEN AND CARBON ANALYSIS

One liter of each sample collected was immediately filtered through a precombusted (450°C for 2 h) 47 mm Whatman glass fiber

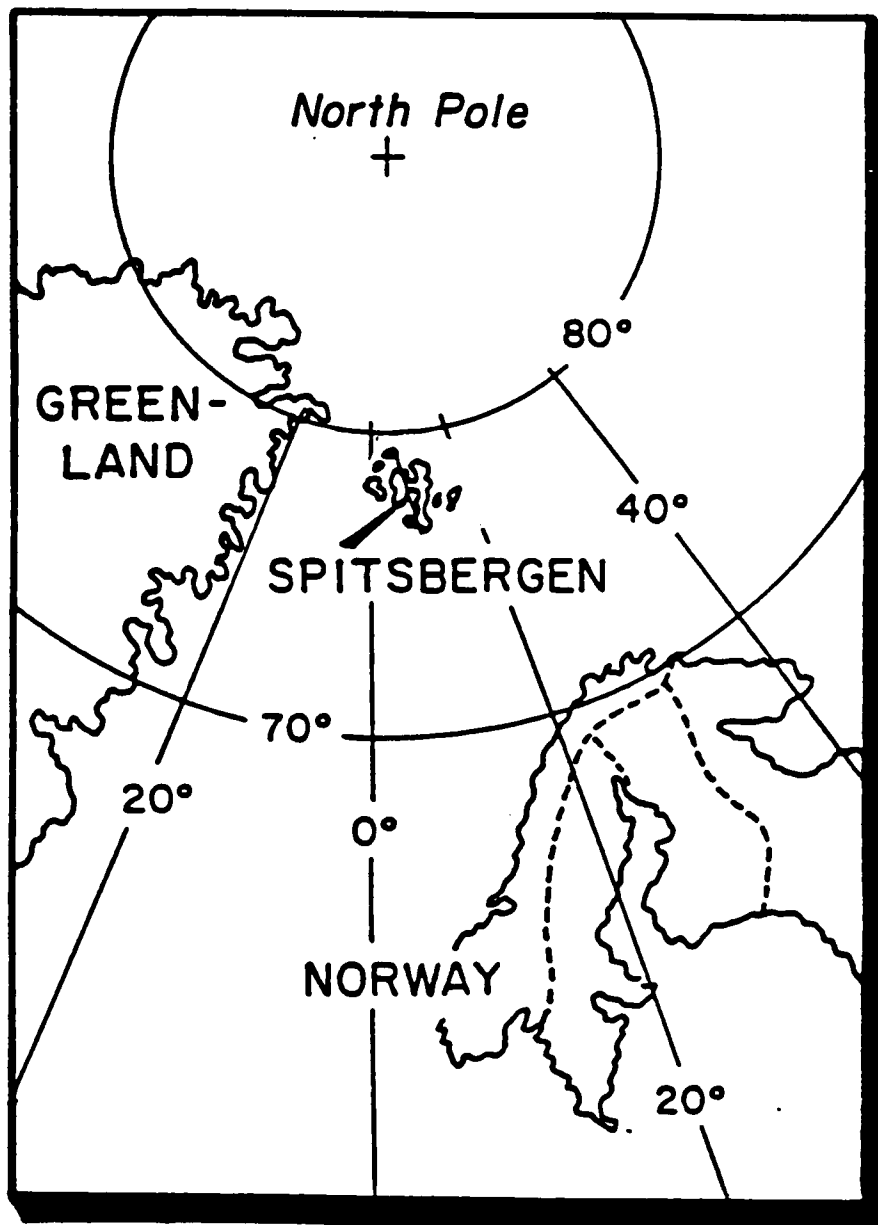


FIGURE 4. Overview of East Greenland Sea.

filter (GF/F) under low pressure, rinsed with 0.001N HCl in filtered sea water to remove inorganic carbonates, and placed in combusted glass vials which were then covered with aluminum foil. Each filter was dried at 60°C and later analyzed for particulate nitrogen and carbon on a Perkin-Elmer 240B Elemental analyzer (Sharp, 1974).

NITRATE AND AMMONIUM UPTAKE MEASUREMENTS

Additional samples were placed in individual 1 liter polycarbonate bottles which were covered with neutral density screens to simulate the irradiance level from which they were collected. Samples for nitrate and ammonium uptake were inoculated with either $^{15}\text{N-NH}_4^+\text{Cl}$ or $^{15}\text{N-KNO}_3^-$. The amount of isotope (99.9% carrier free) added was approximately 10% of ambient nutrient concentration. Ambient concentrations of nitrate and ammonium were obtained from chemical analysis using a continuous flow Technicon AutoAnalyzer II (Eberlein et al., 1983). The isotope was generally not added until two or three hours after collection because of the need to measure ambient nutrient concentrations. After inoculation with isotope, the samples were incubated for approximately 5 h in an on-deck incubator that simulated in situ light conditions and was cooled with continuously-flowing surface seawater. The incubation period was determined after a review of a paper by Harrison (1983), in which he used data from time- course experiments in the Canadian Arctic to demonstrate that low temperatures keep phytoplankton growth rates (and nutrient demands) low. I corroborated this with a time series

in the field that showed no nutrient depletion occurred within 24 h. In addition, the amount of ^{15}N incorporated into particulate matter was adequate for analytical detection. Incubations were terminated by filtering the particulate matter through precombusted 47 mm glass fiber filters which were then rinsed with filtered seawater to remove any residual inorganic ^{15}N . Filters were dried and converted to nitrogen gas using a modified Dumas sample preparation technique (Fiedler & Proksch, 1974) on a Kimazawa Model G-II N-15 Evacuation System. $^{15}\text{N}:^{14}\text{N}$ ratios were then determined on a JASCO N-150 emission spectrometer. Nitrogen uptake rates were calculated using these ratios and the equations of Dugdale & Goering (1967) (see Table 1 for all equations). Particulate nitrogen values used in the equations were those measured at the start of the incubation. Corrections for isotope dilution effects were computed using the equations of Kanda et al. (1987). Ammonium relative preference indices (RPI) and all f-ratios were calculated using the equations of McCarthy (1981) and Eppley & Peterson (1979).

INHIBITION OF AMMONIUM UPTAKE

Additional replicate samples, for the study of inhibition of ammonium uptake, were first inoculated with either prokaryotic inhibitors or eukaryotic inhibitors. Prokaryotic inhibition was achieved using a combination of penicillin (1 mg l^{-1} ; 1647 units mg^{-1}) and vancomycin (200 mg l^{-1}), which stop cell division in prokaryotes (Sherr et al., 1986). Eukaryotic activity was inhibited by a

Table 1. Equations used in the calculation of nitrogen uptake

EQUATION	VARIABLE DEFINITION	REFERENCE
$V = \frac{{}^{15}\text{N}_{\text{Ex}}}{\frac{{}^{15}\text{N}_{\text{Enr}} \times T}{{}^{15}\text{N}_{\text{Enr}}}}$	V = specific uptake rate (h^{-1}) ${}^{15}\text{N}_{\text{Ex}}$ = atom % excess ${}^{15}\text{N}_{\text{Enr}}$ = atom % enrichment T = length of incubation (h)	Dugdale & Goering (1967)
$\rho = V \times \text{PN}$	ρ = absolute uptake rate ($\mu\text{mol l}^{-1}\text{h}^{-1}$) PN = particulate nitrogen (mg m^{-3})	
$\rho = \frac{{}^{15}\text{N}_{\text{Ex}}}{R \cdot T} \cdot \text{PN}$	ρ = absolute uptake rate ($\mu\text{mol l}^{-1}\text{h}^{-1}$) ${}^{15}\text{N}_{\text{Ex}}$ = atom % excess R = exponential avg. of atom % enrichment T = length of incubation PN = particulate nitrogen (mg m^{-3})	
$R = \frac{R_0}{kt [1 - \exp(-kt)]}$	R_0 = atom % enrichment at start of incubation t = length of incubation	Glibert et al. (1982b)
$k = \frac{-\ln[R(t)/R_0]}{t}$	$R(t)$ = atom % enrichment at end of incubation	
$d = \rho \left[\frac{1}{1 + (\ln(P_t/P_0))} \right] \frac{\ln(R_t - {}^{15}\text{n}) - \ln(R_0 - {}^{15}\text{n})}{\ln(R_t - {}^{15}\text{n}) - \ln(R_0 - {}^{15}\text{n})}$	d = regeneration rate ($\mu\text{mol l}^{-1}\text{h}^{-1}$) P_t = ambient NH_4 at end of incubation P_0 = ambient NH_4 at start of incubation ${}^{15}\text{n}$ = ${}^{15}\text{N}$ normal (0.365%)	
$q_c = \rho \times x$	ρ_c = corrected absolute uptake rate ($\mu\text{mol l}^{-1}\text{h}^{-1}$) ρ = absolute uptake rate ($\mu\text{mol l}^{-1}\text{h}^{-1}$)	
$x = \ln(1-b)/b$	x = correction for isotope dilution b = apparent consumption of substrate	Kanda et al. (1987)
$b = (\rho \times T)/(S + S')$	S = ambient concentration of substrate S' = concentration of added tracer (assuming $a=1$)	
$f = \rho_{\text{NO}_3} / (\rho_{\text{NO}_3} + \rho_{\text{NH}_4})$	ρ = absolute uptake ($\mu\text{mol l}^{-1}\text{h}^{-1}$)	Eppley & Peterson (1979)
$\text{RPI} = \frac{V_{\text{NH}_4} / [V_{\text{NO}_3} + V_{\text{NH}_4}]}{[\text{NH}_4] / ([\text{NO}_3] + [\text{NH}_4])}$	RPI = ammonium relative preference index $[\text{NH}_4]$ = ammonium concentration (μM) $[\text{NO}_3]$ = nitrate concentration (μM)	McCarthy et al. (1977)

combination of cycloheximide (200 mg l^{-1}) and colchicine (100 mg l^{-1}), both of which inhibit protein synthesis in eukaryotes (Wheeler & Kirchman, 1986; Sherr et al., 1986). These samples were maintained in an on-deck incubator for a minimum of two hours before the addition of 10% of ambient NH_4^+ concentration of $^{15}\text{N-NH}_4^+\text{Cl}$. The samples were then treated in the same manner as the ammonium uptake samples described above. Controls consisted of additions of all four inhibitors to a single bottle, which was then treated the same as the other samples.

REGENERATION MEASUREMENTS

When regeneration measurements were made, a 2-liter sample was placed in a 2.5 liter container. Then an addition of $^{15}\text{N-NH}_4\text{Cl}$ (99% carrier free) isotope was made, the amount of which was determined to be 10% of the ambient ammonium concentration. One liter was then placed in a 1-liter polycarbonate bottle for ammonium uptake measurements (see NITRATE AND AMMONIUM UPTAKE above). The second liter was immediately filtered for particulate nitrogen analysis. The collected filtrate was measured and 5 ml of carrier $^{14}\text{NH}_4\text{Cl}$ (concentration = 5 uM ml) added. Next, 50 ml was removed from the measured filtrate, with the added carrier, for ambient ammonium analysis. Approximately 700 ml were placed in a 1-liter round bottom boiling flask with 1 ml of MgO slurry, placed on a heating mantle and distilled through a Graham distillation column. Approximately 75 ml of distillate was collected in a polypropylene flask containing 1 ml

of freshly double-distilled H_2O and 35 mg of Union Carbide, #W-85, molecular sieve. The contents of the flask were filtered onto a precombusted 47 mm Whatman glass fiber filter, rinsed with freshly double distilled H_2O and placed in a precombusted glass vial in a $60^\circ C$ drying oven. This procedure was repeated on the filtrate from the ammonium uptake sample that was collected at the end of the incubation period. All filters obtained from this procedure were processed in the same manner as the filters for uptake measurements (see NITRATE AND AMMONIUM UPTAKE above). Rates of regeneration were calculated using these ratios and the Blackburn/Caperon model from Glibert et al. (1982b)(Table 1). Particulate nitrogen values used in the equations were those measured at the start of the incubation. The regeneration apparatus was cleaned initially and between each distillation by rinsing with 10% HCl and then rinsed three times with distilled H_2O . The distillation rig was further cleaned by distilling approximately 100 ml of pre-distilled H_2O . Double-distilled water was used for the MgO slurry, for adding to the sieve and for additional rinsing. Only enough MgO slurry to last for 12 h was made at one time to avoid ammonium contamination.

SUBSTRATE MANIPULATION EXPERIMENTS

The following modification of the Goldman et al. (1987) laboratory experiments was conducted at three stations during ARK V-2. This experiment was performed to examining the effect of substrate C/N ratio. The three stations were chosen to provide

seawater with different levels of biomass. Surface seawater was obtained from bucket casts, and 10 liters were placed in each of three, clear, 16-liter plastic carboys. Initial concentrations of dissolved carbon and nitrogen in the untreated sea water sample were assumed to be in the approximate ratio of 7:1 (Redfield, 1934). To one carboy 2.6 ml of a 233 $\mu\text{mol/ml}$ stock solution of glycine was added to increase the dissolved organic matter C/N substrate ratio to approximately 2:1. A C/N substrate ratio of approximately 10:1 was achieved by adding 2.5 ml of 250 $\mu\text{mol/ml}$ of dextrose to a second carboy. The third carboy was used as a control. These carboys were then incubated in an on deck incubator for 24 h. An additional 10 l of untreated water was immediately used for the following: 1) particulate nitrogen and carbon analysis, 2) nitrate and ammonium uptake, 3) ammonium regeneration and 4) ammonium inhibition measurements. Samples were taken at 0, 6, 12, and 24 h from the control carboy for bacterial enumeration and ambient ammonium concentration measurements. Samples for bacterial enumeration were filtered, concentrated and then stained using acridine orange stain (Hobbie et al., 1977). After 24 h, replicates were taken from each carboy and the previously described measurements made.

ANALYTICAL ERROR

Analysis of analytical error was made for the emission spectrometer and also for the sample preparation and evacuation methodology. Analysis of machine error was determined by finding the

mean and standard deviation for three replicate peaks on single samples. Sample preparation error was determined by taking three aliquots of single samples, running them as replicates and determining mean and standard deviation. These estimates of error showed that there was less than 1% error in the atom percent measurements made by the JASCO N150 and that there was approximately 2% analytical error due to sample preparation.

STATISTICAL ANALYSIS

Due to the problems inherent in oceanographic field work, replicates at each station were not obtained, and consequently, an analysis of variance (ANOVA) was not performed. Without ANOVA an analysis of significant variation can not be done and inferences cannot be made. However, partial correlation regression analyses were run (Statgraphics) for surface ammonium and nitrate uptake and five environmental parameters. These five environmental parameters included ambient nitrogen concentrations, depth of the pycnocline, salinity, and particulate nitrogen concentrations. A multiple regression was then run using the five environmental parameters as well as time and place. These analyses were performed in an attempt to determine points of departure for any future investigation dealing with nitrogen uptake variability and its cause.

3. RESULTS

ARK IV-1

The stations sampled on this cruise were from two distinct areas in the Greenland Sea, the Arctic and Polar Front (Fig. 5). Samples were taken from 12 stations and six isolumes in the area of the Arctic Front, and at six isolumes from 18 stations in the area of the Polar Front.

ARCTIC FRONT

The study region which included the Arctic Front was ice-free at all stations sampled. The pycnocline occurred generally below 100 m, with the depth of the pycnocline determined by a change of 0.1 in the measured, surface, sigma-t values. Sigma-t values are a measure of density computed as $(\text{density} - 1)1000$ (Gross, 1980). The 1% isolume, or depth at which 1% of the surface irradiance was present, was never deeper than 35 m (Fig. 6). Surface levels of nitrate were uniformly high (Fig. 7) and ranged from 6.1 to 11.1 μM . Surface ammonium concentrations ranged from 0.25 to 0.6 μM (Fig. 7).

Specific ammonium uptake ranged from 0.0001 to 0.0022 h^{-1} and specific nitrate uptake ranged from 0.0001 to 0.0035 h^{-1} (Table 2). Mean values for each isolume were obtained by averaging the values for each isolume from all stations sampled. Vertical profiles (Fig. 8) of these mean values (Appendix B-1) showed that mean absolute ammonium uptake rates were between 50 and 75% those of mean absolute

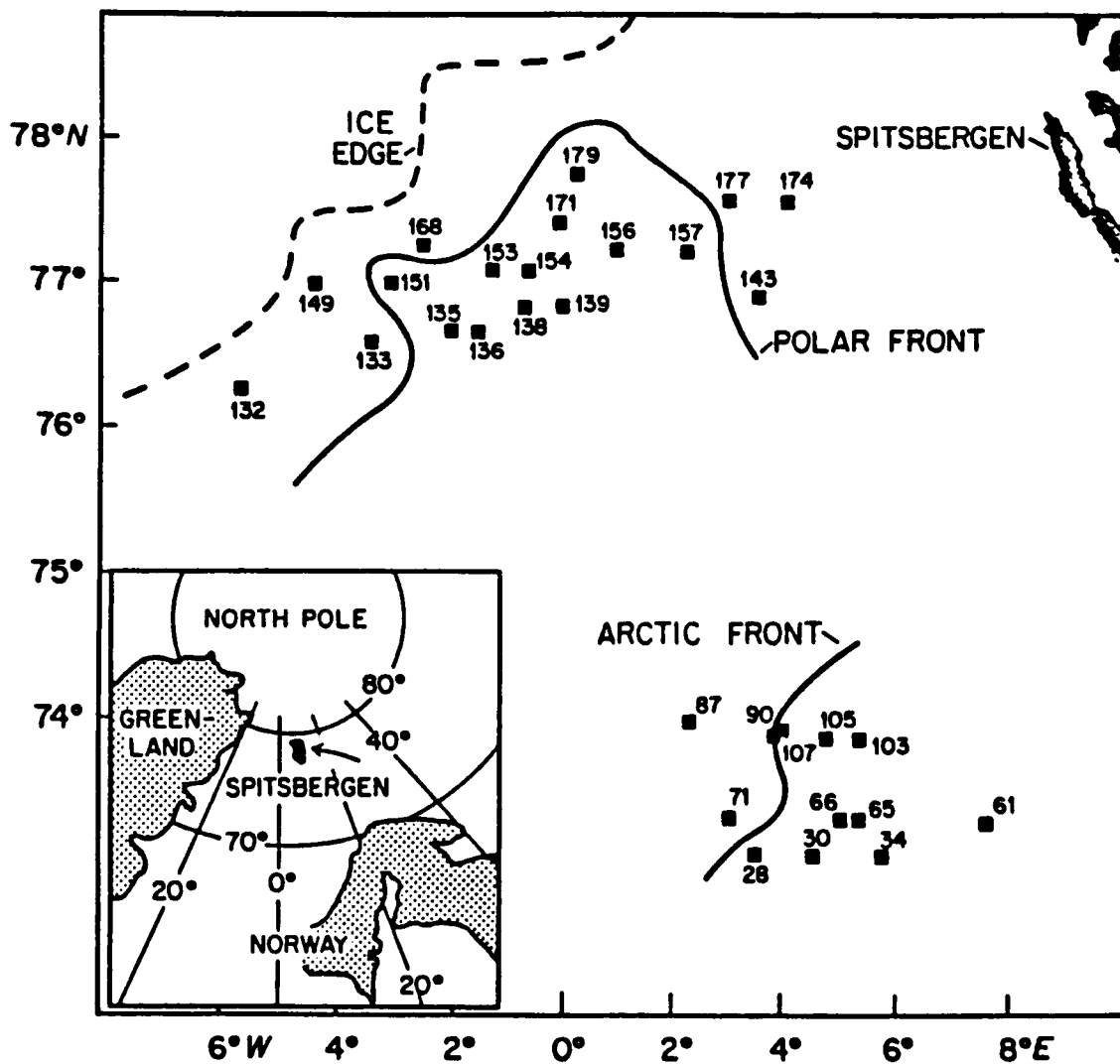


FIGURE 5. Map of Polar and Arctic Front showing station locations at which nitrogen uptake measurements were taken, May, 1987.

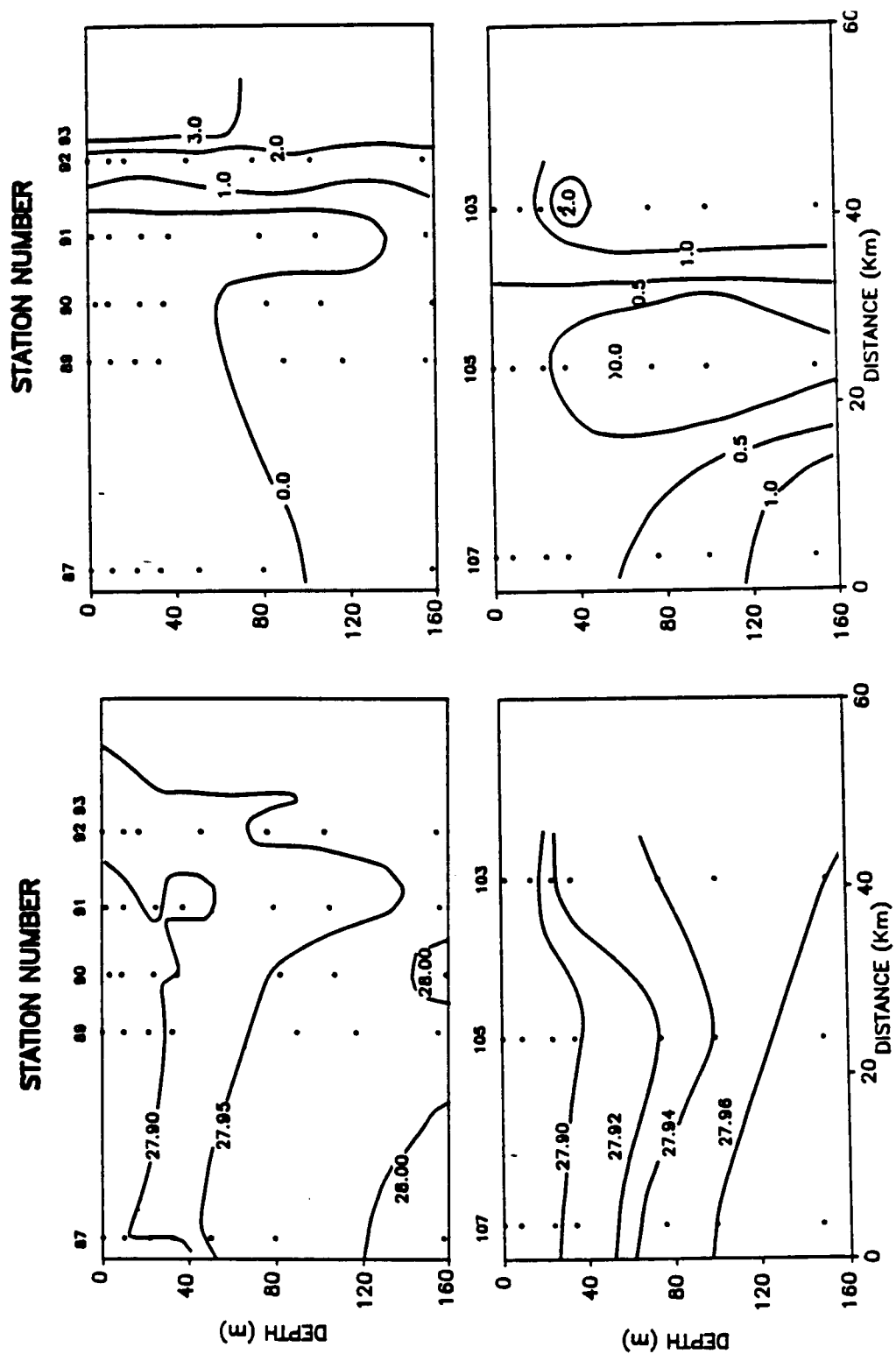


FIGURE 6. Sections of sigma t and temperature (°C) in the upper 160 m along transects at the Arctic Front, ARK IV-1, May, 1987.

