LOWER TROPHIC LEVEL STUDIES IN

THE MARGINAL SEA-ICE ZONE

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A

THESIS

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ABSTRACT

Inorganic nitrogen and carbon uptake by phytoplankton in the Bering

Sea ice-edge zone in April - May 1982 and 1983 was measured using

isotopic tracers ($H^{14}CO_3$, $^{15}NH_4-N$, $^{15}NO_3-N$). The contribution by

ice-related phytoplankton to annual Bering shelf productivity seemed

lower (approximately 0.5 gat N m^{-2} y^{-1}, 50 gC m^{-2} y^{-1}) in 1983 with

respect to 1982 (approximately 1.8 gat N m^{-2} y^{-1}, 78 gC m^{-2} y^{-1}),

presumably due to a deepening of the mixed layer by storms during the

1983 sampling period. Productivity preceding the 1982 and 1983 sampling

periods was not estimated. Upwelling processes met the phytoplankton

nitrogen demands for the duration of the ice-edge bloom (2-3 weeks),

while *in situ* regeneration was usually slow. Neither phosphorus nor

silica seemed to limit the ice-edge bloom (late winter water-column

N:P=5.3 to 9.9 per atoms, 10-30 ugat $Si(OH)_4-Si$ l^{-1}). Taxonomic

information suggests that epontic algae seeded the April - May ice-edge

water column bloom.

AKNOWLEDGEMENTS

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INTRODUCTION

Ecological setting:

The Bering Sea spring marginal sea ice zone is a continuous air-sea-ice interface extending from northern Bristol Bay to the southern part of Anadyr Gulf. At maximum extent (February to March, Webster, 1981; Overland and Pease, 1982), the ice limit roughly parallels the Bering Sea shelf break (figure 1). Spatial variability of events and navigational hazards render synoptic oceanographic coverage difficult. However, a good view of the ice edge can be obtained from synoptic satellite exposures.

Well-defined ice margins may be observed when winds blow from the south, while amorphous margins are characteristic of other wind directions and turbulent water conditions (Pease, 1980; Niebauer, 1983). Dense ice clustering and parallel banding are ice-edge patterns often observed on a scale of 1-100 Km (Martin et al, 1983; Wadhams, 1983; Muench et al, 1983a). Large embayments are common, as are opening and closing polynyas (Bauer and Martin, 1983). Ice thickness is variable, exceeding 5 meters only under ice pressure ridges or floes that may have drifted from the northern Bering and Chukchi Seas.
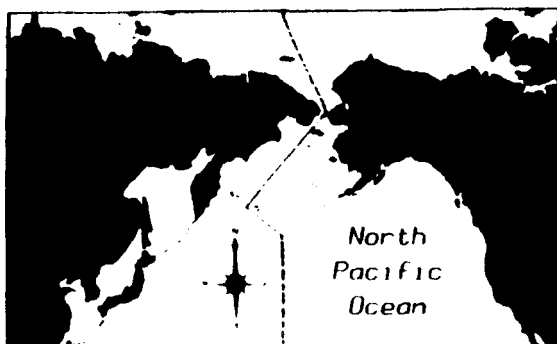
Figure 1:
Approximate ice edge positions
relative to the Bering Sea
shelf break and 'Alpha Helix'
cruise areas []
(lower part of drawing shows
North Pacific Ocean floor
and Aleutian trench).