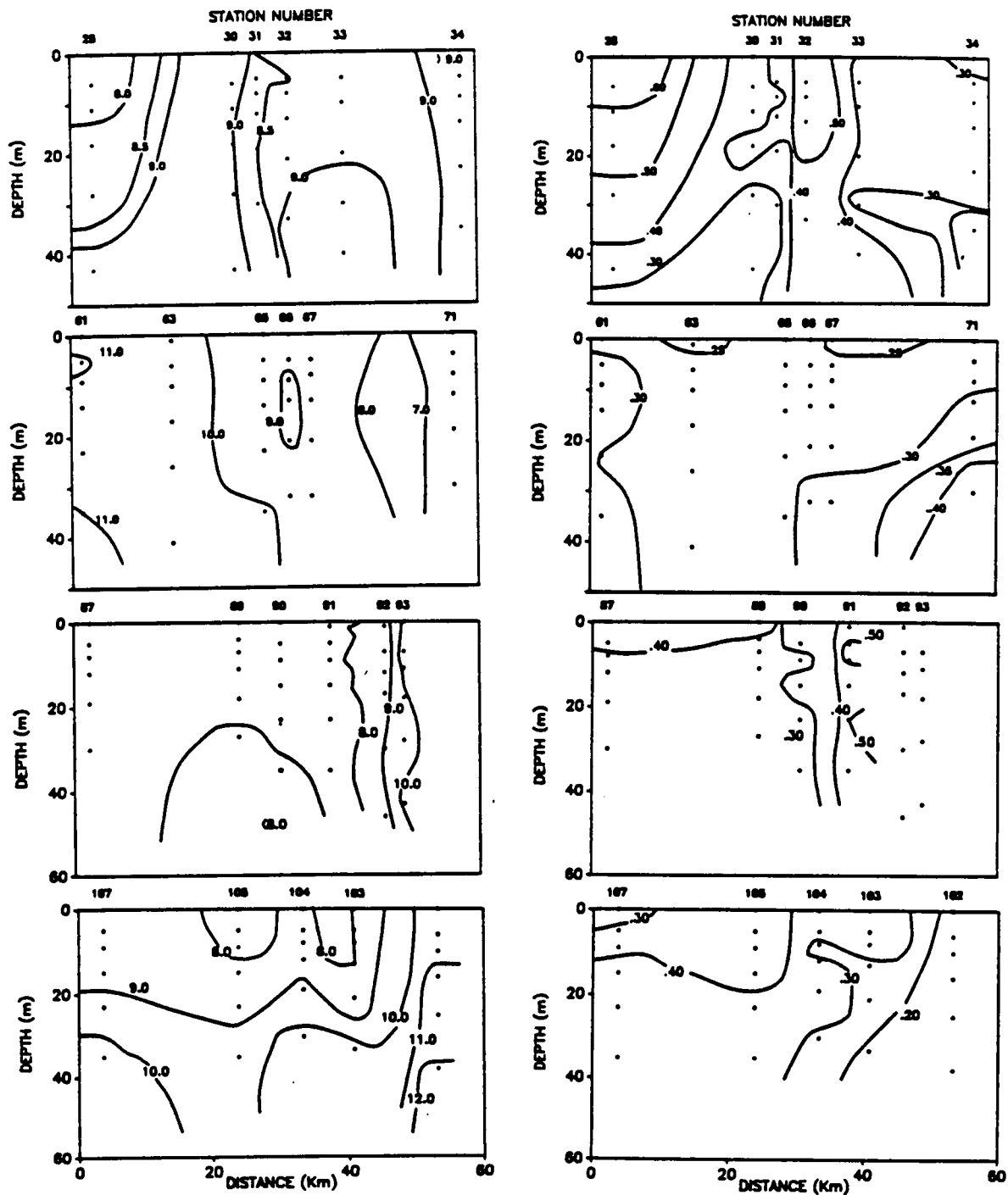


FIGURE 7. Sections of nitrate and ammonium concentrations (μM) in the euphotic zone along transects at the Arctic Front, IV-1, May, 1987.

Table 2. Particulate nitrogen, ammonium and nitrate specific (V) and absolute (ρ) uptake in the region of the Arctic Front. Asterisk denotes particulate nitrogen (PN) values derived from regression of known particulate nitrogen and chlorophyll values. ND = no data

Station No.	%I ₀	PN ($\mu\text{g l}^{-1}$)	Nitrate		Ammonium	
			V (h^{-1})	ρ ($\mu\text{mol l}^{-1} \text{h}^{-1}$)	V (h^{-1})	ρ ($\mu\text{mol l}^{-1} \text{h}^{-1}$)
28	100	*1.30	.0005	.0007	.0016	.0024
	50	0.99	.0009	.0009	.0034	.0034
	30	1.16	.0033	.0038	.0014	.0016
	15	1.96	.0007	.0014	.0012	.0023
	5	1.74	.0017	.0029	.0011	.0019
	1	1.66	.0017	.0017	.0008	.0013
30	100	0.9	.0008	.0008	.0001	.0001
	50	0.77	.0008	.0006	.0008	.0006
	30	0.85	.0002	.0002	.0010	.0009
	15	1.52	.0015	.0022	.0010	.0015
	5	1.46	.0005	.0008	.0005	.0007
	1	0.88	.0003	.0003	.0001	.0001
34	100	1.42	.0016	.0023	.0007	.0010
	50	0.81	.0032	.0026	.0012	.0009
	30	0.63	.0027	.0017	.0022	.0014
	15	0.67	.0024	.0016	.0008	.0005
	5	0.51	.0022	.0011	.0002	.0001
	1	*1.01	ND	ND	.0001	.0001
61	100	1.15	.0035	.0040	.0009	.0010
	50	0.68	.0035	.0024	.0004	.0003
	30	1.44	.0035	.0050	.0003	.0004
	15	1.62	.0014	.0023	.0016	.0027
	5	2.56	.0010	.0026	.0004	.0010
	1	1.48	.0002	.0003	.0005	.0008
65	100	0.90	.0030	.0027	.0008	.0008
	50	1.14	.0038	.0044	.0009	.0011
	30	0.78	.0021	.0016	ND	ND
	15	1.97	.0025	.0050	.0008	.0016
	5	1.04	.0012	.0013	.0008	.0008
	1	1.01	.0016	.0016	ND	ND
66	100	2.61	.0028	.0074	.0004	.0011
	50	0.88	.0028	.0024	.0002	.0001
	30	0.99	.0017	.0016	.0012	.0012
	15	0.81	.0004	.0003	.0007	.0005
	5	1.07	.0002	.0002	.0007	.0007
	1	0.61	.0001	.0001	.0016	.0010

Table 2. cont.

Station No.	SI _o	PN ($\mu\text{g l}^{-1}$)	Nitrate		Ammonium	
			$\frac{V}{(h^{-1})}$	$\frac{\rho}{(\mu\text{mol l}^{-1} h^{-1})}$	$\frac{V}{(h^{-1})}$	$\frac{\rho}{(\mu\text{mol l}^{-1} h^{-1})}$
71	100	3.39	.0021	.0070	.0007	.0025
	50	2.90	.0018	.0052	.0006	.0017
	30	3.01	.0013	.0039	.0007	.0020
	15	3.90	.0014	.0054	.0005	.0018
	5	*3.68	.0001	.0004	.0007	.0026
	1	2.79	.0001	.0004	.0008	.0023
87	100	2.15	.0012	.0026	.0013	.0028
	50	1.77	.0014	.0025	.0015	.0027
	30	*1.79	.0002	.0004	.0012	.0021
	15	1.72	.0007	.0012	.0012	.0020
	5	2.26	.0003	.0008	.0002	.0005
	1	2.23	.0005	.0012	.0005	.0012
90	100	1.41	.0025	.0046	.0001	.0002
	50	1.51	.0025	.0047	.0001	.0002
	30	1.96	.0016	.0031	.0009	.0017
	15	1.82	.0014	.0025	.0001	.0002
	5	1.59	.0013	.0021	.0003	.0005
	1	1.77	.0002	.0003	ND	ND
103	100	1.87	.0022	.0040	.0015	.0029
	50	1.97	.0029	.0057	.0011	.0022
	30	1.93	.0018	.0035	.0003	.0006
	15	1.96	.0011	.0019	.0007	.0012
	5	1.78	.0023	.0051	.0005	.0012
	1	1.01	.0009	.0009	.0003	.0004
105	100	1.71	ND	ND	.0008	.0014
	50	1.79	.0019	.0034	.0009	.0017
	30	1.65	.0011	.0018	.0009	.0015
	15	1.88	.0016	.0031	.0021	.0041
	5	1.59	.0011	.0018	.0008	.0013
	1	1.90	.0003	.0006	.0005	.0016
107	100	1.52	.0029	.0046	.0022	.0034
	50	1.40	.0027	.0040	.0014	.0023
	30	1.42	.0029	.0044	.0015	.0049
	15	1.39	.0015	.0022	.0012	.0039
	5	1.89	.0020	.0039	.0010	.0019
	1	0.88	.0023	.0022	.0015	.0017

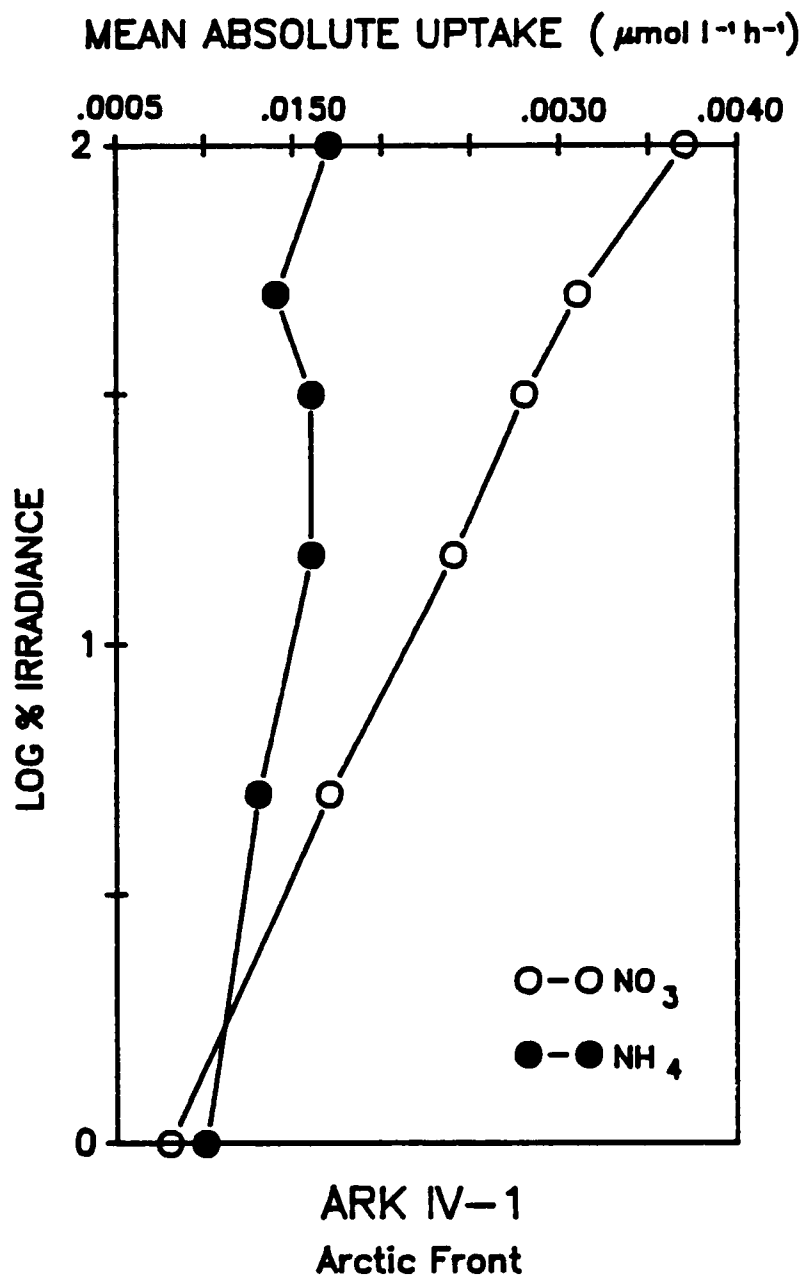


FIGURE 8. Vertical distribution of mean absolute uptake, Arctic Front, ARK IV-1, May, 1987.

nitrate at all depths except at the 1% isolume, and that mean uptake rates decreased with depth for both ammonium and nitrate. Mean nitrate absolute uptake at the 1% isolume was 22% that of surface uptake and for the same depth, mean ammonium absolute uptake was 59% that of the surface, indicating that light availability is affecting nitrate uptake more than ammonium. The standard deviation (for each light depth) for both ammonium and nitrate absolute uptake was not as great as the mean itself (Fig. 9). The standard deviation that was the largest percent of the mean (between 80 and 88%) occurred at the 5 and 1% isolume.

Mean f-ratios were consistent throughout the euphotic zone and averaged 0.62 ($\pm$.08) (Table 3). Ammonium was the preferred nitrogen source, with a relative preference index (RPI) well over 1 and highest at the base of the euphotic zone (Table 3). Although ammonium was preferentially removed, nitrate provided the majority of nitrogen for phytoplankton growth due to its greater availability.

POLAR FRONT

The Polar Front usually coincided with the location of the ice edge (Fig. 5), and 11 of the 18 stations sampled had 2/10 or more ice cover. The pycnocline occurred between 8 and 14 m, which was well above the base of the euphotic zone (depth of the 1% isolume averaged 37 m; Fig. 10). Nitrate concentrations were high at most stations, although reduced to below 3 μ M at one location (Sta. 179; Fig. 11). The lowest nitrate concentrations occurred where ammonium levels were

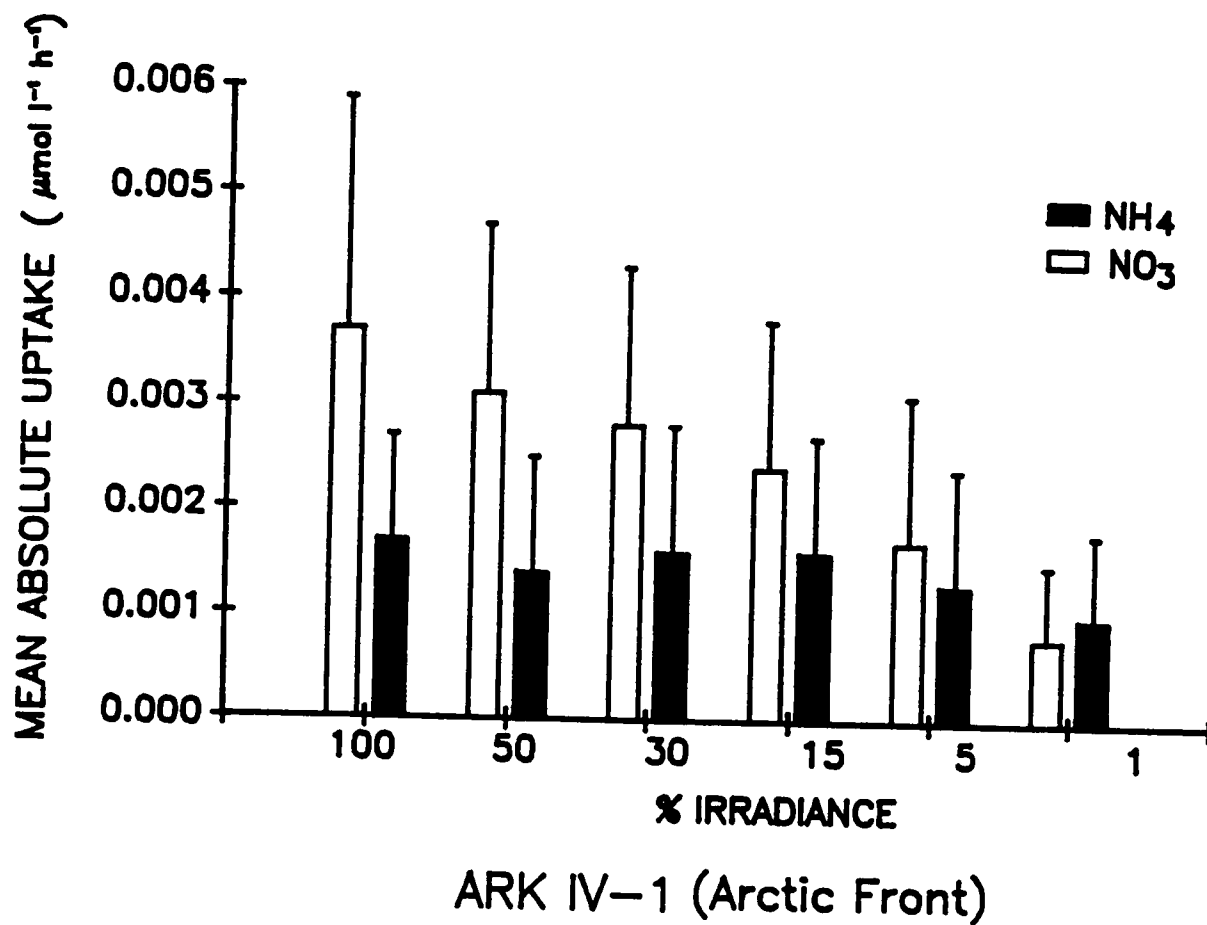


FIGURE 9. Mean absolute uptake and standard deviation, Arctic Front, ARK IV-1, May, 1987.

Table 3. Values for f-ratios and RPI values calculated from mean uptake rates for each isolume in the region of the Arctic Front.

$\%I_0$	f-ratio	RPI
100	0.67	9.00
50	0.70	7.61
30	0.63	9.03
15	0.69	10.59
5	0.55	11.74
1	0.50	14.33

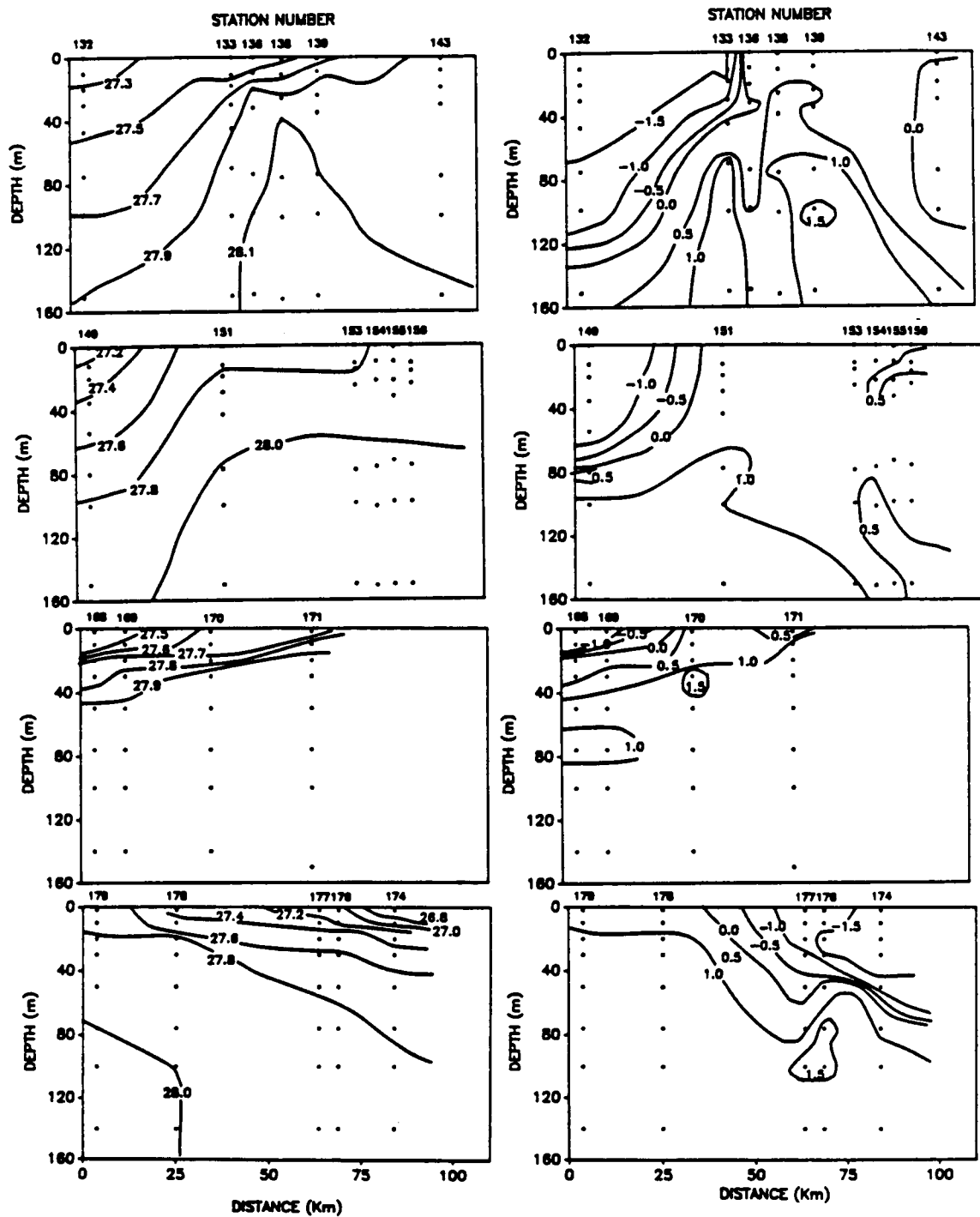


FIGURE 10. Sections of sigma t and temperature (°C) in the upper 160 m along transects at the Polar Front, ARK IV-1, May, 1987.

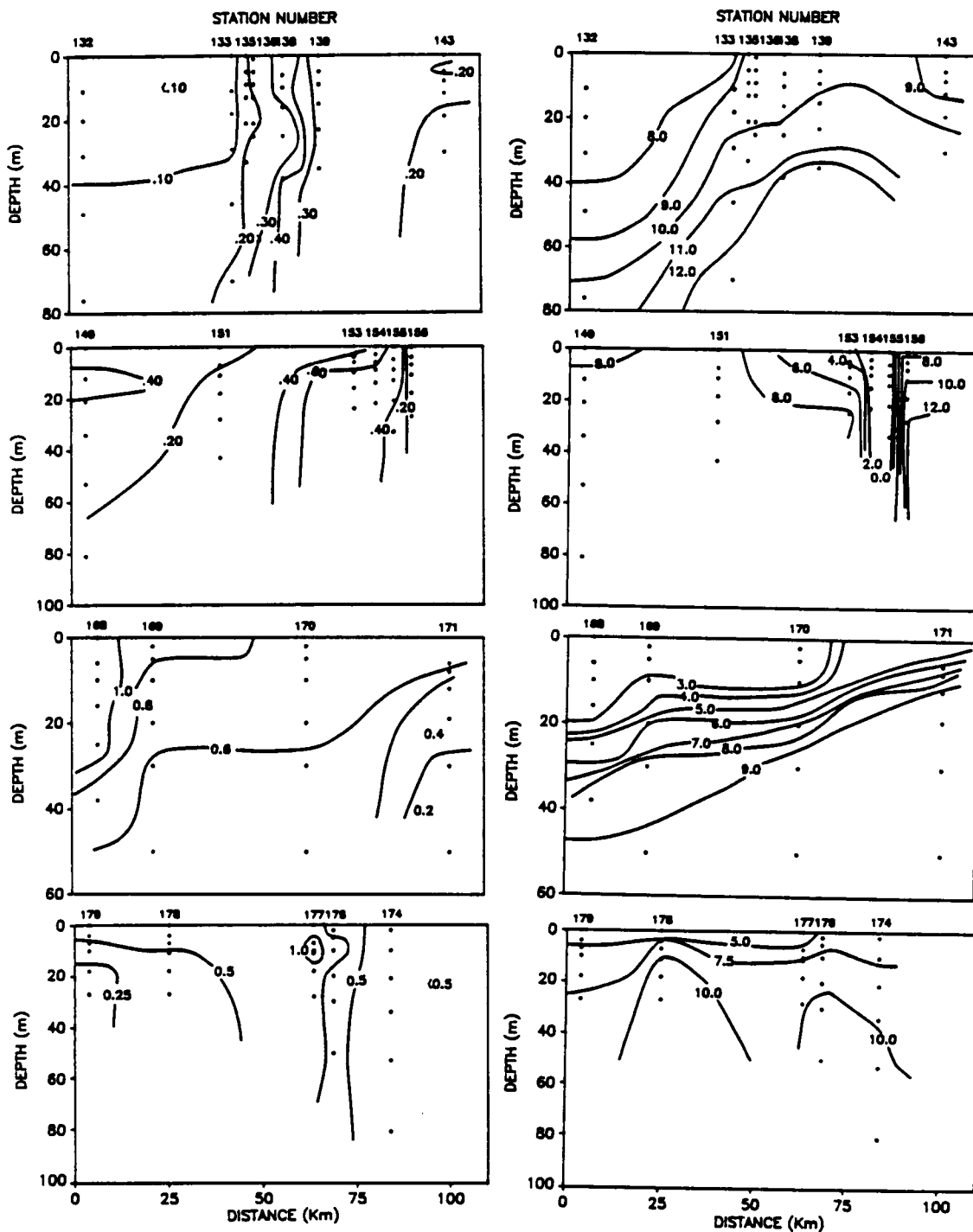


FIGURE 11. Sections of ammonium and nitrate concentrations (μM) along transects at the Polar Front, ARK IV-1, May, 1987.

highest (ammonium concentrations ranged from 0.12 to 0.94 μM ; Fig. 11).

The specific and absolute uptake rates of nitrate and ammonium (Table 4) show that most stations had rates of ammonium uptake which were higher than those of nitrate uptake except at the 1% isolume. For example, the highest ammonium uptake rate measured during the entire cruise occurred at Station 153 (Table 4) and was an order of magnitude higher than the associated nitrate uptake rate. Vertical profiles (Fig. 12) of mean ammonium and nitrate removal (Appendix B-2) indicated a decrease in uptake with depth. Mean absolute nitrate uptake at the 1% isolume was 36% that of surface uptake, but that of ammonium at the 1% isolume was only 11% that of the surface. Ammonium absolute uptake, therefore, was affected more by light availability than nitrate. The standard deviation for absolute ammonium uptake was more than the mean at each isolume through the euphotic zone to the 5% isolume. The standard deviation for absolute nitrate mean was less than the mean through the euphotic zone to the 5% isolume (Fig. 13). The mean f-ratio for all depths was 0.31 (± 0.10). However, there was a large depth-related difference evident between the surface and the 1% isolume where the f-ratio was twice that of the surface, due to the decrease in ammonium uptake at the 1% isolume. Ammonium relative preference index values were well above 1.0, again indicating a strong preference for ammonium (Table 5).

Table 4. Particulate nitrogen, ammonium and nitrate specific (V) and absolute (ρ) uptake rates in the region of the Polar Front. Asterisk denotes particulate nitrogen values derived from regression of known particulate nitrogen and chlorophyll values. ND = no data

Station No.	%I ₀	PN (mg m ⁻³)	Nitrate		Ammonium	
			V (h ⁻¹)	ρ (μ mol l ⁻¹ h ⁻¹)	V (h ⁻¹)	ρ (μ mol l ⁻¹ h ⁻¹)
132	100	0.52	.0099	.0051	.0041	.0022
	50	0.50	.0040	.0020	.0034	.0017
	30	0.33	.0035	.0012	.0032	.0011
	15	0.29	.0037	.0011	.0020	.0006
	5	0.45	.0024	.0011	.0014	.0006
	1	0.29	.0041	.0012	.0016	.0005
133	100	0.55	.0024	.0013	.0028	.0016
	50	0.39	.0033	.0013	.0029	.0011
	30	0.52	.0032	.0016	.0027	.0014
	15	0.28	.0046	.0013	.0023	.0007
	5	0.39	ND	ND	ND	ND
	1	0.36	.0002	.0001	.0020	.0007
135	100	1.56	.0054	.0095	.0051	.0089
	50	2.12	.0059	.0125	.0063	.0161
	30	*3.96	.0037	.0147	ND	ND
	15	1.43	ND	ND	.0043	.0066
	5	1.22	.0030	.0036	.0026	.0033
	1	0.72	.0019	.0013	.0014	.0010
136	100	2.00	.0044	.0088	.0062	.0140
	50	2.17	.0016	.0034	.0083	.0210
	30	2.05	.0032	.0066	.0052	.0120
	15	3.51	.0037	.0128	.0056	.0264
	5	1.88	.0009	.0017	.0036	.0074
	1	0.79	.0017	.0013	.0031	.0025
138	100	1.39	.0055	.0076	.0099	.0148
	50	1.61	.0054	.0088	.0117	.0207
	30	1.64	.0040	.0066	.0112	.0203
	15	1.69	.0049	.0083	.0098	.0185
	5	2.04	.0035	.0072	ND	ND
	1	1.10	.0059	.0064	.0029	.0032
139	100	1.65	.0037	.0061	.0050	.0090
	50	2.00	.0037	.0073	.0043	.0096
	30	2.72	.0048	.0131	.0048	.0130
	15	2.05	.0038	.0077	.0045	.0092
	5	0.23	.0020	.0004	.0041	.0009
	1	0.71	.0041	.0029	.0028	.0020

Table 4. cont.

Station No.	%I ₀	PN (mg m ⁻³)	Nitrate		Ammonium	
			V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
143	100	1.73	.0067	.0115	.0039	.0073
	50	1.79	.0077	.0137	.0065	.0127
	30	1.71	.0050	.0085	.0073	.0139
	15	1.79	.0038	.0068	.0063	.0124
	5	1.05	.0019	.0020	.0048	.0052
	1	0.74	.0050	.0037	.0027	.0021
149	100	0.65	.0050	.0044	.0029	.0019
	50	0.60	.0024	.0025	.0047	.0028
	30	1.75	ND	ND	.0018	.0032
	15	0.34	.0025	.0016	.0027	.0009
	5	0.43	.0016	.0016	.0014	.0006
	1	0.25	.0022	.0012	.0021	.0005
151	100	1.91	.0041	.0078	.0049	.0106
	50	0.71	ND	ND	.0045	.0033
	30	1.81	ND	ND	.0031	.0061
	15	1.32	.0019	.0025	.0026	.0035
	5	1.53	.0005	.0008	ND	ND
	1	0.79	.0010	.0008	.0008	.0007
153	100	3.00	.0015	.0046	.0291	.1200
	50	2.88	.0053	.0152	.0196	.0590
	30	2.51	.0025	.0062	.0200	.0526
	15	2.48	.0017	.0043	.0082	.0208
	5	1.45	.0004	.0006	.0051	.0075
	1	0.76	.0007	.0005	.0108	.0083
154	100	2.74	.0031	.0085	.0040	.0114
	50	2.05	.0030	.0061	.0038	.0081
	30	2.44	ND	ND	.0020	.0050
	15	3.03	.0016	.0047	.0012	.0038
	5	2.55	ND	ND	.0004	.0011
	1	1.61	.0008	.0017	ND	ND
156	100	2.62	.0013	.0035	.0258	.0787
	50	1.16	.0009	.0011	ND	ND
	30	1.85	.0015	.0029	.0166	.0350
	15	0.31	.0010	.0003	.0164	.0052
	5	*0.93	.0002	.0002	.0086	.0080
	1	0.90	.0016	.0015	.0002	.0002

Table 4. cont.

Station No.	%I _o	PN (mg m ⁻³)	Nitrate		Ammonium	
			V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
157	100	3.90	.0018	.0070	.0035	.0144
	50	4.84	.0023	.0110	.0058	.0309
	30	5.84	.0049	.0284	.0056	.0370
	15	4.72	.0022	.0104	.0070	.0378
	5	3.83	ND	ND	.0040	.0161
	1	2.01	ND	ND	.0020	.0040
168	100	2.45	.0016	.0039	.0074	.0188
	50	1.70	ND	ND	.0062	.0109
	30	*2.58	.0008	.0021	.0052	.0134
	15	2.46	.0018	.0044	.0072	.0184
	5	1.49	.0013	.0019	.0058	.0088
	1	0.60	.0008	.0005	.0011	.0007
171	100	1.77	.0018	.0032	.0047	.0085
	50	1.34	.0008	.0011	.0067	.0093
	30	*1.72	.0029	.0050	.0046	.0079
	15	ND	.0042	ND	.0031	ND
	5	*1.52	.0027	.0041	.0027	.0041
	1	1.91	.0031	.0059	.0016	.0032
174	100	0.76	.0012	.0009	.0017	.0014
	50	2.61	.0024	.0064	ND	ND
	30	0.46	.0025	.0011	.0023	.0011
	15	4.92	.0022	.0110	.0039	.0201
	5	6.76	.0021	.0140	.0012	.0081
	1	2.61	.0002	.0007	.0015	.0041
177	100	1.60	.0039	.0063	.0015	.0025
	50	1.65	.0023	.0038	.0023	.0038
	30	0.69	.0026	.0018	ND	ND
	15	0.90	.0015	.0001	.0018	.0016
	5	0.35	.0018	.0006	.0063	.0022
	1	0.35	.0006	.0002	.0008	.0003
179	100	2.79	.0005	.0014	.0026	.0074
	50	2.52	.0011	.0027	.0014	.0036
	30	2.37	ND	ND	.0005	.0011
	15	1.41	ND	ND	.0002	.0003
	5	1.02	.0004	.0004	.0004	.0005
	1	0.44	.0001	.00004	.0003	.0001

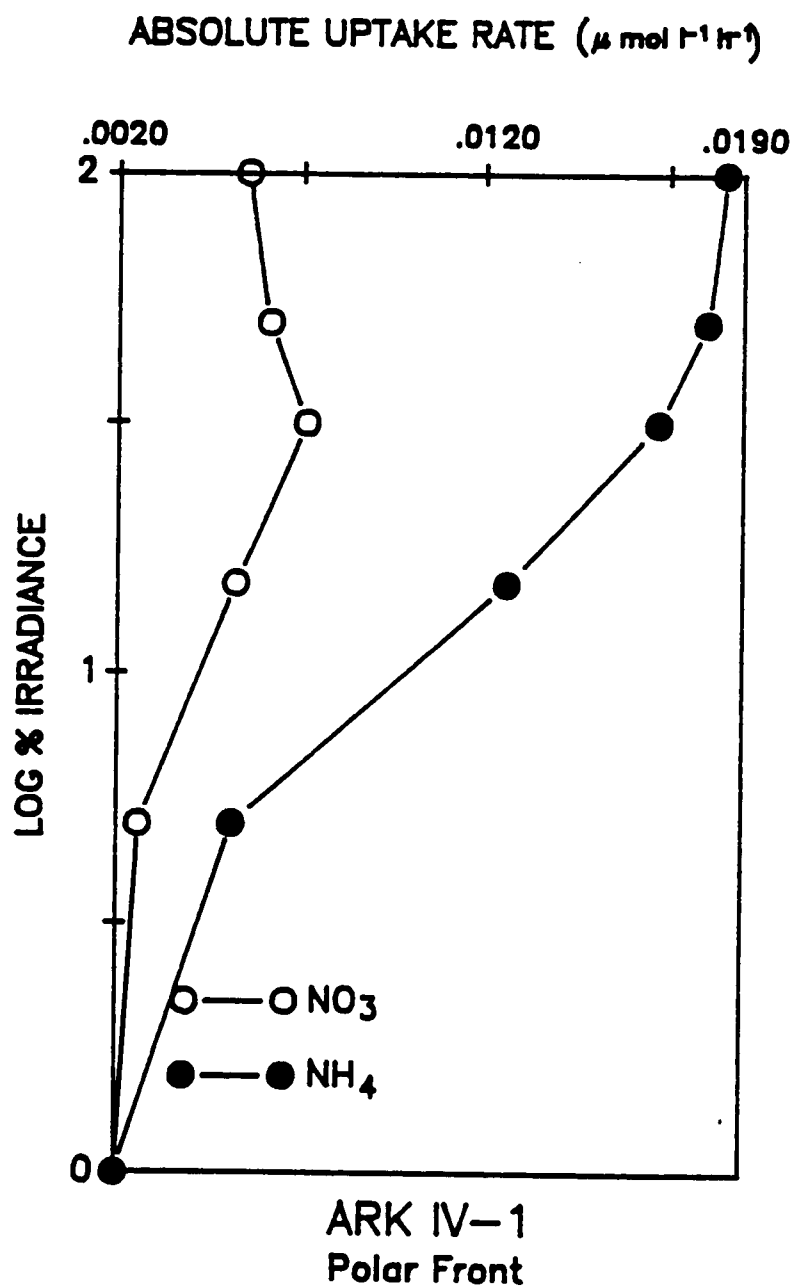


FIGURE 12. Vertical distribution of mean absolute uptake, Polar Front, ARK IV-1, May, 1987.

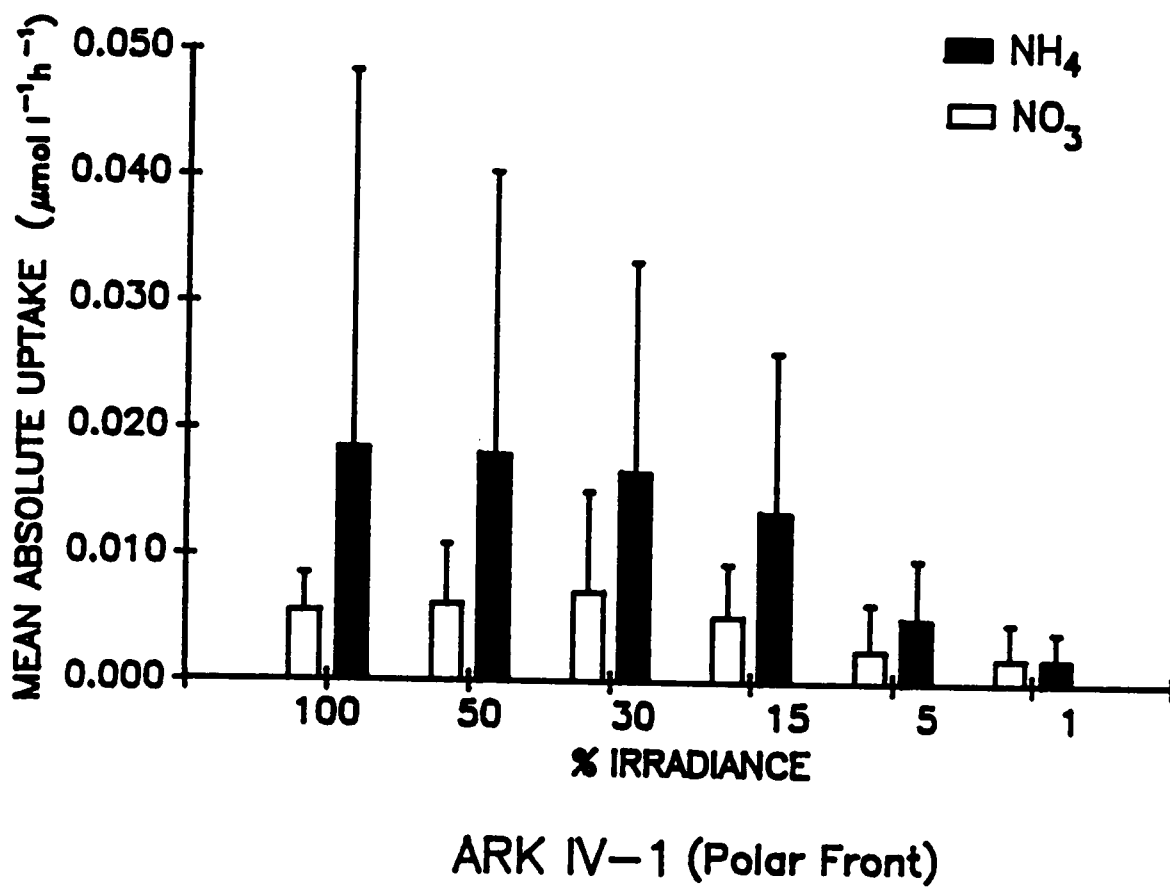


FIGURE 13. Mean absolute uptake and standard deviation, Polar Front, ARK IV-1, May, 1987.

Table 5. Values for f-ratios and RPI values calculated from mean uptake rates for each isolume in the Polar Front.

$\%I_0$	f-ratio	RPI
100	0.23	10.28
50	0.25	10.35
30	0.30	12.42
15	0.29	14.64
5	0.34	17.81
1	0.50	16.27

ARK IV-2

The stations sampled during ARK IV-2 were taken from six standard light depths at 21 stations in the area of the Polar Front during June, 1987. The most northerly transect was at 80°N and the most southerly was between 71 and 72°N. Transects ran approximately east and west and crossed the Polar Front (Fig. 14). Twelve stations had 2/10 or more ice coverage (10/10); Transect 2, at approximately 80°N and 00°E, was entirely free of ice (Fig. 14). The base of the euphotic zone, as measured by the depth of the 1% isolume, was below the pycnocline at all stations (Fig. 15). Transect 2 in the Fram Strait had surface temperatures above 1°C along the entire transect while all other transects had stations with temperatures both above and below. Due to the distance between transects, data will be examined by transect as well as for the entire region.

Surface concentrations of nitrate ranged from 0.06 to 7.33 μM and varied between stations as well as through depth and between transects (Fig. 16). The limits of detection for ambient ammonium and nitrate are approximately .01 μM (Eberlein et al., 1983), and nitrate was undetectable at the 50% isolume at Stations 208, and 215, at the 15% isolume at Stations 215 and at the 50 and 5% isolumes at Station 213. All these stations were on Transect 2, which was the most northerly transect and crossed the Fram Strait. The highest concentration of nitrate occurred at the 1% isolume at Station 189 in the first transect. Nitrate concentrations increased with depth

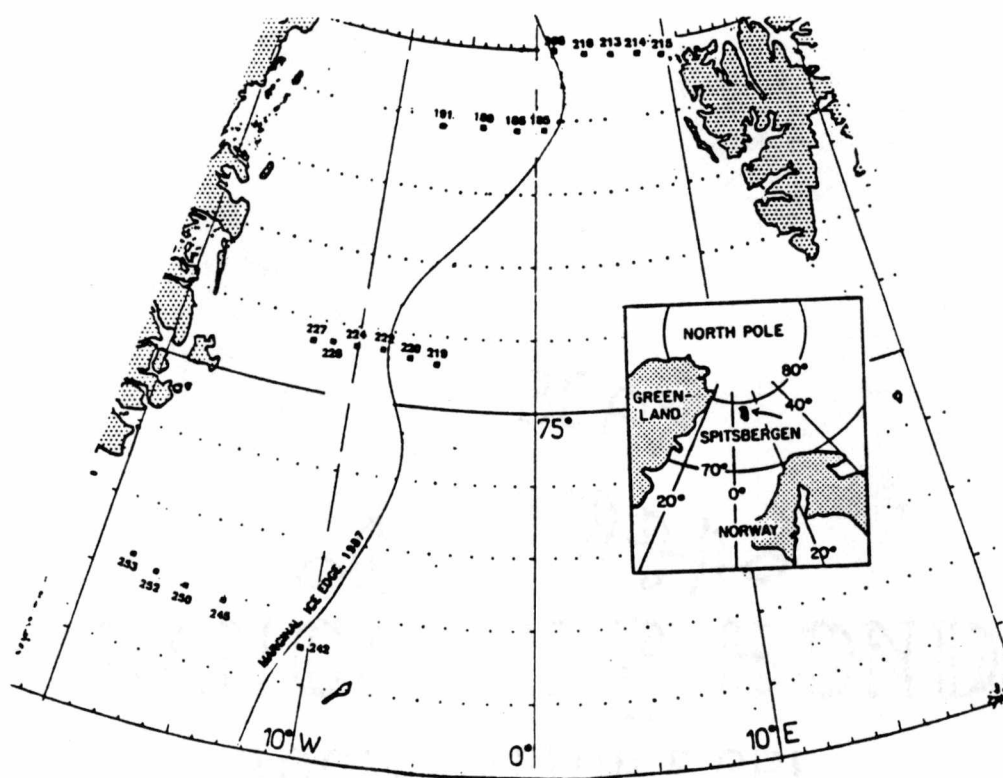


FIGURE 14. Map of Polar Front showing station locations at which nitrogen uptake measurements were taken, ARK IV-2, June, 1987.