———————————   4 May, 1982
— — — — — — —   26 April, 1983
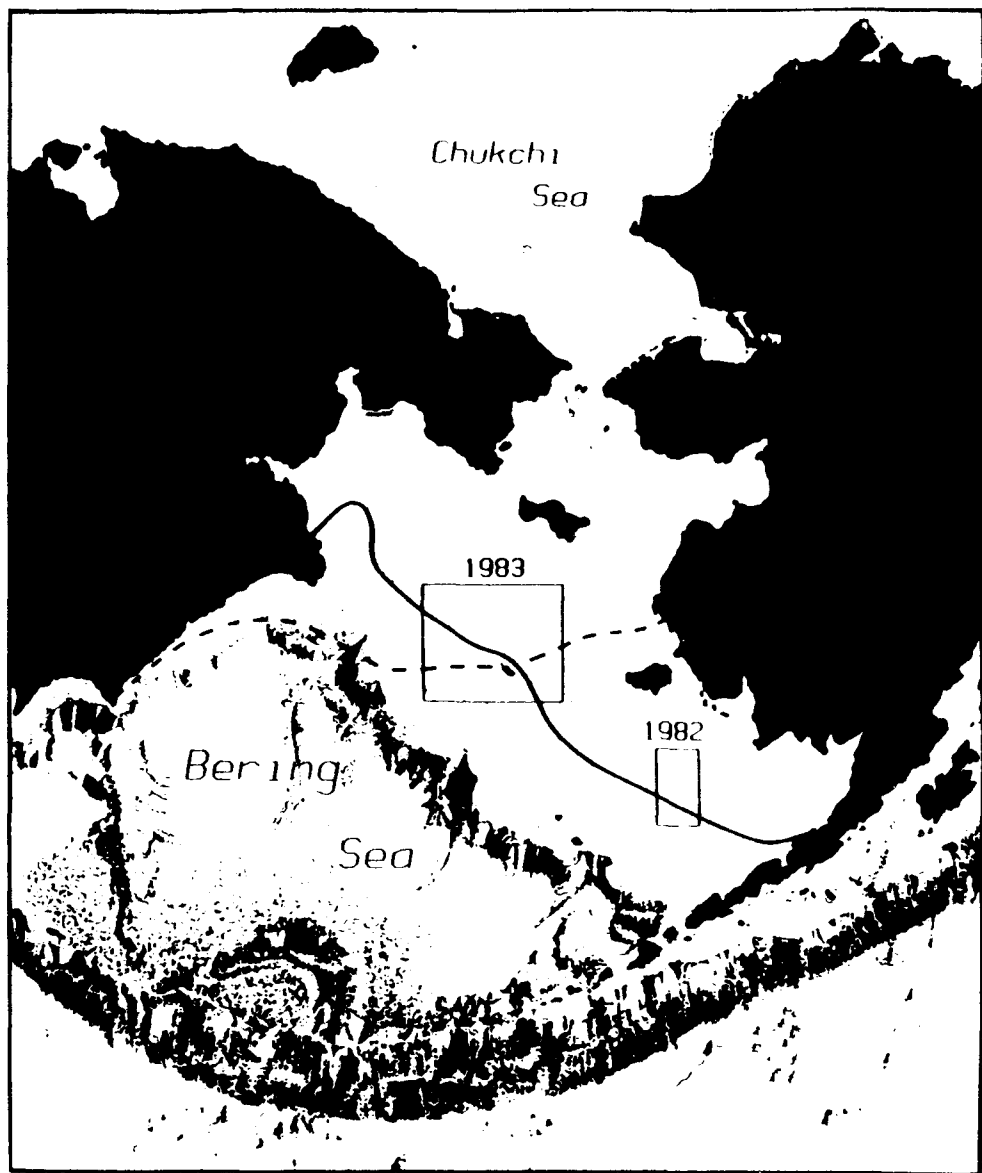
January - February oceanographic observations of the Bering Sea shelf and its ice-edge habitat reveal an almost completely mixed, cold (<-1.70°C) water column (McRoy and Goering, 1974a). Weak frontal structures, caused by continuous melting at the ice edge, characterize this habitat in winter (Overland and Pease, 1982; Roed and O'Brien, 1983; Muench, 1983; Niebauer and Alexander, in prep.). High levels of all nutrients have been recorded in the area in February - March (Muench et al, 1983b; McRoy and Goering, 1974a; Alexander, pers. comm.; Schell, pers. comm.).

The Bering Sea seasonal ice cover begins to retreat in March - April, shortly after reaching maximum extent. As the snow cover on the ice melts, the entire ice pack decays rapidly. The Bering Sea is ice-free by late May or early June. The sequence of events is tied to weather changes (Niebauer, 1980, 1983; Niebauer et al., 1981; Alexander and Niebauer, 1981; Webster, 1981; Overland and Pease, 1982).