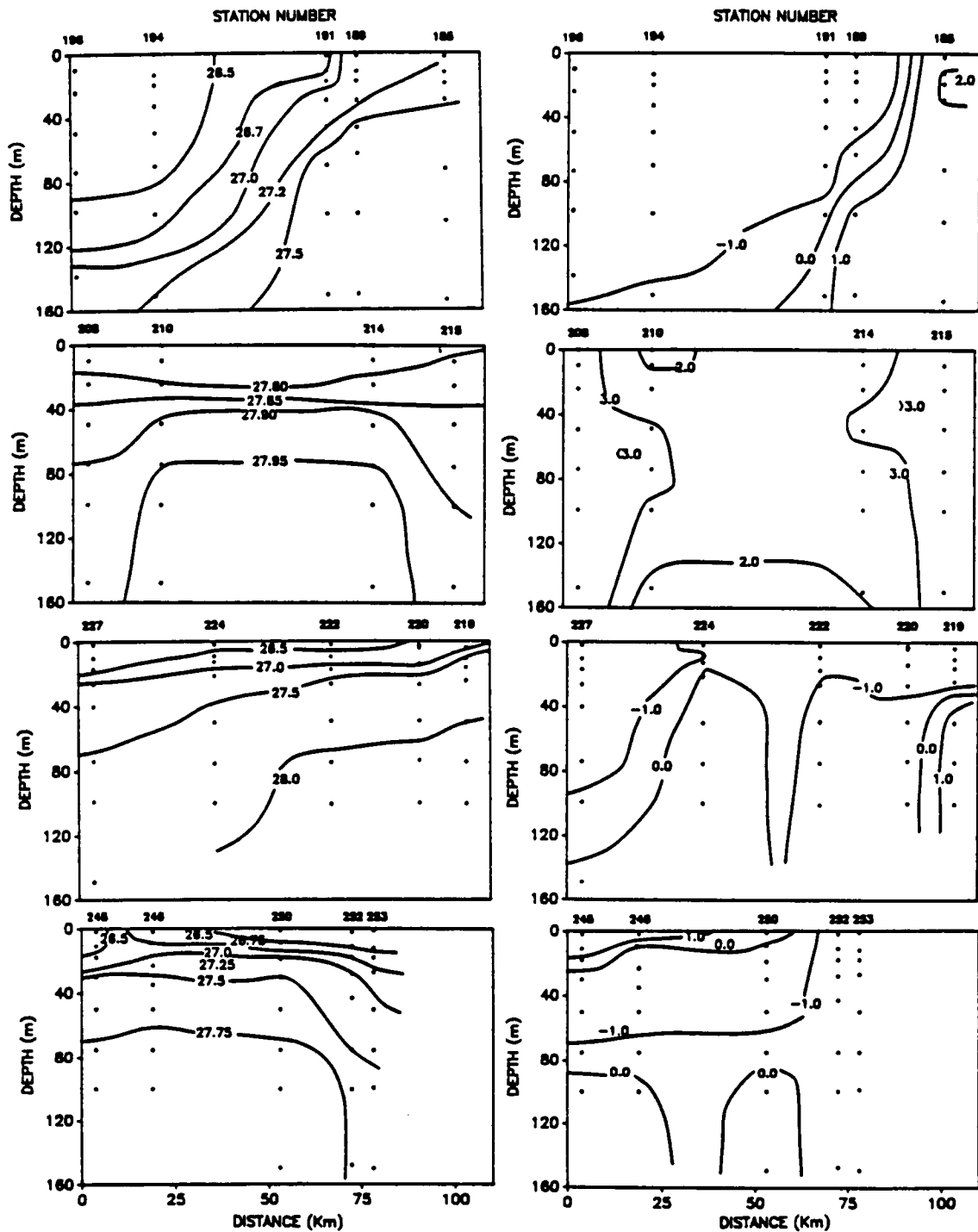


FIGURE 15. Sections of sigma t and temperature ($^{\circ}\text{C}$) along transects at the Polar Front, ARK IV-2, June, 1987.

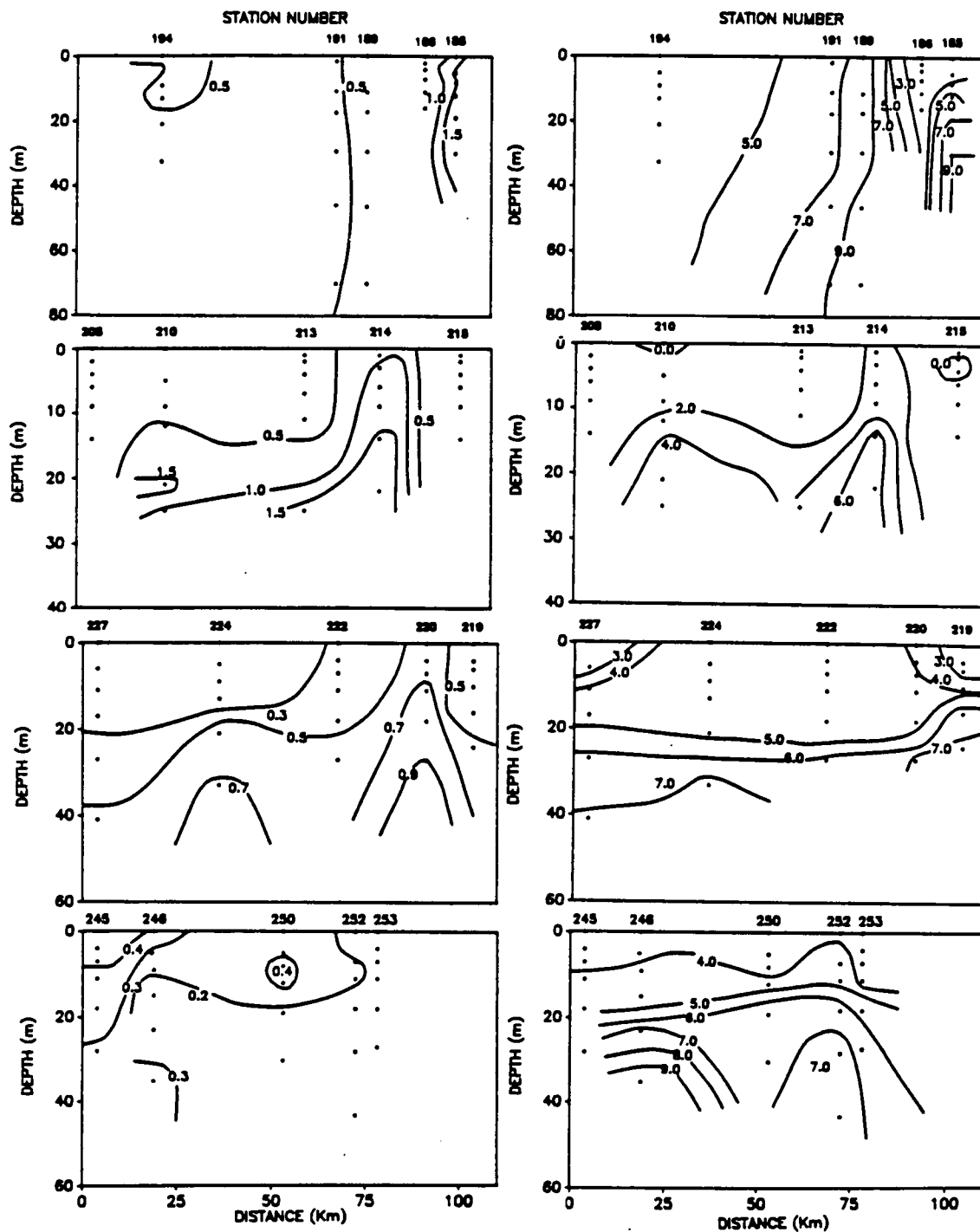


FIGURE 16. Sections of ammonium and nitrate concentrations (μM) along transects at the Polar Front, ARK IV-2, June, 1987.

at each station and for all transects (Fig. 16).

Surface ammonium concentrations ranged from 0.30 to 1.25 μM . The lowest ammonium concentration was 0.11 μM at the 30% isolume at station 224, and the highest was 2.44 μM at the 30% isolume at Station 248. Station 185 contrasted with the other stations sampled in that it had high ammonium concentrations throughout the euphotic zone, with an average concentration of 1.49 μM . Ammonium concentrations increased with depth on Transect 2 and 3 and decreased with depth on Transect 4 (Fig. 16).

The maximum and minimum specific nitrate uptake rates for this cruise occurred on the same transect (Transect 2), at two stations (214 & 215; Table 6) that were approximately 33 km apart. The minimum value was 0.0001 h^{-1} (Station 215) and the maximum was 0.0231 h^{-1} (Station 214). Station 215 had consistently low specific uptake rates through depth, with a mean of only 0.00013 h^{-1} ($^{+} 0.00005$). Nitrate concentrations at this station were 0.01 μM or less and ammonium concentrations averaged 0.39 μM ($^{+} 0.04$). Nitrate concentrations for Station 214 ranged from 1.18 μM at the surface to 8.79 μM at the 1% isolume. The ammonium concentrations at this station went from 0.74 to 1.74 μM at the 1% isolume. Nitrate absolute uptake rates ranged from 0.0001 to 0.0451 $\mu\text{mol l}^{-1} \text{ h}^{-1}$ at Stations 194 and 185, respectively. The highest rate for each isolume (except 50%) occurred at Station 195, which was in a small area of open water within the 10/10 ice coverage (Table 6).

Specific ammonium uptake rates ranged from 0.0001 (Station

Table 6. Particulate nitrogen, ammonium and nitrate specific (V) and absolute (ρ) uptake rates for ARK IV-2, June, 1987. Asterisk denotes particulate nitrogen values derived from regression of known chlorophyll and particulate nitrogen values. ND = no data

Station No.	%I ₀	PN ($\mu\text{g l}^{-1}$)	Nitrate		Ammonium	
			V (h^{-1})	ρ ($\mu\text{mol l}^{-1} \text{h}^{-1}$)	V (h^{-1})	ρ ($\mu\text{mol l}^{-1} \text{h}^{-1}$)
185	100	2.0	.0025	.0050	.0050	.0101
	50	1.6	.0021	.0034	.0059	.0098
	30	2.3	.0055	.0126	.0070	.0166
	15	5.1	.0048	.0243	.0076	.0041
	5	1.0	.0022	.0023	.0056	.0059
	1	0.6	.0017	.0010	.0039	.0023
186	100	4.4	.0032	.0142	.0109	.0613
	50	5.0	.0045	.0225	.0071	.0421
	30	4.0	.0043	.0169	.0124	.0619
	15	4.2	.0045	.0192	.0125	.0712
	5	4.7	.0027	.0126	.0212	.1270
	1	3.7	ND	ND	.0113	.0659
189	100	0.9	.0038	.0046	.0053	.0043
	50	1.3	.0023	.0056	.0071	.0094
	30	0.7	.0030	.0035	.0037	.0026
	15	1.3	.0036	.0074	.0048	.0062
	5	1.2	.0029	.0068	.0022	.0027
	1	1.4	.0033	.0084	.0039	.0054
194	100	1.0	.0061	.0060	.0019	.0019
	50	0.3	.0041	.0011	.0037	.0010
	30	1.4	.0040	.0056	.0045	.0065
	15	1.1	.0031	.0033	.0041	.0045
	5	1.2	.0011	.0013	.0038	.0047
	1	0.7	.0006	.0005	.0149	.0116
195	100	0.1	.0022	.0013	.0040	.0005
	50	0.1	.0016	.0001	.0043	.0003
	30	0.5	.0015	.0007	.0040	.0019
	15	0.3	.0012	.0004	.0027	.0008
	5	0.04	.0010	.0001	.0042	.0002
	1	0.03	.0005	.00004	.0029	.0001
208	100	4.7	.00003	.0001	.0065	.0360
	50	4.1	.00007	.0003	.0044	.0196
	30	5.5	.00002	.0001	.0052	.0338
	15	2.0	.0003	.0013	.0058	.0124
	5	4.4	.0001	.0016	.0045	.0225
	1	6.5	.0011	.0177	.0035	.0255

Table 6. cont.

Station No.	%I ₀	PN ($\mu\text{g l}^{-1}$)	Nitrate		Ammonium	
			$\frac{V}{h^{-1}}$	$\frac{\rho}{(\mu\text{mol l}^{-1} h^{-1})}$	$\frac{V}{h^{-1}}$	$\frac{\rho}{(\mu\text{mol l}^{-1} h^{-1})}$
210	100	1.3	.0027	.0036	.0108	.0152
	50	2.0	.0023	.0047	.0098	.0289
	30	1.9	ND	ND	.0096	.0205
	15	1.8	.0043	.0094	.0118	.0236
	5	1.1	.0007	.0023	.0118	.0127
	1	0.7	.0019	.0025	.0082	.0054
213	100	2.0	.0019	.0038	.0142	.0357
	50	1.4	.0016	.0023	.0158	.0260
	30	1.7	.0017	.0029	.0176	.0376
	15	1.9	.0011	.0022	.0153	.0354
	5	1.8	.0007	.0013	.0136	.0302
	1	0.6	.0169	.0101	.0771	.0495
214	100	3.8	.0046	.0292	ND	ND
	50	2.8	.0057	.0317	.0028	.0079
	30	2.1	.0072	.0334	.0052	.0112
	15	2.5	.0072	.0396	.0085	.0221
	5	ND	.0205	ND	.0153	ND
	1	1.5	.0231	.0667	.0153	.0263
215	100	4.7	.0002	.0021	.0031	.0161
	50	4.5	.0001	.0011	.0104	.0542
	30	3.1	.0001	.0012	.0085	.0325
	15	3.3	.0001	.0009	.0080	.0339
	5	3.8	.0001	.0011	.0082	.0400
	1	3.4	.0002	.0014	.0082	.0362
219	100	3.8	.0005	.0076	.0036	.0119
	50	3.7	.0063	.0075	.0036	.0149
	30	3.5	.0062	.0078	.0024	.0092
	15	3.5	.0041	.0090	.0029	.0107
	5	1.8	.0025	.0058	.0050	.0092
	1	0.9	.0014	.0013	.0043	.0038
220	100	1.5	.0061	.0203	.0047	.0074
	50	1.5	.0055	.0188	.0048	.0073
	30	2.4	.0060	.0321	.0046	.0118
	15	2.1	.0072	.0300	.0064	.0138
	5	2.3	.0019	.0085	.0103	.0249
	1	2.3	.0030	.0165	.0061	.0150

Table 6. cont.

Station No.	$\%I_0$	PN ($\mu\text{g l}^{-1}$)	Nitrate		Ammonium	
			$\frac{V}{(h^{-1})}$	$\frac{\rho}{(\mu\text{mol l}^{-1} h^{-1})}$	$\frac{V}{(h^{-1})}$	$\frac{\rho}{(\mu\text{mol l}^{-1} h^{-1})}$
222	100	4.7	.0030	.0229	.0062	.0334
	50	4.4	.0034	.0228	.0077	.0418
	30	5.1	.0035	.0269	.0055	.0337
	15	6.8	.0027	.0254	.0049	.0436
	5	8.4	.0016	.0224	.0040	.0474
	1	4.5	.0011	.0131	.0081	.0418
224	100	1.5	.0030	.0071	.0025	.0040
	50	1.0	.0041	.0056	.0022	.0022
	30	1.2	.0032	.0056	.0024	.0029
	15	1.7	.0031	.0080	.0010	.0018
	5	1.1	.0015	.0034	.0099	.0109
	1	1.1	.0031	.0070	.0055	.0062
226	100	1.0	ND	ND	.0036	.0037
	50	0.9	.0050	.0056	.0027	.0026
	30	0.5	ND	ND	.0034	.0019
	15	0.8	.0066	.0071	.0033	.0029
	5	0.4	.0020	.0018	.0036	.0016
	1	0.2	.0023	.0011	ND	ND
227	100	2.8	ND	ND	.0052	.0168
	50	2.3	.0042	.0115	.0055	.0145
	30	1.9	ND	ND	ND	ND
	15	0.6	ND	ND	.0053	.0033
	5	1.5	.0008	.0039	.0039	.0060
	1	0.6	.0024	.0027	.0041	.0025
242	100	2.1	.0030	.0039	.0032	.0068
	50	2.3	ND	ND	.0036	.0081
	30	2.0	.0027	.0054	.0033	.0067
	15	*3.4	.0030	.0102	.0027	ND
	5	2.2	.0022	.0033	.0023	.0050
	1	*2.2	.0014	.0031	.0016	.0035
250	100	2.0	.0001	.0040	.0056	.0119
	50	2.8	.0020	.0083	.0087	.0244
	30	2.6	.0004	.0050	.0083	.0242
	15	1.6	.0054	.0093	.0088	.0150
	5	1.1	.0042	.0048	.0061	.0074
	1	0.6	.0014	.0022	.0041	.0026

Table 6. cont.

Station No.	%I ₀	PN ($\mu\text{g l}^{-1}$)	Nitrate		Ammonium	
			V (h^{-1})	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h^{-1})	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
252	100	0.8	.0138	.0128	.0013	.0015
	50	0.7	ND	ND	.0005	.0004
	30	0.9	.0117	.0121	.0036	.0026
	15	0.7	.0081	.0071	.0001	.0001
	5	0.7	.0134	.0114	ND	ND
	1	0.6	.0121	.0097	ND	ND
253	100	2.2	ND	ND	.0027	.0059
	50	1.7	ND	ND	.0016	.0027
	30	1.4	ND	ND	.0049	.0068
	15	1.2	.0023	.0014	.0014	.0017
	5	1.7	.0032	.0028	ND	ND
	1	0.1	.0037	.0003	ND	ND

252) to 0.0771 h^{-1} (Station 213). The maximum specific ammonium uptake at Station 213 coincided with an ambient ammonium level of $1.95 \text{ } \mu\text{M}$ at that isolume. Ambient nitrate levels at this station were less than $0.1 \text{ } \mu\text{M}$ through the 1% isolume where it increased to $4.65 \text{ } \mu\text{M}$. Absolute ammonium uptake ranged from 0.0001 (Station 195) to $0.1270 \text{ } \mu\text{mol l}^{-1} \text{ h}^{-1}$ (Station 210), which was comparable to $0.12 \text{ } \mu\text{mol l}^{-1} \text{ h}^{-1}$ from the Polar Front, ARK IV-1.

Average values for absolute ammonium uptake at each depth and transect (Table 7) showed uptake to be higher than mean nitrate specific uptake at all depths on Transects 1 and 2. Transect 3 had average values of nitrate uptake higher than ammonium at the 50 and 30% isolume and Transect 4 had nitrate uptake values higher than ammonium at the surface. Transect 4 had both ammonium and nitrate specific uptake mean values that were lower at the 1% isolume than at the surface, although this decrease was not consistent throughout the water column.

Mean absolute ammonium uptake calculated for each isolume for the entire area was higher than mean specific nitrate specific uptake at all isolumes (Appendix B-3). Mean absolute nitrate uptake was between 50 and 60% that of ammonium at the surface through the 15% isolume, but decreased to between 35 and 45% at the 5 and 1% isolume (Appendix B-3). Both nitrate and ammonium specific uptake increased with depth (Fig. 17). This increase was greater for specific ammonium uptake, with surface specific nitrate uptake being 79% of uptake at the 1% isolume and surface specific ammonium uptake 50%

Table 7. Mean ammonium and nitrate absolute (ρ) and specific (V) uptake rates for each isolume, ARK IV-2, June, 1987.

%I ₀	Nitrate		Ammonium	
	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
Transect 1				
100	.0034	.0052	.0049	.0135
50	.0026	.0051	.0051	.0107
30	.0037	.0076	.0063	.0179
15	.0034	.0103	.0063	.0247
5	.0020	.0040	.0074	.0281
1	.0015	.0015	.0074	.0171
Transect 2				
100	.0019	.0052	.0087	.0258
50	.0021	.0052	.0086	.0273
30	.0018	.0047	.0092	.0271
15	.0026	.0057	.0099	.0255
5	.0044	.0052	.0107	.0264
1	.0086	.0107	.0228	.0286
Transect 3				
100	.0025	.0083	.0043	.0121
50	.0048	.0080	.0044	.0138
30	.0051	.0092	.0036	.0119
15	.0034	.0107	.0040	.0146
5	.0017	.0039	.0061	.0188
1	.0022	.0031	.0047	.0167
Transect 4				
100	.0056	.0077	.0032	.0058
50	.0020	.0020	.0036	.0047
30	.0049	.0049	.0050	.0093
15	.0047	.0051	.0033	.0053
5	.0061	.0055	.0042	.0062
1	.0047	.0028	.0029	.0026

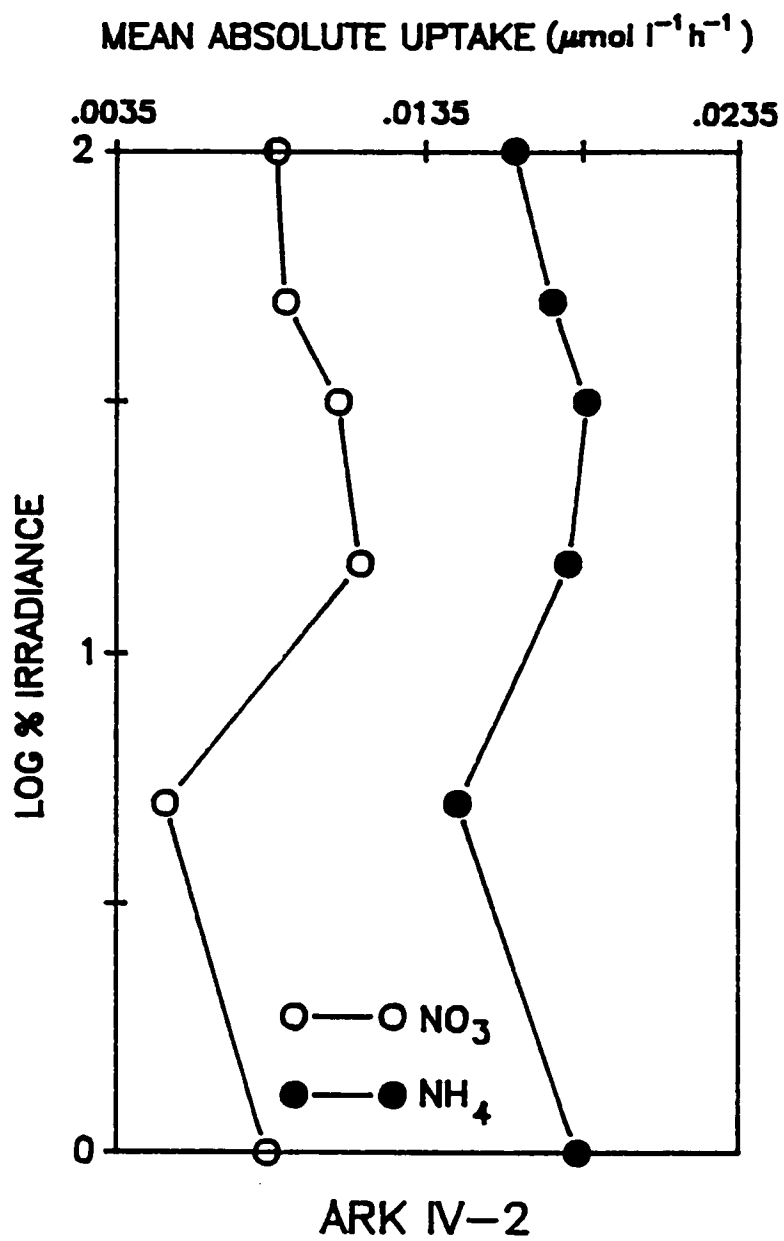


FIGURE 17. Mean absolute uptake, Polar Front, ARK IV-2, June, 1987.

that of the 1% isolume rate. Absolute nitrate uptake at the 1% isolume decreased slightly with depth, whereas absolute ammonium uptake increased slightly. Variability around the mean as expressed by standard deviation (Fig. 18) was equal to $\pm 5\%$ of the mean value at all isolumes for both nitrate and ammonium absolute uptake, except at the 1% isolume where it was twice the nitrate mean and 25% of the ammonium mean.

Mean f-ratios for each transect show variations between transects (Table 8) in terms of new production except for Transect 2. On all transects the surface f-ratios were greater than at the 1% isolume and Transects 1, 2 and 3 had f-ratios below 0.50 at all depths. Transect 4 had f-ratios above 0.50 at the surface and the 1% isolume. Mean f-ratios for the entire area were less than 0.50 and decreased with depth (Table 9). RPI values, as in previous results, were over 1, indicating a preference for ammonium that increased with depth (Table 9).