The Bering-Chukchi Sea ice edge behaves as a biological concentration region for large numbers of organisms (Alexander, 1980, 1981). The most obvious of these organisms are mammals on a year-round basis (Fay, 1974, 1981; Burns et al, 1981), and birds on a seasonal time scale (Divoky, 1981).

Phytoplankton blooms can develop at the ice edge as the sea-ice melting rate increases with spring warming (Marshall, 1957; McRoy and Goering, 1974a, 1974b; Alexander and Niebauer, 1981; Niebauer et al, 1981). The ice-edge bloom develops under conditions different from the Bering Shelf phytoplankton bloom described by Goering and Iverson

(1980), Sambrotto and Goering (1980), Sambrotto (1983) and Sambrotto *et al* (in prep.). Ice meltwater, rather than temperature increases, induce water column stability at the ice edge. Similar observations to the Bering Sea ice-edge system are reported for other ice-affected waters (Bunt, 1968; Buinitsky, 1977; Hoshiai, 1977, 1981; Hsiao, 1980; Ainley and Jacobs, 1981; El-Sayed and Taguchi, 1981; Hoshiai and Fukuchi, 1981).

Few studies on late-winter (February - May), ice-related primary production have been accomplished (McRoy, Goering and Shiels, 1972; McRoy and Goering, 1974a; Alexander and Cooney, 1979; Alexander and Chapman, 1981; Alexander and Niebauer, 1981; C. Sancetta, pers. comm.). The underside of the seasonal ice cover provides a platform on which epontic (under-ice) algae can grow at rapid rates (Meguro and Fukushima, 1966; Horner and Alexander, 1972; Alexander, 1974; Horner, 1977; Clasby *et al*, 1976; Taniguchi *et al*, 1976; Pautzke, 1979; Alexander and Chapman, 1981; Takahashi, 1981; Schell *et al*, 1982), from perhaps as early as mid-February in a warm year (McRoy, Goering and Shiels, 1972). The ice-edge bloom occurs in the water column in late April or early May (Niebauer, Alexander and Cooney, 1981; Alexander and Niebauer, 1981; Schandelmeier and Alexander, 1981), but its exact timing and duration escape easy forecasting.

Marshall (1957) examines the ice-edge phytoplankton bloom in the western Barents Sea and proposes Sverdrup's (1953) critical depth hypothesis as an explanation for its development. Sverdrup's hypothesis states that water column net primary productivity will be positive when the ratio of the mixed layer depth (MLD) to the critical depth becomes

less than 1, given unlimited light and nutrient conditions. Niebauer,
Alexander and Cooney (1981) and Alexander and Niebauer (1981) support
this view, suggesting that primary producers at the Bering Sea ice edge
flourish due to enhanced water column stability and increased light
levels in a nutrient-rich environment.

Alexander and Niebauer (1981) and Niebauer and Alexander (in prep.)
find evidence of upwelling at the spring ice margin and of interaction
between the moving ice edge and the relatively stationary Bering
inner-shelf (50 m isobath) front (Kinder and Schumacher, 1981). They
suggest that such events may extend the life of the bloom, but the
mechanisms of upwelling at the ice edge are not clear yet (Foldvik and
Kvinge, 1977; Clarke, 1978; Buckley et al, 1979; Roed and O'Brien,
1983; Niebauer and Freed, pers. comm.).

In the fall, the oceanography of the Bering Sea is different than
in the spring. The ice edge begins to advance southward in October and
November from the Chukchi Sea and the south-facing coasts of the
northern Bering Sea (Fay, 1974; Shapiro and Burns 1975a, 1975b; Muench
and Ahlnäs, 1976; Burns et al, 1981; Pease, 1981). At this time,
environmental stresses limit the productivity of lower trophic level
communities: available light diminishes, nutrient concentrations are
low, storms continuously mix the water column, ice formation contributes
to instability by salt extrusion from the freezing surface waters and
salinity increases throughout the water column, while surface
temperatures quickly dip below 0°C. In these arctic-subarctic areas, a
definite fall bloom, as found in most temperate seas (Parsons et al,
1977), is not seen, except in restricted parts of the northern Bering

Sea and Bering Strait (Dawson, 1965; Arsenyev and Voytov, 1968; Taniguchi, 1969; McRoy, Goering and Shiels, 1972; Alexander, pers. comm.), where high nutrient concentrations occur.