Regeneration measurements were completed at the surface and 1% isolumes at Stations 185, 186, 194, and 215, and at the surface at Station 213 and 1% isolume at Station 224 (Table 10). Ratios of uptake:regeneration indicate that at Station 186 rates of uptake were greater than regeneration rates at both the 100 and 1% isolume. At Station 194, regeneration was greater than uptake at the surface and at the 1% isolume. The difference between uptake and regeneration was always greater at the surface than at depth. Five out of the eight samples measured had more uptake than regeneration.

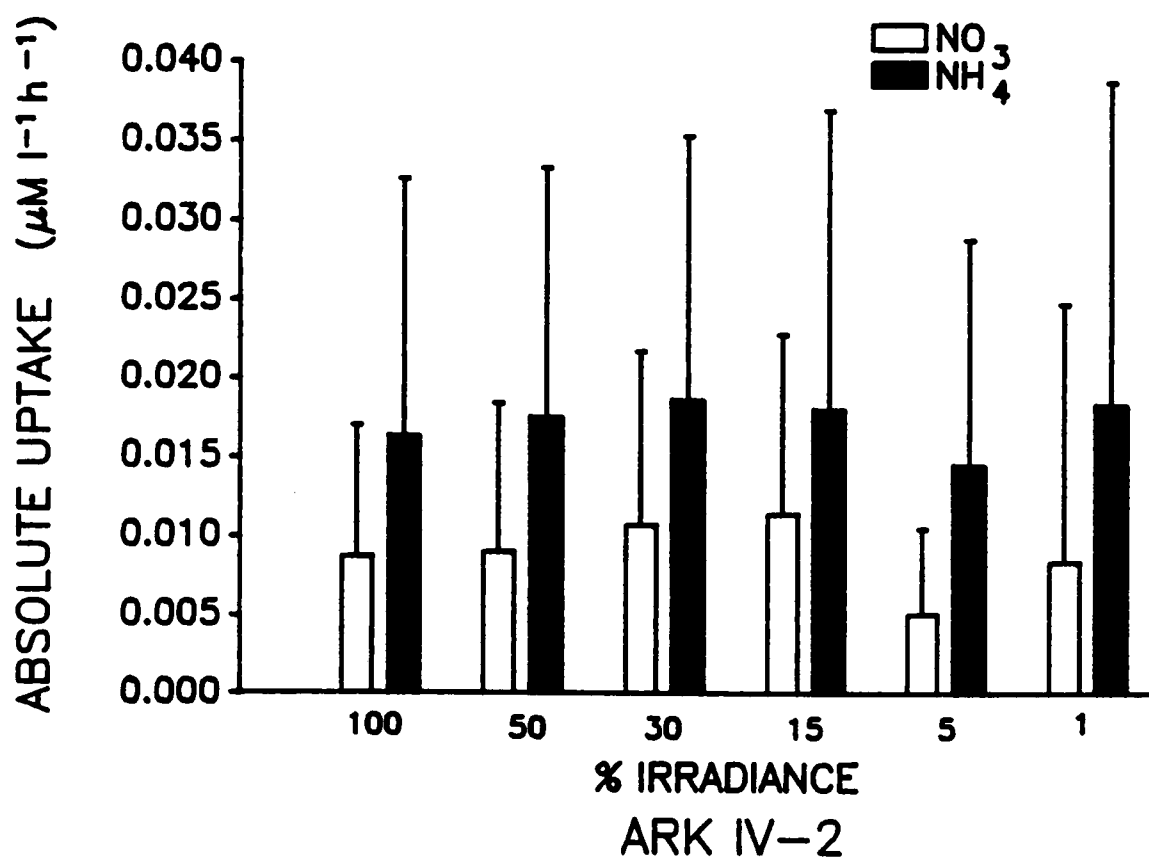


FIGURE 18. Mean absolute uptake with standard deviation, Polar Front, ARK IV-2, June, 1987.

Table 8. Average f-ratios calculated for each Transect, ARK IV-2.

	$\%I_0$	f-ratio
Transect 1	100	0.28
	50	0.32
	30	0.30
	15	0.29
	5	0.12
	1	0.08
Transect 2	100	0.17
	50	0.16
	30	0.15
	15	0.18
	5	0.16
	1	0.27
Transect 3	100	0.41
	50	0.37
	30	0.44
	15	0.42
	5	0.17
	1	0.16
Transect 4	100	0.60
	50	0.30
	30	0.35
	15	0.49
	5	0.47
	1	0.54

Table 9. Values for f-ratios and RPI values calculated from mean uptake rates for each isolume, ARK IV-2, June 1987.

$\%I_0$	f-ratio	RPI
100	0.30	5
50	0.29	4
30	0.29	5
15	0.31	5
5	0.15	12
1	0.20	10

Table 10. Ammonium uptake (ρ) and regeneration rates for stations from ARK IV-2, June, 1987. Uptake and regeneration were calculated using equations from Glibert et al. (1982b)

Station No.	%I ₀	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	REGENERATION ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	ρ/REGEN
185	100	.1120	ND	-
	1	.0278	ND	-
186	100	.7823	.3129	2.5
	1	.5572	.3980	1.4
194	100	.1797	.3353	0.5
	1	.3109	1.7638	0.2
213	100	4.0006	2.9084	1.4
	1	.9201	ND	-
215	100	1.0202	.7043	1.4
	1	1.7876	3.2377	0.6
224	100	ND	ND	-
	1	.1769	.0960	1.8

ARK V-2

Polarstern cruise ARK V-2 occurred during June 1988 in the East Greenland Sea and in the Fram Strait between Spitsbergen and Greenland. The samples taken came from four transects ranging from 71 to 78°N and from 18°W to 9°E (Fig. 19). Samples were taken from 100, 50 and 1% isolumes at 16 stations, from 100 and 1% isolumes at five stations, and from the surface at two additional stations between transects 1 and 2. Ice was encountered at 18 of the 25 stations and ice cover ranged from 1/10 to 8/10. Station 65 on the second transect, Stations 79, 81 and 82 on the third transect and Stations 96 through 104 on the fourth transect were free of ice. This cruise covered approximately the same area as ARK IV-2, June, 1987 (Fig. 20). The pycnocline was well defined and the euphotic zone was above or within the pycnocline at all stations during this cruise (Fig. 21).

Surface concentrations of nitrate ranged from undetectable at Station 65 to 5.43 μM at Station 87. The highest concentration observed was 8.60 μM at the 1% isolume at Station 87. Transect 4 had the least variation in surface concentrations, with nitrate below 1.0 μM at all stations. The other transects had one or more stations with concentrations of nitrate below 0.5 μM (Fig. 22). Surface ammonium concentrations ranged from 0.14 μM at Stations 79 and 96, to 1.07 μM at Station 73. The highest concentration was 3.20 μM at the 1% isolume at Station 81. Average nitrate and ammonium concentrations for each transect were higher at the 1% isolume than

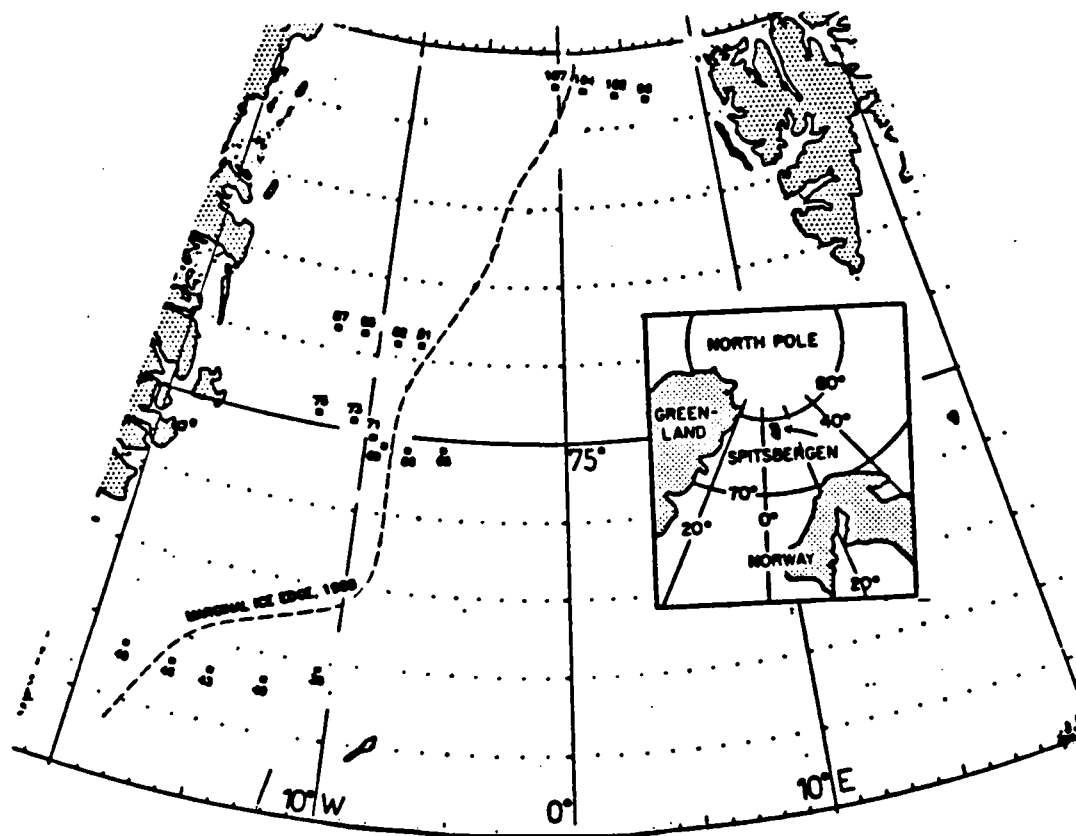


FIGURE 19. Map of Polar Front showing stations at which nitrogen uptake measurements were taken, ARK V-2, June, 1988.

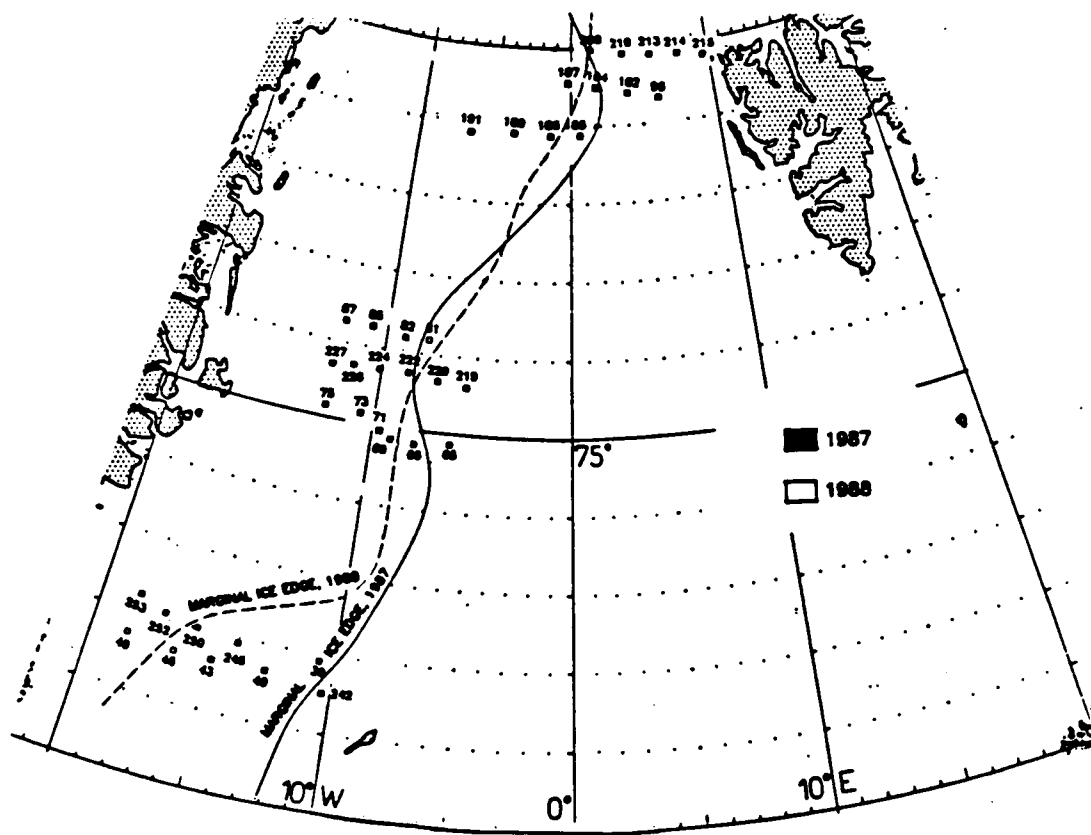


FIGURE 20. Station map, Polar Front, ARK IV-2, ARK V-2.

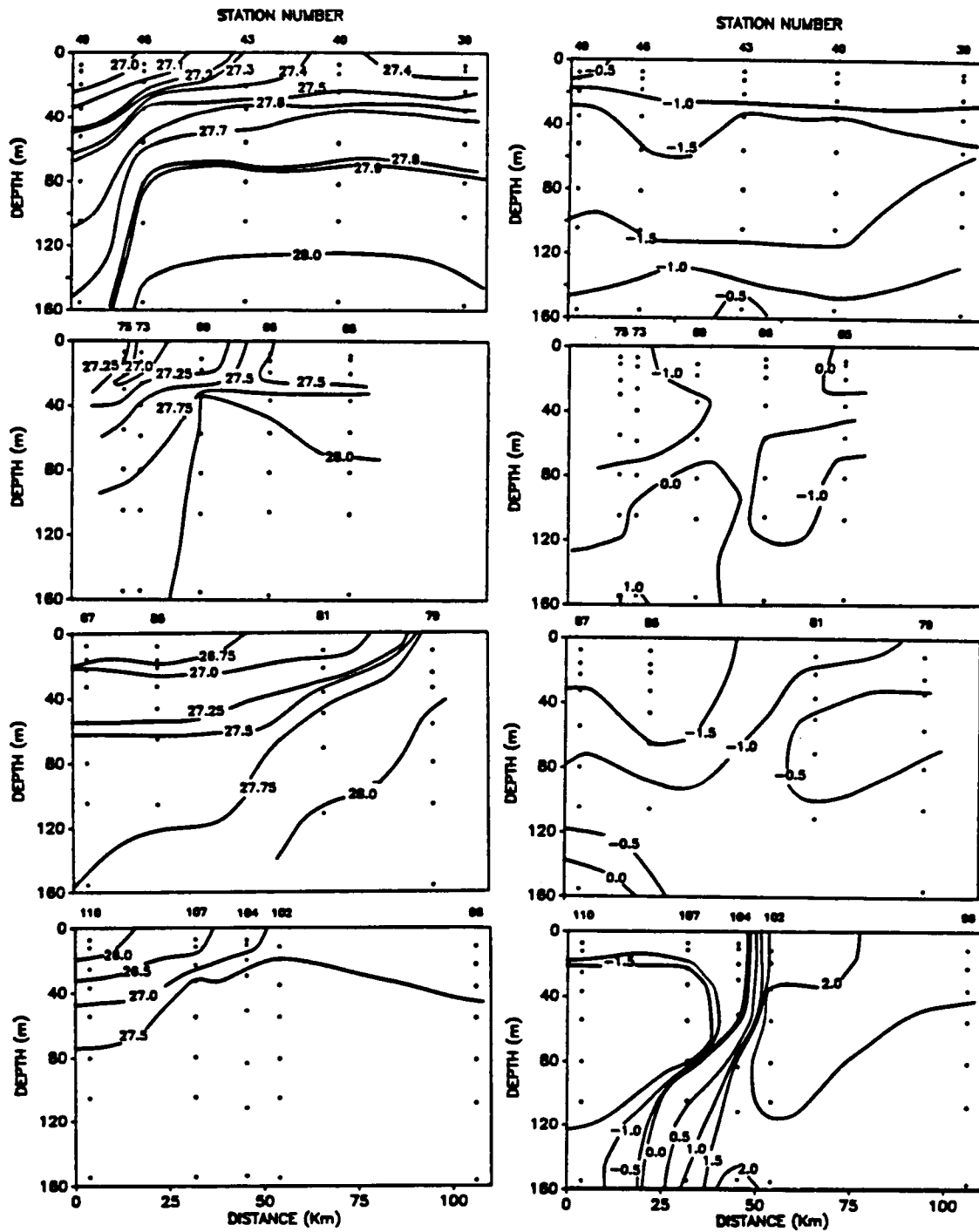


FIGURE 21. Sections of sigma t and temperature (°C) along transects at the Polar Front, ARK V-2, June, 1988.

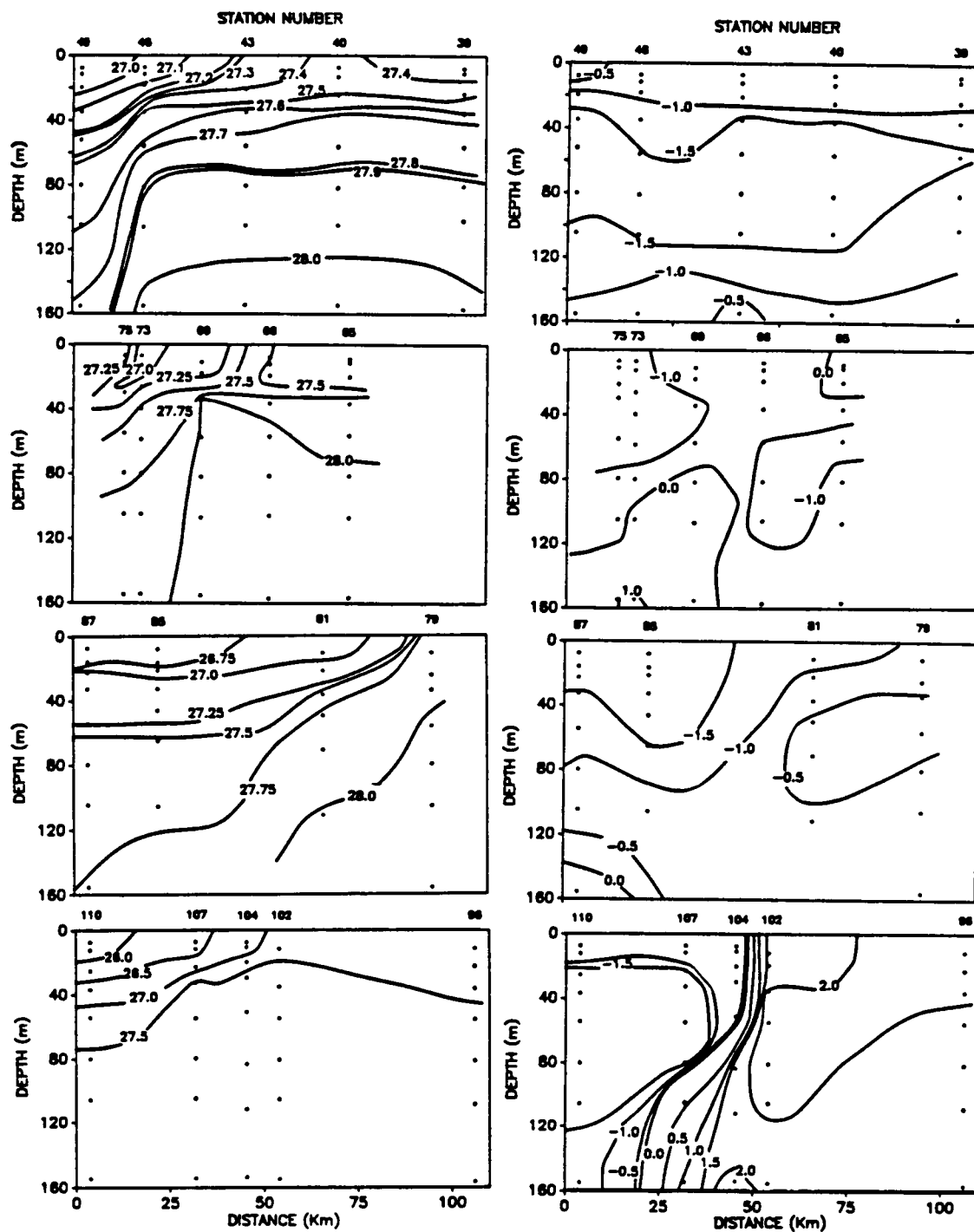


FIGURE 22. Sections of ammonium and nitrate concentrations (μM) along transects at the Polar Front, ARK V-2, June, 1988.

at the surface.

Minimum and maximum values for uptake varied greatly, with specific nitrate uptake rates ranging from 0.0001 h^{-1} at Station 43 to 0.0043 h^{-1} at Station 102. Absolute nitrate uptake rates ranged from $0.0002 \mu\text{mol l}^{-1} \text{ h}^{-1}$ at Station 87 to $0.0228 \mu\text{mol l}^{-1} \text{ h}^{-1}$ at Station 96 (Table 11). Specific ammonium uptake rates ranged from 0.0007 h^{-1} at Station 43 to 0.0129 h^{-1} at Station 66. Absolute rates of ammonium uptake ranged from $0.0003 \mu\text{mol l}^{-1} \text{ h}^{-1}$ at Station 87 to $0.0538 \mu\text{mol l}^{-1} \text{ h}^{-1}$ at Station 63 (Table 11).

Mean values for each isolume calculated for each transect (Table 12) show differences between transects, but not to the extent seen in June, 1987. Both specific and absolute mean ammonium uptake rates were higher than nitrate specific and absolute rates at most stations, with surface nitrate specific mean rates 55% of surface ammonium specific mean rates (Appendix B-4). On this cruise mean absolute uptake rates were higher at the surface than at the 1% isolume for both ammonium and nitrate (Fig. 23). Standard deviations calculated for both ammonium and nitrate absolute uptake showed a decrease in variability for nitrate and an increase in variability for absolute ammonium uptake with depth (Fig. 24). Mean f-ratios calculated for each depth and each transect demonstrate variability in amount of new production between transects as well as through depth (Table 13). On transect 4, the surface f-ratio was 3 times that of the 1% isolume. Mean f-ratios calculated for each isolume for the entire area were low and consistent through the 1% isolume

Table 11. Particulate nitrogen, ammonium and nitrate specific (V) and absolute (ρ) uptake rates, ARK V-2, June, 1988. Asterisk denotes particulate nitrogen derived from a regression of known particulate nitrogen and chlorophyll values. ND = no data

Station No.	%I ₀	PN (mg m ⁻³)	Nitrate		Ammonium	
			V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
39	100	7.49	.0005	.0038	.0032	.0430
	50	4.45	.0030	.0134	.0019	.0099
	1	1.50	.0010	.0018	.0018	.0028
40	100	4.95	.0003	.0016	.0010	.0053
	50	4.81	.0011	.0053	.0023	.0135
	1	2.88	.0004	.0012	.0007	.0021
43	100	5.99	.0008	.0050	.0013	.0092
	50	4.10	.0001	.0005	.0013	.0061
	1	6.00	.0001	.0012	.0002	.0012
46	100	6.15	.0006	.0037	.0031	.0217
	50	6.93	ND	ND	.0031	.0263
	1	2.20	.0009	.0020	.0003	.0007
49	100	1.40	.0030	.0042	.0008	.0012
	50	1.66	.0044	.0097	.0002	.0004
	1	ND	ND	ND	ND	ND
65	100	3.67	.0006	.0020	.0023	.0093
	50	*4.84	.0006	.0029	.0045	.0208
	1	5.09	.0001	.0008	.0005	.0011
66	100	4.72	.0003	.0014	.0051	.0206
	50	4.31	.0006	.0026	.0052	.0152
	1	2.87	.0004	.0011	.0023	.0093
69	100	2.16	.0018	.0040	.0020	.0045
	50	1.81	.0030	.0055	.0036	.0069
	1	2.29	.0007	.0017	.0026	.0062
71	100	1.13	.0026	.0030	.0029	.0033
	50	*1.03	.0009	.0009	.0026	.0027
	1	1.05	.0013	.0013	.0010	.0010
73	100	0.97	.0011	.0011	.0027	.0026
	50	0.96	.0007	.0007	.0006	.0006
	1	0.67	.0023	.0015	.0016	.0011

Table 11. cont.

Station No.	%I _o	PN (mg m ⁻³)	Nitrate		Ammonium	
			$\frac{V}{(h^{-1})}$	$\frac{\rho}{(\mu mol\ l^{-1}\ h^{-1})}$	$\frac{V}{(h^{-1})}$	$\frac{\rho}{(\mu mol\ l^{-1}\ h^{-1})}$
75	100	0.96	.0008	.0008	.0014	.0014
	50	0.98	.0008	.0008	.0014	.0013
	1	0.74	.0004	.0003	.0010	.0007
79	100	6.28	.0011	.0072	.0015	.0094
	50	5.34	.0028	.0150	.0012	.0071
	1	6.35	.0005	.0030	.0004	.0027
81	100	1.27	.0006	.0008	.0015	.0019
	50	ND	ND	ND	ND	ND
	1	*1.47	.0002	.0003	.0020	.0046
82	100	1.25	.0021	.0026	.0090	.0119
	50	1.37	.0022	.0030	.0048	.0069
	1	1.78	.0009	.0016	.0007	.0012
85	100	0.40	.0030	.0012	.0034	.0014
	50	1.28	.0023	.0030	.0024	.0031
	1	1.36	.0016	.0022	.0012	.0017
87	100	0.66	.0020	.0013	.0030	.0020
	50	0.43	.0028	.0012	.0017	.0007
	1	0.19	.0030	.0006	.0015	.0003
96	100	5.31	.0043	.0228	.0003	.0023
	50	ND	ND	ND	ND	ND
	1	5.67	.0007	.0040	.0014	.0050
99	100	2.56	ND	ND	.0047	.0157
	50	ND	ND	ND	ND	ND
	1	2.38	.0021	.0050	.0113	.0358
102	100	1.22	.0015	.0033	.0044	.0054
	50	ND	ND	ND	ND	ND
	1	1.14	.0013	.0015	.0006	.0007
104	100	2.01	.0032	.0064	.0037	.0078
	50	ND	ND	ND	ND	ND
	1	0.84	.0006	.0005	.0007	.0006

Table 11. cont.

Station No.	%I ₀	PN (mg m ⁻³)	Nitrate		Ammonium	
			^V (h ⁻¹)	^ρ (μmol l ⁻¹ h ⁻¹)	^V (h ⁻¹)	^ρ (μmol l ⁻¹ h ⁻¹)
107	100	0.37	.0023	.0009	.0039	.0041
	50	ND	ND	ND	ND	ND
	1	1.07	.0010	.0011	.0037	.0039
110	100	12.11	.0011	.0121	.0009	.0115
	50	ND	ND	ND	ND	ND
	1	1.58	.0010	.0016	ND	ND

Table 12. Mean values of absolute (ρ) and specific (V) ammonium and nitrate uptake calculated for each isolume and for each transect, ARK V-2, June, 1988.

%I _o	Nitrate		Ammonium	
	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
Transect 1				
100	.0010	.0037	.0019	.0161
50	.0012	.0053	.0017	.0112
1	.0014	.0015	.0006	.0007
Transect 2				
100	.0012	.0021	.0027	.0070
50	.0011	.0022	.0030	.0075
1	.0009	.0011	.0015	.0032
Transect 3				
100	.0018	.0031	.0037	.0056
50	.0025	.0056	.0025	.0045
1	.0012	.0015	.0012	.0021
Transect 4				
100	.0025	.0127	.0030	.0115
50	ND	ND	ND	ND
1	.0014	.0033	.0035	.0092

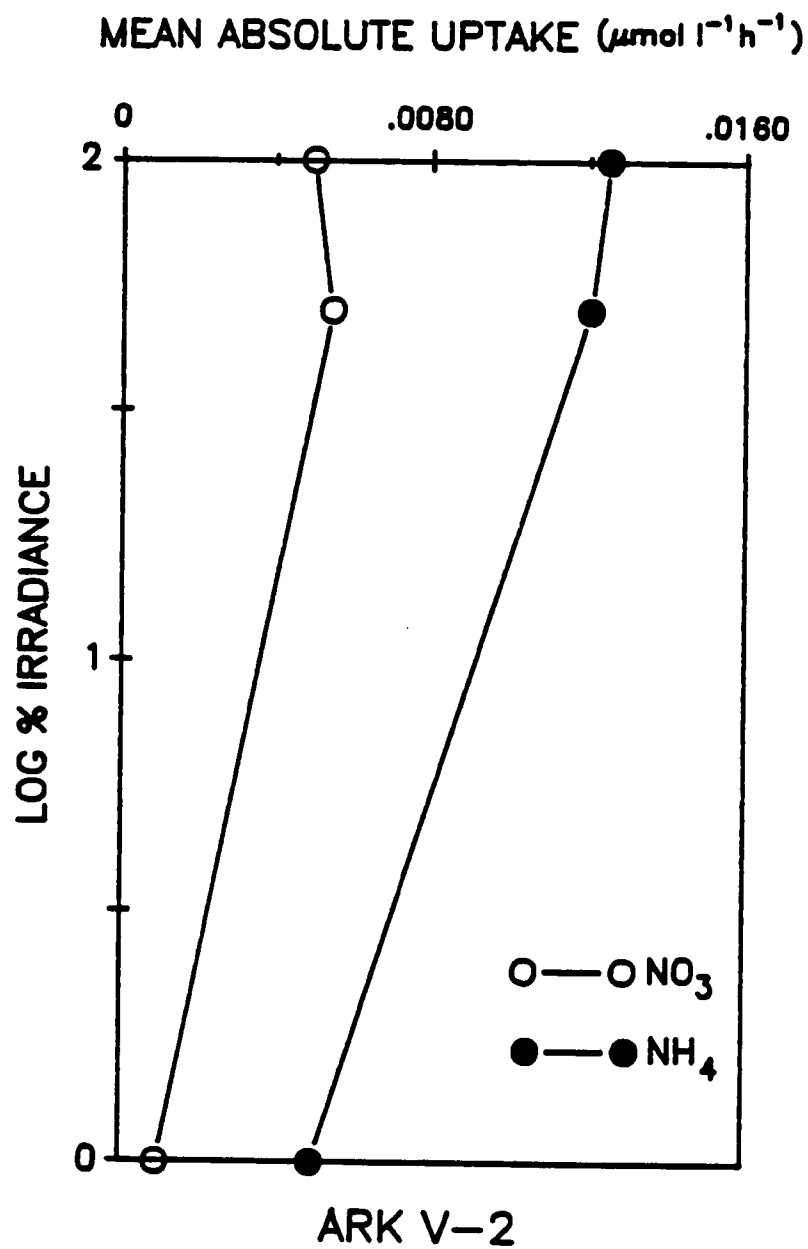


FIGURE 23. Mean absolute uptake, Polar Front, ARK V-2, June, 1988.

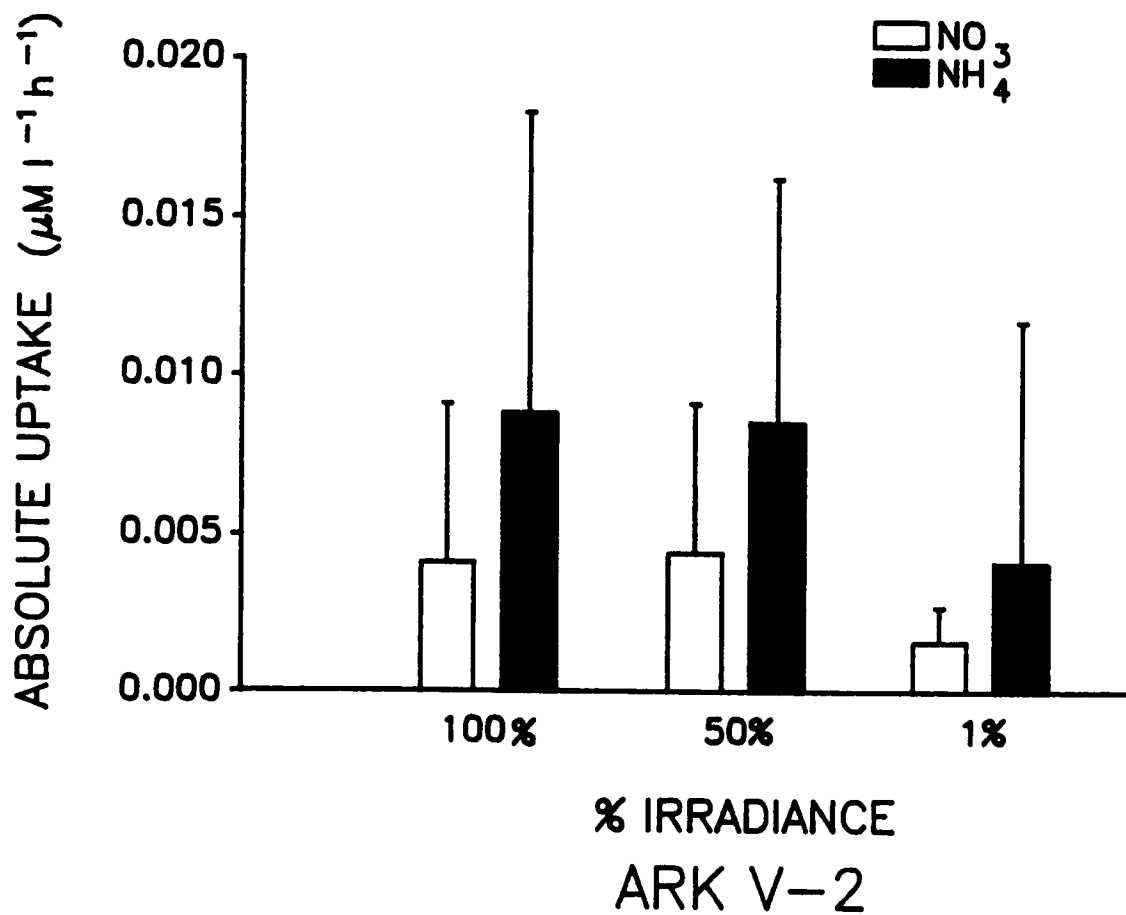


FIGURE 24. Mean absolute uptake with standard deviation, Polar Front, ARK V-2, June, 1988.

Table 13. Values for f-ratios calculated from mean uptake rates for each transect and each isolume. ARK V-2, June, 1988.

	%I ₀	f-ratio
Transect 1	100	0.19
	50	0.32
	1	0.45
Transect 2	100	0.23
	50	0.23
	1	0.26
Transect 3	100	0.31
	50	0.56
	1	0.42
Transect 4	100	0.52
	50	ND
	1	0.33

and RPI values were approximately 4 at each depth, indicating a preference for ammonium (Table 14).

Regeneration experiments were completed at the 100% isolume at 20 stations, at the 50% isolume at 12 stations, and 14 stations had regeneration measured at the 1% isolume. Of the 41 samples, 7 had uptake to regeneration ratios of one, indicating uptake and regeneration at parity. Twenty-one samples had ratios higher than one, indicating uptake greater than regeneration, and 11 had ratios less than one, or regeneration higher than uptake (Table 15). Of the ratios below 1, six were 0.9 and could be considered equal to one. At Station 66 and 75 where the ratios were 0.7 and 0.2, respectively, high regeneration rates were expected in view of the fact that ambient ammonium values were over 1 μM .

Data on the inhibition of ammonium uptake were obtained from surface samples at six stations on this cruise (Table 16). If eucaryotic activity is the major source of ammonium assimilation, then bottles with eucaryotic inhibitors should have lower uptake than those with no inhibitors and also lower uptake rates than bottles with procaryotic inhibitors. Control bottles should have no activity. At stations 39 through 49 ammonium uptake rates were greater in samples with eucaryotic-inhibitors than those with procaryotic inhibitors. At Station 43, eucaryotic inhibited bottles had ammonium specific uptake rates that were 8 times those of the uninhibited samples; however at this station total inhibition of both eucaryotic and procaryotic uptake was not achieved in the control

Table 14. Values for f-ratios and RPI values calculated from mean uptake rates for each isolume, ARK V-2, June, 1988.

%I	f-ratio	RPI
100	0.33	3.78
50	0.33	4.44
1	0.30	3.55

Table 15. Absolute (ρ) uptake and regeneration values for stations during ARK V-2, June, 1988. Absolute values were calculated using Glibert et al. (1982b) equation 11 and regeneration is calculated using equation 5 from Glibert et al. (1982b).

Station No.	%I ₀	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	REGENERATION ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	ρ/REGEN
39	100	.6777	.6760	1.0
	50	.2110	.1845	1.1
	1	.0758	.0892	0.9
40	100	.1506	.1448	1.0
	50	.1931	.1940	1.0
	1	.0570	.0601	1.0
43	100	.3448	.3156	1.1
	50	.2405	.2134	1.1
	1	.2115	.1135	1.9
49	100	.0392	.0255	1.3
	50	.0352	.0348	1.0
	1	ND	ND	ND
65	100	.2712	.0304	8.9
	50	.5946	.5212	1.1
	1	ND	ND	ND
66	100	.1553	.1834	0.9
	50	.0631	.0692	0.9
	1	.0635	.0983	0.7
69	100	.0605	.0726	0.8
	50	.0377	.0386	1.0
	1	.0462	-.0045	ND
71	100	.0244	.0076	3.2
	50	ND	ND	ND
	1	.0100	.0054	1.9
73	100	.0218	.0203	1.1
	50	.0157	.0127	1.2
	1	.0154	.0138	1.1
75	100	.0215	.0148	1.5
	50	.0256	.0174	1.5
	1	.0109	.0633	0.2

Table 15. cont.

Station No.	%I ₀	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	REGENERATION ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	ρ/REGEN
79	100	.3711	ND	-
	50	.2149	ND	-
	1	.2223	.2514	0.9
81	100	.0462	.0410	1.1
	50	ND	ND	-
	1	.0730	.0797	0.9
82	100	.0158	.0142	1.1
	50	.0246	.0168	1.5
	1	.0083	ND	-
85	100	.0086	.0063	1.4
	50	.0180	.0451	0.4
	1	ND	ND	-
87	100	.0073	.0094	0.8
	50	.0054	.0062	0.9
	1	.0012	.0065	1.8
96	100	.0690	.0392	1.8
	50	ND	ND	-
	1	.1151	ND	-
99	100	.0647	.0420	1.5
	50	ND	ND	-
	1	.1174	.1208	1.0
Mean	100	.1437	.1037	1.7
	50	.1220	.1128	1.1
	1	.0753	.0773	1.0

Table 16. Inhibition data for ammonium specific (V) and absolute (ρ) uptake samples, ARK V-2, June, 1988. ND = no data

INHIBITOR	AMMONIUM	
	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
STATION 39		
No inhibitor	.0039	.0701
Procaryotic inhibitor	.0000	.0000
Eucaryotic inhibitor	.0036	.0575
Both inhibitors	ND	ND
STATION 40		
No inhibitor	.0010	.0053
Procaryotic inhibitor	.0001	.0005
Eucaryotic inhibitor	.0004	.0019
Both inhibitors	.0000	.0000
STATION 43		
No inhibitor	.0013	.0092
Procaryotic inhibitor	.0008	.0049
Eucaryotic inhibitor	.0085	.0999
Both inhibitors	.0008	.0049

Table 16. cont.

INHIBITOR	AMMONIUM	
	V (h^{-1})	ρ ($\mu\text{mol l}^{-1} h^{-1}$)
STATION 49		
No inhibitor	.0008	.0012
Procaryotic inhibitor	.0000	.0000
Eucaryotic inhibitor	.0036	.0575
Both inhibitors	ND	ND
STATION 51		
No inhibitor	.0005	.0002
Procaryotic inhibitor	.0004	.0002
Eucaryotic inhibitor	.0004	.0002
Both inhibitors	.0000	.0000
STATION 63		
No inhibitor	.0054	.0270
Procaryotic inhibitor	.0033	.0179
Eucaryotic inhibitor	.0007	.0034
Both inhibitors	.0000	.0000

bottle. Only at Station 63 did the eucaryotic-inhibited bottle demonstrate lower uptake rates than the procaryotic-inhibited and uninhibited bottles, although at Station 51 the eucaryotic inhibited bottle had uptake similar to that of both the procaryotic and uninhibited bottles.

At each of three stations, uptake rates, regeneration measurements and inhibition experiments were made on three carboys of surface sea water, each with a different dissolved organic C:N ratio. The surface waters chosen for these experiments were taken at stations with particulate nitrogen concentrations of 7.5 (Station 39), 5.1 (Station 63) and $0.47 \mu\text{mol l}^{-1}$ (Station 51). Station 63 was originally used because it had a secchi depth of 6 m, which was nearly one half that of the 11 recorded at Station 39. Particulate carbon nitrogen measurements indicated, however, that it had a particulate matter value between that of Stations 39 and 51, and therefore, the attenuation of irradiance within the water column must have been due to some other factor.

Bacterial counts from samples at the start of the experiments, showed differences in bacterial numbers among the three stations (Table 17), with the lowest abundances occurring at Station 63 and the highest at Station 51 (which also had the lowest particulate carbon concentration). Because of the low precision of the method used for enumeration (Hobbie et al., 1977), bacteria were probably present at Station 63 but in numbers too low to detect with this method. Bacterial numbers on control samples after incubation for 24 h

Table 17. Data from substrate experiment Ark V-2, June, 1988. x 0 represents samples inoculated with no previous incubation period; x 24 samples inoculated after a 24 incubation.

Substrate		PN ($\mu\text{g l}^{-1}$)	Nitrate (μM)	Ammonium (μM)	Bacteria (cells ml^{-1})
STATION 39					
Control	x 0	7.49	3.31	0.16	20,979
	x 24	8.01	0.92	0.29	82,978
Glycine	x 24	7.83	ND	0.66	15,309
Dextrose	x 24	7.63	ND	0.30	14,884
STATION 51					
Control	x 0	0.47	5.73	0.39	87,507
	x 24	ND	5.76	0.56	10,716
Glycine	x 24	0.61	5.58	1.01	71,442
Dextrose	x 24	0.75	5.70	0.96	29,673
STATION 63					
Control	x 0	5.08	0.39	0.46	8,505
	x 24	4.77	0.01	0.55	< 1,000
Glycine	x 24	4.51	0.00	1.00	11,130
Dextrose	x 24	4.98	0.03	0.87	< 1,000

increased at Station 39, but decreased at Station 51. Bacteria in both the glycine and dextrose-enriched samples differed at each of the three stations, but the bacterial numbers were always higher in glycine-enriched water than in dextrose-enriched. Ambient ammonium concentrations increased through time in the enriched as well as the unenriched sea water at each station (Table 17). Nitrate concentration appeared to decrease in the substrate-enriched samples, suggesting that substrate enrichment enhanced nitrate uptake despite the insufficient time for cycling of particulate nitrogen and regeneration.

Specific and absolute nitrate uptake rates were different between samples with the different C:N ratios, as were absolute ammonium uptake rates (Table 18). Specific ammonium uptake in dextrose-enriched samples did not change noticeably between stations, although it did in glycine-enriched samples. Absolute ammonium uptake to regeneration ratios for these data show close coupling at Station 39 for three C:N ratios and parity or higher at Station 63 (Table 19). Station 51, however, showed less regeneration than uptake, and these samples had the highest bacterial counts.

When inhibitors were added in this experiment, each station produced different results (Table 20). At station 39, procaryotic uptake (eucaryotic inhibited) was nearly equal to the uptake in the sample with no inhibitors, but only 10% of uninhibited uptake in the glycine-enriched and 5% in the dextrose-enriched. Eucaryotic uptake (procaryotic inhibited) was only evident in the samples from the

Table 18. Nitrate and ammonium specific (V) and absolute (ρ) uptake for substrate experiment. ND = no data

Substrate	NITRATE		AMMONIUM	
	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)
STATION 39				
Control x 0	.0037	.0280	.0039	.0701
x 24	ND	ND	ND	ND
Glycine x 24	.0034	.0264	.0119	.1540
Dextrose x 24	.0052	.0400	.0059	.0724
STATION 51				
Control x 0	.0035	.0016	.0026	.0012
x 24	.0029	.0014	.0035	.0016
Glycine x 24	.0052	.0032	.0046	.0028
Dextrose x 24	.0035	.0026	.0056	.0043
STATION 63				
Control x 0	.0051	.0238	.0065	.0537
x 24	.0067	.0334	.0094	.1062
Glycine x 24	.0033	.0151	.0091	.0883
Dextrose x 24	.0036	.0178	.0058	.0427

Table 19. Ammonium absolute (ρ) uptake, and regeneration, data for substrate experiment, ARK V-2, June 1988.

Substrate		ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	Regeneration ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	ρ/REG
STATION 39				
Control	x 0	.0701	.0699	1.0
Glycine	x 24	.1540	.1779	0.9
Dextrose	x 24	.0724	.0760	1.0
STATION 51				
Control	x 0	.0012	.0016	0.8
Glycine	x 24	.0028	.0065	0.4
Dextrose	x 24	.0043	.0283	0.2
STATION 63				
Control	x 0	.0537	.0345	1.6
Glycine	x 24	.0883	.0887	1.0
Dextrose	x 24	.0427	.0397	1.1

Table 20. Inhibition data for ammonium specific (V) and absolute (ρ) uptake on substrate enriched samples, ARK V-2, June, 1988. ND = no data

TREATMENT	AMMONIUM	
	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1}\text{h}^{-1}$)
STATION 39		
NO ADDED SUBSTRATE		
No inhibitor	.0039	.0701
Procaryotic inhibitor	.0000	.0000
Eucaryotic inhibitor	.0036	.0575
Both inhibitors	.0000	.0000
GLYCINE		
No inhibitor	.0085	.0906
Procaryotic inhibitor	.0000	.0000
Eucaryotic inhibitor	.0008	.0073
Both inhibitors	.0000	.0000
DEXTROSE		
No inhibitor	.0042	.0430
Procaryotic inhibitor	.0046	.0427
Eucaryotic inhibitor	.0006	.0049
Both inhibitors	.0000	.0000

Table 20. cont.

TREATMENT	AMMONIUM	
	V (h^{-1})	ρ ($\mu\text{mol l}^{-1}h^{-1}$)
STATION 51		
NO ADDED SUBSTRATE		
No inhibitor	.0014	.0007
Procaryotic inhibitor	.0011	.0006
Eucaryotic inhibitor	.0009	.0004
Both inhibitors	.0000	.0000
GLYCINE		
No inhibitor	.0007	.0004
Procaryotic inhibitor	.0014	.0008
Eucaryotic inhibitor	.0006	.0004
Both inhibitors	.0015	.0011
DEXTROSE		
No inhibitor	.0019	.0014
Procaryotic inhibitor	.0015	.0011
Eucaryotic inhibitor	.0006	.0004
Both inhibitors	.0015	.0011

Table 20. cont.

TREATMENT	AMMONIUM	
	V (h ⁻¹)	ρ ($\mu\text{mol l}^{-1}\text{h}^{-1}$)
STATION 63		
NO ADDED INHIBITOR		
No inhibitor	.0082	.0747
Procaryotic inhibitor	.0018	.0091
Eucaryotic inhibitor	.0030	.0166
Both inhibitors	.0008	.0042
GLYCINE		
No inhibitor	.0080	.0643
Procaryotic inhibitor	.0000	.0000
Eucaryotic inhibitor	.0030	.0137
No inhibitors	ND	ND
DEXTROSE		
No inhibitor	.0047	.0312
Procaryotic inhibitor	.0020	.0103
Eucaryotic inhibitor	.0035	.0184
Both inhibitors	ND	ND

dextrose-enriched sea water where it was nearly equal to that of the uninhibited sample. At Station 51 uptake occurred in the controls for the two substrate-enriched samples; therefore, for these two experiments the exact amount of uptake for eucaryotes and procaryotes cannot be determined. The bacteria at this station may have been more resistant to the antibiotics, preventing a complete elimination of bacterial uptake; however, characterization of bacteria in these samples is unavailable. In unenriched seawater, where total inhibition was demonstrated, eucaryotic uptake was greater than procaryotic; this also occurred in the dextrose- and glycine-enriched sea water. Total elimination of uptake was not achieved in any of experiments from station 63, but it appears that procaryotic uptake may have been greater than eucaryotic uptake.

Because each different station began with different parameters and produced different results, the many variables involved make it difficult to determine cause and effect. However, it can be noted that 1) there were different patterns resulting from different dissolved organic C:N ratios, 2) that bacteria appeared to grow better in the glycine-enriched sea water and 3) that there was little difference in ammonium uptake rates between dextrose and glycine-enriched samples when eucaryotes were inhibited.

TOTAL PRODUCTION

Primary production can be calculated from measurements of nitrate and ammonium. Table 21 contains production estimated in this

Table 21. Production estimated from absolute uptake rates converted into carbon units by converting molar to weight units and multiplying these by the carbon:nitrogen ratio observed at that station. Rates were then integrated through the euphotic zone. Integrated rates of production are based on ammonium and nitrate uptake rates in units of $\text{mg C m}^{-2} \text{ d}^{-1}$ and f-ratios are calculated on integrated rates of primary productivity.

Study	Nitrate	Ammonium	Total	f-ratio
ARK IV-1 (Arctic) May, 1987	147	67	215	.69
ARK IV-1 (Polar) May, 1987	218	557	776	.28
ARK IV-2 June, 1987	281	684	966	.29
ARK V-2 June, 1988	162	293	456	.36

manner. Total production is broken down into "new" and regenerated production for each cruise and for the Arctic and Polar Front on cruise ARK IV-1. From these calculations we see that the percentage of total production that was "new" was approximately three times greater in the Arctic Front than in the Polar Front in May, 1987. These calculations also indicate that the percentage of total production that was "new" production was greater at the Arctic Front in May of 1987 than at the Polar in May, 1987, June, 1987 or June of 1988. However, the total amount of production was always greater in the Polar front area during all three cruises and in June of 1977 was 4 times that of the production at the Arctic Front.

4. DISCUSSION

Phytoplankton growth is the base of all energy transformations within marine food webs. In addition phytoplankton growth also directly affects the global carbon budget by removing inorganic carbon from surface waters, causing a flux of CO_2 into the ocean. This is particularly true for the Greenland Sea where the role of phytoplankton production in the biogeochemical cycle of carbon is thought to be substantial (Peng et al., 1987). However, the permanence of this role depends on the amount of biogenic carbon that is removed from the surface layers of the ocean. Despite the fact that this can be determined by the use of ammonium and nitrate uptake rates, until this study very little had been done to determine these rates in the East Greenland Sea (Smith & Kattner, 1989; Kristiansen & Lund, 1989). These data cover both the Arctic Front and the Polar Front in the same month and an extended portion of the Polar Front over a two-year period. Therefore, they represent a more complete view of ammonium and nitrate uptake rates in the Greenland Sea than had previously been obtained. Previous nitrate and ammonium specific uptake rates measured by Smith & Kattner (1989) in spring, 1984, of 0.0039 and 0.0028 h^{-1} for nitrate and ammonium, respectively, were similar to values from the Arctic Front and the Polar Front, June, 1988. The Arctic and Polar Front values were also similar to values of Kristianson & Lund in the Barents Sea (1989) in spring, 1987, who found specific nitrate and ammonium surface uptake of 0.0015 and

0.0024 h^{-1} respectively in the vicinity of the Polar Front and of 0.0026 and 0.0031 h^{-1} for nitrate and ammonium, respectively, in the Arctic Front region. Values of specific nitrate and ammonium uptake at the surface in the region of the Polar Front in 1987 were higher than both Smith & Kattner's and Kristianson & Lund's measurements. However, the surface, mean absolute ammonium uptake at the Polar Front, 1987 is similar to that found by Müller-Karger & Alexander (1986) of 0.0071 h^{-1} in the spring and summer in the southeastern Bering Sea, a region considered to be significantly more productive (Smith, 1987). Their mean specific nitrate uptake value of 0.0208 h^{-1} was five times higher than the highest mean specific nitrate surface uptake value from this study. The values from these three cruises are within the range of what has been previously found in the spring and summer in northern polar regions. The extent of the range of values found in other studies emphasizes the possibility of a great deal of variability within this area.

Production

Total production calculations made from ammonium and nitrate uptake measurements in the vicinity of the Arctic and Polar Fronts indicated that the amount of total production was different in each area. This was also true of the amount of new production available in each area. Despite the fact that the Arctic Front in May, 1987 had twice the percentage of nitrate based or "new" production as the Polar Front, the total production of the Polar Front was 3.6 times

that of the Arctic Front. This results in a difference in the absolute amount of production available for export. The Polar Front contributed more "new" as well as total production than the Arctic Front in all three studies. Using the uptake rates of ammonium and nitrate at both the Polar and Arctic Front in May, 1987, we can see that these two areas together contributed approximately $991.91 \text{ mg C m}^{-2} \text{ d}^{-1}$ to the euphotic zone and $366.39 \text{ mg C m}^{-2} \text{ d}^{-1}$ for flux to depth. Integrated values of primary production are not available from other studies for the area of the Arctic Front, however, Smith et al. (1987) reported calculated values of $426 \text{ mg C m}^{-2} \text{ d}^{-1}$ at the Polar Front in June - July, 1984. This value is slightly more than half that determined for the Polar Front in May, 1987 and less than half that determined for the Polar Front in June, 1987. However, the June, 1988 mean was very similar to that of the Smith et al. (1987). These differences indicate interannual differences in production.

Calculated f-ratios indicated that the percentage of nitrate based production at the Arctic Front was twice that of the ammonium, which suggests a system depending on nitrate brought up from depth. The Polar Front during all three studies had low f-ratios, and therefore must rely on heterotrophic processes to maintain production. The same physical processes that allow for the development of extensive heterotrophic populations (i.e., water column stability) also reduce the flux of nitrate into the upper layers. For the Polar Front to increase its percentage of "new" production, more nitrate must be brought into the system. When

stratification breaks down because of freezing processes along the Polar Front, irradiance becomes a limiting factor. Events such as eddies may bring about short-term instability that increases the amount of nitrate, but these probably dissipate before light limitation becomes too great. Whether short-term instability was occurring in the East Greenland Sea and what its effects were during the years of this study is unknown, but during a year of significant eddy generation "new" production could be increased.

It appears from this study that the region of the Polar Front was more important in terms of the amount of production available for export from the system than the Arctic Front, even though the latter was producing a higher percentage of its total production as new production. Due to the frontal dynamics involved with the Arctic Front (deep pycnocline, lack of low salinity melt water, etc.), the Arctic Frontal system probably never becomes ammonium based. If it does, it is unlikely that it will remain so for any significant length of time because of the physical processes in the area. However, the region of the Arctic Front may never contribute as much new production as the Polar Front because these same processes put a limit on the amount of production occurring. In addition, the total production as well as "new" production in the Polar Front can be increased with physical forcing events such as eddies, (Niebauer & Smith, 1989).

Uptake Variability

It is evident from the magnitude of the differences between production in the Arctic and Polar Frontal regions that there was variability between the two areas both in the total amount of production and also in the extent to which the different forms of nitrogen are being utilized. Station-to-station variability, examined in terms of standard deviation around the mean of each isolume in each area, indicated that the Arctic Front had less variability than the Polar Front. No replications were made, and therefore, an analysis of variance (ANOVA) was not attempted to determine the variability within the data. A partial correlation was performed in order to establish which factors are associated with the variability in ammonium and nitrate uptake rates and to determine the direction of future studies.

Absolute nitrate and ammonium uptake rates, particulate nitrogen, ambient ammonium and nitrate concentrations and the depth of the pycnocline were used in the partial correlation analysis (Appendix C). The most obvious difference between the Arctic and Polar Fronts was the depth of the pycnocline, especially in relationship to the base of the euphotic zone. A significant negative correlation ($r = -.734$) was seen with depth of the pycnocline and absolute ammonium uptake in the Arctic Front. A deep mixed layer appeared to have more of an effect on ammonium uptake than on nitrate uptake, whereas a shallow mixed layer had relatively little effect on either nitrate nor ammonium absolute uptake. This

does not appear to be due to changes in ambient concentrations since there was not a significant correlation between either ambient nitrate nor ammonium concentrations and the depth of the pycnocline.

Pycnocline depth usually affects irradiance and nutrient concentration, however, the partial correlation analysis failed to reveal a relationship between ambient nitrogen concentration and uptake rates. Therefore, the effects of irradiance on ammonium and nitrate uptake in this region need to be examined with greater detail. Irradiance availability may play a more pronounced role in ammonium uptake than nitrate, as indicated by a lack of significant correlation between nitrate uptake and pycnocline. Previous studies of the dependence of uptake on irradiance in polar regions have produced contrasting results. Olson (1980) found during late winter/early spring in Antarctic waters that nitrate uptake ceased in the dark, whereas ammonium uptake was approximately half that found in the light. Glibert et al. (1982a), however, found in the spring in the Scotia Sea that nitrate uptake was virtually the same in the dark as in the light, while ammonium uptake was only 30-50% of that in the light. Nelson & Smith (1986) in the Ross Sea and Smith & Kattner (1989) in the Fram Strait found that nitrate uptake at the 1% isolume was not as low as ammonium uptake at the same light level. Although nitrate uptake would be expected to be lower than ammonium uptake at depth, due to energetic considerations (McCarthy, 1980), Thompson et al. (1989) suggested that the use of nitrate relative to that of ammonium is of little energetic importance in terms of growth

rate at low photon flux densities. This is substantiated in an analysis of experiments by Smith & Harrison (unpubl.) that indicate that there is only a weak dependency of nitrate and ammonium uptake on irradiance. Changes in uptake rates may also be the result of obtaining samples of phytoplankton which had been moving throughout the euphotic zone and maintaining them at set irradiances. MacIsaac & Dugdale (1972) found that water from the 50% isolume, when incubated at 100% irradiance, experienced a reduction in both specific nitrate and ammonium uptake. In this study, mean specific ammonium uptake rates demonstrated a sharper increase at the 5% isolume than at the preceding three. Increased uptake rates at the 1% isolume could be due to photo-inhibition of organisms from a deeply mixed water column, when they are brought to the surface. However, this is unlikely given the density distribution. Ice coverage might also produce populations adapted to low irradiances, but Transect 2 had no ice coverage and exhibited increased uptake with depth. Depth of mixing does appear to affect ammonium uptake. Further study of irradiance quantity and quality in these two regions and its effects on uptake is needed.

The only other significant correlations ($P < 0.05$) found were those positive correlations between particulate nitrogen and absolute nitrate uptake in May, 1987 at both the Arctic Front ($r = 0.701$) and Polar Front ($r = 0.663$) and between particulate nitrogen and ammonium absolute uptake in June, 1987, and 1987 ($r = 0.676$) and June 1988 ($r = 0.826$) at the Polar Front. These correlations are explained by the

fact that as the uptake rate of a particular form of nitrogen increase, the atom% from that form increases in the particulate portion.

A multiple regression was run using absolute ammonium and nitrate uptake as dependent variables and date and place as independent variables (Appendix C). This resulted in a high level of significance for absolute ammonium uptake with time ($P = 0.006$) and place ($P = 0.027$), but nothing of significance for nitrate uptake. The strong regression between ammonium uptake and date and place again supports the hypothesis that the difference between the two areas may be a result of differences in pycnocline depth and its relationship to the euphotic zone. The high level of significance for time may be related to interannual variability due to large scale physical forcing (i.e., global climate conditions) resulting in mesoscale physical forcing (i.e., time and duration of ice extent).

It appears that there is variability between ammonium and nitrate uptake and that this variability can be accounted for by physical forcing dynamics between the two areas. This results in differences in total and new production. It also appears that irradiance may play a more significant role in ammonium uptake than nitrate as indicated by a lack of correlation with nitrate uptake and pycnocline. A replicated study at the Arctic and Polar Front could validate this analysis.

Regeneration

The highest uptake rates were found to occur at stations with the shallowest pycnocline, where stratification could create conditions conducive to the development of larger populations of heterotrophs (e.g. microzooplankton, macrozooplankton, bacteria) in association with the temporal sequence of a phytoplankton bloom (Cushing, 1959). This in turn appears to have resulted in a community dominated by heterotrophic processes. It has been shown that ammonium is a major fraction of nitrogen used by phytoplankton under many circumstances (Dugdale & Goering, 1967; Eppley & Peterson, 1979). For phytoplankton to rely primarily on reduced nitrogen, the rates of regeneration must equal or exceed the total nitrogen requirements of phytoplankton. In a seasonal study of NH_4^+ regeneration in Vineyard Sound, MA, Glibert (1982) found that regeneration rates greatly exceeded uptake rates in the spring months, but were approximately equal to the NH_4^+ uptake rates in the warm, summer months. Cochlan (1986) also found regeneration rates on the Scotian Shelf to equal those of uptake in July. Other studies have observed that regeneration rates were generally equal to or greater than NH_4^+ rates (Harrison, 1978; Axler et al., 1981). Additional studies (Caperon et al., 1979; Paasche & Kristiansen, 1982; Harrison et al., 1983) have reported that uptake usually exceeds regeneration. The regeneration data from June, 1987 showed uptake rates generally exceeding regeneration measurements by at least 40%. The stations measured in this study were utilizing both

nitrate and ammonium, therefore, the possibility of an increase in standing stocks existed. In June, 1988 the system showed a tighter coupling of uptake and regeneration, indicating that more regeneration was occurring. Ammonium remineralization and utilization were approximately in balance at this time. Production in an approximate state of equilibrium and flux out of the system would lead to a decrease in standing stocks unless replaced by production based on nitrate vertically advected from depth.

Bacterial Utilization of Ammonium

Although historically it has been assumed that phytoplankton are responsible for most of the inorganic nitrogen uptake in the euphotic zone of marine environments (Dugdale & Goering, 1967), exceptions have been observed (Eppley et al., 1977; Laws et al., 1985, Wheeler & Kirchman, 1986). Various experimental approaches have been used to demonstrate that heterotrophic bacteria are a sink for dissolved organic nitrogen in marine environments (Billen, 1984). However, bacterial production appears to be substantially higher than the maximum measured uptake rates of dissolved amino acids (Williams, 1984; Wheeler & Kirchman, 1986), and therefore, another source of nitrogen for bacteria should be considered.

Inhibition measurements done in the Greenland Sea were not entirely satisfactory due to a lack of bacterial numbers for samples and the occurrence of uptake in certain control bottles. The measurements do indicate, however, that bacterial uptake of ammonium

may account for a significant percentage of total ammonium uptake in the surface waters of the Greenland Sea. If heterotrophs were utilizing ammonium, the circumstances under which this occurred were also of importance. Goldman et al. (1987) measured nitrogen uptake of natural marine bacteria grown in the laboratory on differing substrates. They found that ambient ammonium concentrations increased with increasing C:N ratio of the initial substrate. This was not inconsistent with our findings from experiments where ammonium concentration always increased more in the sample with the lower C:N ratio. They also found that there was a distinct trend of increasing regeneration with increasing C:N ratio of the substrate. This did occur at the station with a particulate nitrogen value less than $1.0 \text{ } \mu\text{mol m}^{-3}$, but not at the two stations with particulate nitrogen values greater than $1.0 \text{ } \mu\text{mol m}^{-3}$.

There is currently no published data on the use of inhibitors on substrate manipulation for natural marine assemblages, and my results were not always satisfactory due to uptake in the control bottles. However, the use of inhibitors may be helpful in determining the relative extent of heterotrophic uptake. This must be taken into consideration when looking at differences in uptake due to changes in C:N ratio. Because each station started out with different parameters and produced different results, the many variables involved make it difficult to determine cause and effect. Inconsistencies in uptake rates may have resulted from the presence or absence in varying quantities of heterotrophs, although more data

are needed to support this hypothesis.

This study confirmed that many factors influence the ability of procaryotes to utilize ammonium, including differences in dissolved organic C:N ratio. Further examination of this problem with natural assemblages should include careful replication as well as experiments to determine the amount of inhibitors needed to control procaryotic and eucaryotic uptake. Measurements should also be made of the C:N ratio of the sea water after initial substrate manipulation and at the end of the experiment. In addition, some analysis of community structure should be made. This would help determine if variability between sampling areas is due to variability the biological component or the rates of each component. This hypothesis is supported by the fact that differences occurred between stations in bacterial counts, as well as rates of uptake between eucaryotic and procaryotic-inhibited samples. Bacteria may be a sink for ammonium under certain conditions, and a more detailed and closely controlled set of experiments could reveal the extent of this sink.

5. Conclusions

Ecological data can often be viewed as a product of either an experimental or observational approach (Ludwig & Reynolds, 1989). An experimental approach presupposes that the community is subject to experimental manipulations, while an observational approach makes measurements over a range of conditions imposed by nature rather than by the researcher. Because care was taken to add only trace amounts of nutrient in an effort not to change nutrient conditions, the uptake measurements made during this study fall under the category of observational approach. These observations were then used to determine contributions to carbon flux. The secondary goals of studying temporal and spatial variability as well as inhibition and substrate manipulation were made in an attempt to elicit patterns that would lead to the formation of causal hypotheses that may then be tested with further work.

Inference to locations and times other than those sampled are not sought here due to the paucity of statistical analysis. However, the large number of samples taken contributes to the validity of mean uptake values. Statistical analysis indicates that variation between years and between frontal areas is a real expression of the space/time variations of this polar region. Differences in the Greenland Sea area are undoubtedly due to differences in environmental factors on both spatial and temporal bases. The cause and effect of these temporal differences may be due to frontal

dynamics at the Arctic front that are different from those of the Polar Front (i.e., marginal ice dynamics). Statistical analysis has indicated that the difference in pycnocline depth between the Polar and Arctic Front has been may play a major role in differing uptake rates as well as differing forms of nitrogen being predominately taken up between the two areas. The difference in pycnocline depth is directly related to the fact that the Polar Front marginal ice edge produces water column stratification, which does not occur at the Arctic Front. These differences create variability on the small, meso- and large scale and also ultimately lead to differences in biotic communities. This hypothesis is supported by the fact that differences occurred between stations in bacterial counts as well as rates of uptake between eucaryotic- and procaryotic-inhibited samples. That bacteria may be a sink for ammonium under certain conditions was also demonstrated, and a more detailed and closely controlled set of experiments could reveal the extent of this sink.

Conclusions drawn in regard to the objectives set forth for this study are as follows:

1. f- ratios for the Arctic Front indicate that approximately 70% of total primary production at the Arctic front is in the form of new production.

2. f- ratios for the Polar Front indicate that approximately 30% of total production at the Polar Front is in the form of new production.

3. The total production at the Polar Front was consistent between May and June of 1987.

4. The absolute amount of "new" production contributed to the East Greenland Sea was less at the Arctic Front during the sampling period than during any of the three sampling periods at the Polar Front.

5. Variability in absolute ammonium uptake occurred between the two frontal regions. This variability may have been due to a difference that occurred between the two areas in regards to the depth of the pycnocline in relation to the depth of the euphotic zone.

6. Experimental results indicate that bacteria are utilizing ammonium as a source of nitrogen, and therefore, may be competing with phytoplankton for this nutrient.

7. Bacteria utilization of ammonium is affected by the C:N ratio of the dissolved organic matter in sea water.

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APPENDICES

APPENDIX A

Nutrient and Particulate Nitrogen Data

A-1. Nutrient and biomass data from six light depths in the region of the Arctic Front. Asterisk indicates particulate nitrogen values calculated from chlorophyll a values using a Particulate nitrogen:Chlorophyll ratio of 2.25:1. ND = no data

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl a (ug l ⁻¹)
28	100	0	7.9	.6	*1.30	.62
	50	6	7.9	.65	.99	.54
	30	11	8.0	.61	1.16	.37
	15	18	8.0	.52	1.96	1.23
	5	28	8.3	.46	1.74	1.53
	1	43	9.1	.32	1.66	1.02
30	100	0	9.2	.35	.95	.55
	50	7	9.1	.36	.77	.58
	30	13	9.1	.37	.85	.48
	15	20	9.1	.41	1.52	.87
	5	31	9.4	.27	1.46	1.20
	1	49	9.8	.22	.88	.83
34	100	0	9.4	.28	1.42	1.22
	50	5	9.3	.36	.81	ND
	30	9	9.3	.36	.63	.52
	15	14	9.3	.35	.67	.45
	5	23	9.4	.34	.51	.45
	1	35	9.4	.23	*1.01	.46
61	100	0	10.9	.25	1.15	1.09
	50	5	11.1	.34	.68	.91
	30	9	10.8	.34	1.44	1.19
	15	14	10.8	.36	1.62	1.03
	5	23	10.8	.29	2.56	1.87
	1	35	11.0	.35	1.48	.82
65	100	1	9.8	.28	.9	1.6
	50	5	9.7	.28	1.14	1.68
	30	9	9.7	.28	.78	1.69
	15	14	9.6	.29	1.97	2.31
	5	23	9.7	.29	1.04	2.18
	1	35	10.1	.28	1.01	1.39
66	100	1	9.0	.23	2.61	1.36
	50	5	9.0	.27	.88	ND
	30	8	9.0	.28	.99	1.23
	15	13	8.9	.29	.81	1.31
	5	21	8.9	.29	1.07	1.37
	1	33	9.3	.34	.61	.97

A-1. cont

Station No.	%I _o	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m^{-3})	Chl a ($\mu\text{g l}^{-1}$)
71	100	0	6.1	.27	3.39	2.65
	50	4	6.1	.27	2.90	3.09
	30	8	6.0	.26	3.01	1.07
	15	15	6.0	.31	3.90	2.23
	5	19	6.1	.38	3.68	1.75
	1	30	6.4	.45	2.79	1.81
87	100	0	7.8	.46	2.15	2.0
	50	5	7.7	.42	1.77	1.79
	30	8	7.7	.38	1.79	1.73
	15	12	7.6	.36	1.72	1.55
	5	19	7.6	.35	2.26	1.58
	1	30	7.8	.37	2.23	1.33
90	100	0	7.9	.27	1.41	1.27
	50	5	7.9	.27	1.51	1.16
	30	8	7.9	.33	1.96	1.40
	15	12	7.8	.29	1.82	1.40
	5	19	7.8	.32	1.59	1.42
	1	30	8.1	.32	1.77	1.61
103	100	0	8.0	.37	1.87	1.33
	50	5	8.0	.33	1.99	1.41
	30	9	8.0	.32	1.93	1.51
	15	13	8.0	.26	1.78	.60
	5	21	8.4	.22	2.27	1.13
	1	33	10.3	.11	1.45	1.03
105	100	0	7.7	.47	1.71	.81
	50	6	7.8	.42	1.79	.75
	30	9	7.8	.42	1.65	.90
	15	15	8.1	.47	1.88	.89
	5	23	8.4	.35	1.59	.79
	1	35	9.1	.35	1.90	1.18
107	100	0	8.8	.38	1.52	.87
	50	5	8.9	.41	1.4	.9
	30	9	8.9	.42	1.42	.92
	15	15	8.9	.38	1.39	.89
	5	23	9.2	.30	1.89	.89
	1	35	10.2	.35	2.74	.91

A-2. Nutrient and biomass data from six light depths in the region of the Polar Front. ND = no data

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl a (ug l ⁻¹)
132	100	0	7.4	.25	.52	.52
	50	11	7.8	.23	.5	ND
	30	20	7.9	.23	.33	.30
	15	31	8.0	.24	.29	.19
	5	49	8.8	.14	.45	.09
	1	76	10.4	.17	.29	.07
133	100	0	7.8	.28	.55	.26
	50	11	8.5	.41	.39	.22
	30	18	9.0	.27	.52	.20
	15	29	10.1	.25	.28	.08
	5	46	11.6	.19	.39	.07
	1	70	12.3	.21	.36	.05
135	100	0	9.1	.15	1.56	1.63
	50	5	9.2	.16	2.12	1.77
	30	9	9.2	.10	*3.96	1.76
	15	13	9.5	.14	1.43	1.89
	5	21	9.7	.11	1.22	1.87
	1	33	10.6	.12	.72	.82
136	100	1	8.7	.25	2.0	1.21
	50	5	8.8	.29	2.17	1.56
	30	9	9.0	.20	2.05	1.86
	15	13	9.2	.17	3.51	2.11
	5	21	10.0	.17	1.88	2.81
	1	25	10.9	.23	.79	ND
138	100	0	9.4	.49	1.39	.76
	50	6	9.3	.49	1.61	1.21
	30	10	9.2	.48	1.64	1.37
	15	16	9.4	.38	1.69	1.25
	5	25	10.7	.32	2.04	1.71
	1	38	12.5	.40	1.1	.63
139	100	0	9.4	.26	1.65	1.53
	50	5	9.8	.24	2.0	2.17
	30	9	9.8	.28	2.72	2.38
	15	15	10.1	.26	2.05	2.54
	5	23	10.6	.25	.23	.92
	1	35	12.3	.27	.71	.39

A-2. cont.

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl ^a (ug l ⁻¹)
143	100	0	8.9	.21	1.73	1.32
	50	5	8.9	.30	1.79	1.40
	30	8	8.7	.29	1.71	1.51
	15	12	8.9	.29	1.79	1.71
	5	19	9.8	.36	1.05	1.01
	1	30	10.1	.31	.74	.65
149	100	0	7.6	.43	.65	.31
	50	12	8.2	.60	.6	.30
	30	21	8.7	.4	1.75	.21
	15	34	9.3	.32	.34	.20
	5	53	10.3	.14	.43	.15
	1	81	11.3	.18	.25	.08
151	100	0	9.2	.23	1.91	1.42
	50	7	9.1	.20	.71	2.16
	30	11	9.1	.22	1.81	2.76
	15	18	9.5	.17	1.32	2.20
	5	28	9.6	.19	1.53	2.20
	1	43	11.2	.18	.79	1.37
153	100	0	4.0	.94	3.0	2.47
	50	4	4.6	.77	2.88	2.72
	30	6	5.3	.61	2.51	3.09
	15	10	6.2	.45	2.48	3.02
	5	16	7.3	.35	1.45	2.51
	1	24	9.2	.37	.76	.98
154	100	0	7.2	.50	2.74	1.96
	50	3	7.3	.45	2.05	2.1
	30	6	7.3	.45	2.44	1.56
	15	9	7.7	.33	3.03	1.82
	5	14	7.8	.22	2.55	1.64
	1	22	8.9	.23	1.61	1.42
156	100	0	8.0	.1	2.62	1.79
	50	5	7.8	.17	1.16	2.45
	30	9	7.7	.14	1.85	2.46
	15	13	10.2	.15	.31	2.86
	5	21	11.4	.17	.93	1.51
	1	33	12.8	.17	.90	.36

A-2. cont.

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl a (ug l ⁻¹)
157	100	0	4.6	.91	3.9	2.79
	50	4	4.7	.98	4.84	3.48
	30	7	5.1	.89	5.84	3.55
	15	11	5.5	.83	4.72	3.75
	5	18	6.2	.87	3.83	3.51
	1	27	7.4	.93	2.01	2.81
168	100	0	3.1	1.2	2.45	1.66
	50	6	3.1	1.25	1.7	1.73
	30	10	3.3	1.26	2.58	2.71
	15	16	4.0	1.15	2.46	3.68
	5	25	6.2	1.07	1.49	1.32
	1	38	9.3	.65	.6	.76
171	100	0	6.0	.73	1.77	1.61
	50	5	7.5	.65	1.34	1.84
	30	8	8.8	.55	1.72	1.26
	15	12	11.5	.43		ND
	5	19	12.5	.26	1.52	1.11
	1	30	13.0	.13	1.91	.28
174	100	2	5.8	.18	.76	.48
	50	10	6.6	.21	2.61	.83
	30	21	7.8	.43	.46	.44
	15	34	7.8	.43	4.92	.16
	5	53	7.6	.92	6.76	.14
	1	81	10.5	.43	2.61	.16
177	100	0	3.6	.03	1.6	1.30
	50	7	5.0	1.10	1.65	1.08
	30	10	6.6	1.10	.69	ND
	15	11	6.4	1.08	.90	.81
	5	18	8.0	.78	.35	.55
	1	28	9.1	.61	.35	.48
179	100	0	2.7	.88	2.79	3.14
	50	4	3.9	.66	2.52	3.81
	30	7	5.7	.34	2.37	1.45
	15	11	6.3	.32	1.41	.95
	5	18	7.4	.63	1.02	.79
	1	27	9.3	.81	.44	.66

A-3. Nutrient and biomass data from six light depths in the region of the Polar Front, June 1987. Asterik indicates particulate nitrogen values calculated from chlorophyll a values using a PN:Chl ratio of 2.25:1. ND = no data

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl <i>a</i> (ug l ⁻¹)
185	100	0	.97	1.25	2.0	.55
	50	5	1.47	1.52	1.6	.38
	30	8	3.71	1.43	2.3	.52
	15	12	5.55	1.48	5.1	1.44
	5	19	6.98	1.67	1.0	.42
	1	30	9.17	1.59	0.6	.23
186	100	0	.85	.54	4.4	1.62
	50	2	1.09	.54	5.0	2.47
	30	4	1.54	.61	4.0	1.68
	15	7	1.52	.53	4.2	1.8
	5	11	.38	.47	4.7	2.4
	1	16	1.44	.62	3.7	1.72
189	100	0	7.33	.84	0.8	ND
	50	11	7.35	.84	1.3	ND
	30	18	7.35	.82	0.7	ND
	15	29	8.49	.57	1.3	ND
	5	46	10.18	.55	1.2	ND
	1	70	10.87	.75	1.4	ND
191	100	0	5.32	.43	1.3	ND
	50	11	5.35	.45	0.7	ND
	30	18	5.61	.43	ND	ND
	15	29	6.7	.43	ND	ND
	5	46	7.25	.39	ND	ND
	1	70	8.98	.38	ND	ND
194	100	0	3.29	.45	1.8	.64
	50	5	3.29	.42	1.6	.58
	30	9	3.27	.45	1.4	.75
	15	13	3.27	.45	1.1	.69
	5	21	3.27	.39	1.2	.51
	1	33	4.00	.39	0.7	.09
195	100	0	3.29	.43	0.54	.13
	50	7	3.33	.42	0.54	.11
	30	12	3.44	.41	0.5	.08
	15	19	3.54	.36	0.3	.03
	5	30	3.55	.37	0.04	.03
	1	46	3.58	.33	0.03	.02

A-3. cont.

Station No.	%I _o	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl ^a (ug l ⁻¹)
208	100	0	.10	.43	4.7	ND
	50	2	.00	.41	4.1	ND
	30	4	.01	.42	5.5	ND
	15	6	.09	.40	2.0	ND
	5	9	.01	.38	4.4	ND
	1	14	.05	.43	6.5	ND
210	100	0	.04	.46	2.6	.97
	50	5	.50	.43	5.2	3.49
	30	9	.76	.45	1.9	1.60
	15	12	3.57	.55	1.8	ND
	5	21	5.11	1.15	1.1	1.40
	1	25	6.93	.98	0.7	ND
213	100	1	.06	.37	4.0	ND
	50	2	.00	.39	4.1	ND
	30	4	.00	.39	3.4	ND
	15	7	.00	.44	3.9	ND
	5	11	.00	.34	3.5	ND
	1	25	4.65	1.95	1.2	ND
214	100	1	1.18	.74	3.8	ND
	50	3	2.26	1.06	2.8	1.39
	30	6	3.51	1.28	2.1	ND
	15	9	3.50	1.27	2.5	ND
	5	14	7.80	1.81	ND	ND
	1	22	8.79	1.74	1.5	ND
215	100	1	.01	.40	4.7	ND
	50	2	.00	.43	4.5	ND
	30	4	.01	.40	3.1	ND
	15	6	.00	.33	3.3	ND
	5	9	.01	.41	3.8	ND
	1	14	.01	.34	3.4	ND
219	100	0	.73	.30	3.8	1.36
	50	4	.67	.33	3.7	1.44
	30	6	1.27	.29	3.5	1.33
	15	10	4.89	.35	3.5	2.18
	5	16	6.82	.49	1.8	1.38
	1	24	7.68	.66	1.4	1.27

A-3. cont.

Station No.	%I _o	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl <i>a</i> (ug l ⁻¹)
220	100	0	3.26	.51	1.5	.83
	50	4	3.24	.52	1.5	.46
	30	7	3.18	.59	2.4	.88
	15	11	3.22	.75	2.1	.64
	5	18	3.75	1.07	2.3	1.25
	1	27	8.76	.91	2.3	.82
222	100	0	3.12	.50	4.7	.52
	50	4	3.02	.43	4.4	.75
	30	7	3.08	.41	5.1	.44
	15	11	3.04	.33	6.8	1.94
	5	18	3.35	.27	8.4	2.35
	1	27	6.29	.60	4.5	.76
224	100	0	4.28	.12	1.5	1.13
	50	5	4.29	.23	1.0	1.08
	30	9	4.17	.11	1.2	1.57
	15	13	4.20	.12	1.7	.92
	5	21	4.55	.63	1.1	1.01
	1	33	9.39	.86	1.1	.68
226	100	0	3.75	.25	1.0	1.16
	50	7	4.10	.29	0.9	.9
	30	11	4.32	.32	0.5	.84
	15	18	4.90	.26	0.8	.61
	5	28	7.93	.20	0.4	1.0
	1	43	9.62	.23	0.2	.41
227	100	0	2.61	.23	2.8	5.44
	50	6	2.51	.24	2.3	3.79
	30	11	2.70	.26	1.9	3.9
	15	17	4.80	.28	0.6	.41
	5	27	6.71	.39	1.5	1.20
	1	41	7.70	.52	0.6	1.31
242	100	0	3.79	.30	3.8	2.51
	50	2	3.88	.35	3.6	1.68
	30	4	3.98	.36	2.0	1.74
	15	7	4.06	.32	*3.4	2.16
	5	11	4.74	.41	2.2	1.56
	1	16	4.92	.33	*2.2	1.44

A-3. cont.

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl _a (ug l ⁻¹)
250	100	0	3.46	.35	2.0	.60
	50	5	3.21	.37	2.8	1.30
	30	8	3.01	.47	2.6	2.0
	15	12	4.17	.42	1.6	1.66
	5	19	6.29	.27	1.1	1.09
	1	30	6.95	.29	0.6	.56
252	100	0	3.76	.29	0.8	.77
	50	7	4.67	.38	0.7	.64
	30	11	4.32	.31	0.9	.69
	15	18	6.36	.24	0.7	.22
	5	28	7.89	.24	0.7	.19
	1	43	9.17	.26	0.6	.13
253	100	0	1.36	.24	2.2	ND
	50	4	1.82	.19	1.7	ND
	30	7	2.64	.22	1.4	ND
	15	11	3.00	.25	1.2	ND
	5	18	5.11	.23	1.7	ND
	1	27	6.38	.21	.1	ND

A-4. Nutrient and biomass data from three light depths.
 Asterisk indicates particulate nitrogen values calculated from
 chlorophyll a values using a Particulate nitrogen:Chlorophyll ratio
 of 2.25:1. ND = no data.

Station No.	%I ₀	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (mg m ⁻³)	Chl a (ug l ⁻¹)
39	100	0	3.31	.16	7.49	4.41
	50	5	4.15	.15	4.45	4.09
	1	30	7.77	.16	1.50	0.63
40	100	0	.12	.38	4.95	6.97
	50	5	.12	.37	4.81	6.86
	1	25	5.79	.93	2.88	4.57
43	100	0	.03	.34	5.99	4.68
	50	2	.02	.26	4.10	4.68
	1	16	.38	.24	6.00	4.68
46	100	0	3.68	.41	6.15	3.52
	50	3	3.82	.34	6.93	5.51
	1	21	7.85	.44	2.20	1.58
49	100	0	2.27	.36	1.40	0.83
	50	5	2.52	.51	1.66	2.16
	1	30	5.62	.75	*2.20	2.77
65	100	0	0.00	.32	3.67	1.32
	50	3	0.04	.29	*4.84	1.26
	1	22	0.05	.38	5.09	1.65
66	100	0	0.84	.67	4.72	0.88
	50	5	0.54	.54	4.31	1.06
	1	30	5.95	2.35	2.87	0.45
69	100	0	1.76	.64	2.16	0.49
	50	4	1.90	.67	1.81	0.46
	15	18	1.37	.60	2.29	0.50
71	100	0	3.95	.98	1.13	0.16
	50	5	3.95	1.01	*1.03	0.17
	1	30	4.85	1.71	1.05	0.22
73	100	0	4.18	1.07	0.97	0.28
	50	8	4.18	1.02	0.96	0.28
	1	54	8.58	1.44	0.67	0.12

A-4. cont.

Station No.	%I _o	Depth (m)	NO ₃ (μmol)	NH ₄ (μmol)	PN (m mg ⁻³)	Chl _a (ug l ⁻¹)
75	100	0	4.58	.39	0.96	0.32
	50	6	4.58	.34	0.98	0.34
	1	38	6.01	1.27	0.74	0.33
79	100	0	0.34	.14	6.28	0.98
	50	3	0.34	.17	5.34	1.06
	1	11	0.38	.21	6.35	1.02
81	100	0	2.69	.45	1.27	0.21
	50	6	2.32	.78	*1.47	0.21
	1	38	3.87	3.20	2.23	0.32
82	100	0	2.20	.50	1.25	0.17
	50	4	2.08	.55	1.37	0.19
	1	27	0.51	.80	1.78	0.24
85	100	0	5.36	.32	1.36	0.28
	50	6	5.34	.31	1.28	0.26
	1	41	8.40	.39	.40	0.11
87	100	0	5.43	.37	.66	0.30
	50	7	5.36	.33	.43	0.27
	1	43	8.60	.38	.19	0.10
96	100	0	0.25	.14	5.31	1.05
	1	16	1.97	.62	4.73	0.64
99	100	0	0.70	.19	2.56	0.65
	1	24	0.71	.17	2.38	0.60
102	100	0	8.03	.55	1.22	1.05
	1	22	1.24	.31	1.14	1.07
104	100	0	0.77	.28	2.01	0.50
	1	38	7.75	1.52	.84	0.24
107	100	0	4.02	.24	.37	0.23
	1	43	8.02	.21	1.07	0.14
110	100	0	3.68	.19	ND	0.18
	1	49	6.94	.12	1.58	0.05

Appendix B

Mean Ammonium and Nitrate Uptake

B-1. Mean ammonium and nitrate specific (V) and absolute (ρ) uptake rates in the region of the Arctic Front. n = number of samples.

%I _o	Nitrate		Ammonium	
	V (h ⁻¹)	(n)	V (h ⁻¹)	(n)
100	.0021	12	.0009	13
50	.0024	13	.0010	13
30	.0019	12	.0011	11
15	.0014	12	.0010	12
5	.0012	12	.0006	12
1	.0007	12	.0006	10

%I _o	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)		ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	
	(n)		(n)	
100	.0037	11	.0017	12
50	.0031	12	.0014	12
30	.0028	11	.0016	11
15	.0024	12	.0016	11
5	.0017	11	.0013	12
1	.0008	11	.0010	11

B-2. Mean ammonium and nitrate specific (V) and absolute (ρ) uptake rates in the region of the Polar Front. n = number of samples.

%I _o	Nitrate		Ammonium	
	V (h ⁻¹)	(n)	V (h ⁻¹)	(n)
100	.0041	17	.0070	18
50	.0035	17	.0062	16
30	.0042	14	.0063	15
15	.0040	15	.0056	16
5	.0029	14	.0040	14
1	.0027	17	.0022	17

%I _o	Nitrate		Ammonium	
	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	(n)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	(n)
100	.0055	18	.0185	18
50	.0061	16	.0180	16
30	.0071	11	.0167	13
15	.0052	14	.0135	15
5	.0026	14	.0047	12
1	.0020	17	.0020	17

B-3. Mean ammonium and nitrate absolute (ρ) and specific (V) uptake rates for each isolume, ARK IV-2, June, 1987. n = number of samples.

%I _o	Nitrate		Ammonium	
	V (h ⁻¹)	(n)	V (h ⁻¹)	(n)
100	.0033	17	.0051	17
50	.0031	17	.0055	18
30	.0040	16	.0061	17
15	.0037	18	.0059	17
5	.0033	19	.0075	16
1	.0043	16	.0109	16

%I _o	Nitrate		Ammonium	
	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	(n)	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	(n)
100	.0062	17	.0142	17
50	.0059	17	.0144	18
30	.0069	16	.0169	17
15	.0081	18	.0181	17
5	.0036	19	.0211	16
1	.0048	16	.0188	16

B-4. Mean values of absolute (ρ) and specific (V) ammonium and nitrate uptake calculated for each isolate, ARK V-2, June, 1989. n = number of samples.

%I _o	Nitrate		Ammonium	
	V (h ⁻¹)	(n)	V (h ⁻¹)	(n)
100	.0016	22	.0029	23
50	.0018	15	.0028	16
1	.0011	22	.0017	21
%I _o	ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)		ρ ($\mu\text{mol l}^{-1} \text{ h}^{-1}$)	
		(n)		(n)
100	.0041	22	.0088	23
50	.0041	15	.0084	16
1	.0016	22	.0041	21

Appendix C

Partial Correlation Coefficients

C-1. Partial Correlations (Pearson product-moment correlations), Arctic Front, May, 1987.

	NO ₃ Rho	NH ₄ Rho	NO ₃	NH ₄	PN	Depth of Pycnocline
NO ₃ Rho	1.0000	-0.0820	-0.3692	-0.6528	0.7352	0.0444
NH ₄ Rho	-0.0820	1.0000	-0.3235	0.7179	0.3016	-0.8891
NO ₃	-0.3692	-0.3232	1.000	-0.0797	-0.7425	0.6023
NH ₄	-0.6528	0.7179	-0.0797	1.000	-0.1587	-0.6865
PN	0.7352	0.3016	-0.7425	-0.1587	1.000	-0.4806
Depth of Pycnocline	0.0444	-0.8891	0.6023	-0.6865	-0.4806	1.000

C-2. Partial Correlations (Pearson product-moment correlations), Polar Front, May, 1987.

	NO ₃ Rho	NH ₄ Rho	NO ₃	NH ₄	PN	Depth of Pycnocline
NO ₃ Rho	1.0000	-0.0861	0.4832	-0.2476	0.2110	0.4375
NH ₄ Rho	-0.0861	1.0000	-0.1924	0.2617	0.4781	-0.3208
NO ₃	0.4832	-0.1924	1.000	-0.6471	-0.4327	0.3476
NH ₄	-0.2476	0.2617	-0.1924	1.000	0.5760	-0.1811
PN	0.2110	0.4781	-0.4327	0.5760	1.000	-0.2582
Depth of Pycnocline	0.4375	-0.3208	0.3476	-0.1811	-0.2582	1.000

C-3. Partial Correlations (Pearson product-moment correlations), Polar Front, June, 1987.

	NO ₃ Rho	NH ₄ Rho	NO ₃	NH ₄	PN	Depth of Pycnocline
NO ₃ Rho	1.0000	0.2092	0.1882	-0.0021	0.0773	-0.4301
NH ₄ Rho	0.2092	1.0000	-0.5173	-0.2626	0.7885	-0.2968
NO ₃	0.1882	-0.5173	1.000	0.2140	-0.6461	0.0966
NH ₄	-0.0021	-0.2626	0.2140	1.000	-0.2786	0.4886
PN	0.0773	0.7885	-0.6461	-0.2786	1.000	-0.4074
Depth of Pycnocline	-0.4301	-0.2968	0.0966	0.4886	-0.4074	1.000

C-4. Partial Correlations (Pearson product-moment correlations), Polar Front, June, 1988.

	NO ₃ Rho	NH ₄ Rho	NO ₃	NH ₄	PN	Depth of Pycnocline
NO ₃ Rho	1.0000	-0.0419	-0.3856	-0.4063	0.3906	0.5700
NH ₄ Rho	-0.0419	1.0000	-0.1053	-0.1828	0.7069	0.1683
NO ₃	-0.3856	-0.1053	1.000	0.2617	-0.5588	-0.3054
NH ₄	-0.4063	-0.1828	0.2617	1.000	-0.3759	-0.1150
PN	0.3906	0.7069	-0.5588	-0.3759	1.000	-0.2582
Depth of Pycnocline	0.5700	0.1683	-0.3054	-0.1150	0.3200	1.000

VITA

Nancy Knowlton Keene was born in Tulsa, Oklahoma on March 23, 1947. She attended primary and secondary schools in Oklahoma City, Oklahoma and Lawton, Oklahoma and graduated from Lawton High School, Lawton, Oklahoma in May of 1965. The following September she attended Cameron College for two semesters. The following year she attended Central State University and graduated in May, 1969 with a Bachelor of Science degree in Science. In September of 1969 she attended the University of Oklahoma Medical Center and in August of 1970 she graduated with a Registered Medical Technologist certification. In September of 1979 she entered Graduate School at Texas A & M University in College Station, Texas. In May of the following year she graduated with a Master's of Education Degree. In September of 1985 she entered the Graduate School at the University of Tennessee, Knoxville, TN. She received the Doctor of Philosophy degree in the field of Ecology in August, 1990.