Statement of the problem: Research objectives

The study of primary production in the ice-edge zone is important since this is the base of a food web which supports several animal populations. Transfer and distribution of the primary products through the ice-related trophic structure is not yet well understood (Alexander, 1980; Niebauer, Alexander and Cooney, 1981). The relationship between oceanographic variables (nutrients, light, temperature, density structure) and primary production at the ice edge needs to be resolved.

Estimates of the contribution of each of the Bering Sea primary production phases (epontic, ice edge, spring open shelf, summer and fall) to Bering Sea annual carbon and nitrogen budgets are important for understanding the biological dynamics of the Bering Sea shelf (Hood, 1983). A comprehensive ecological picture has not yet emerged from research conducted in the area, and apparent interannual variations in production regimes remain to be resolved (Sambrotto and Goering, 1983; Alexander, pers. comm.).

This study was undertaken to provide information with which to characterize production regimes at the ice-edge habitat. The early spring Bering Sea ice-related phytoplankton primary production and its carbon and nitrogen budget are examined. In particular, this thesis attempts to determine the relative importance of various nutrient sources to the ice-edge bloom, differentiating between biological and

physical nitrogen supply mechanisms. The physiological responses of the algae were of concern, and experiments were designed to address the response of phytoplankton from various depths to varying light intensities and/or nitrogen nutrient concentrations.

This research should contribute to a long-term understanding of ice-edge habitats, helping in the resolution of trophic pathways in ice-affected shallow shelves. In view of possible commercial exploitation of Bering Sea oil reserves, the present study may be of help in assessing anthropogenic effects in ice-covered areas.

MATERIALS AND METHODS

Ice Edge Cruises

The data presented in this thesis were collected from the R/V *Alpha Helix* (Institute of Marine Science, University of Alaska, Fairbanks).

Alpha Helix Cruise HX022

Between 16 October and 1 November, 1981, Bering Sea, Bering Strait and Chukchi Sea chlorophyll a was measured along the cruise track. Nitrate (NO_3-N) and ammonia (NH_4-N) uptake by phytoplankton was estimated at 71°21'N, 166°11'W in ice-covered waters.

HX025 AND HX043 cruises

R/V *Alpha Helix* cruises 025 and 043 visited the Bering Sea ice margin during spring 1982 and spring 1983, respectively (table 1, figure 1). Sampling during HX025 was restricted to a small area in NW Bristol Bay. Sampling in 1983 started a week earlier than in 1982. 1983 stations were occupied east, north and west of St. Matthew Island.

Table 1. Alpha Helix 025 and 043 cruises: Coordinates of area sampled and cruise dates.

	HX025	HX043
Sampling:	30 April 1982	21 April 1983
to	11 May 1982	6 May 1983
Lat N	56°30' - 58°35'	59°30' - 62° 0'
LongW	164° 0' - 166° 0'	170° 0' - 176° 0'

This work was carried out in conjunction with a broader investigation of the oceanographic regime at the retreating ice edge in spring. My results will be interpreted against the background of physical data provided by J. Niebauer and nutrient data provided by V. Alexander. The methods used in obtaining the above information are given in Niebauer and Alexander (in prep.).

Nitrogen stable isotope uptake experiments:

The ^{15}N tracer procedure used in all cruises was originally described by Neess et al (1962) and Dugdale and Goering (1967). Reviews of assumptions and limitations involved in the ^{15}NH$_4$-N and ^{15}NO$_3$-N uptake method can be found in Alexander (1970), McCarthy et al (1977), Harrison (1978), Caperon et al (1979), Glibert et al (1982) and Collos (1983).

^{15}N uptake measurement assumptions:

For purposes of the uptake experiments, the following assumptions were made:

Nitrogen uptake is assumed to be only externally controlled, by nutrient concentration and light intensity (Goldman, 1977; Collos and Slawyk, 1980), and internal cell nutrient pools may be neglected.

Under certain conditions N-uptake obeys Michaelis-Menten type kinetics (i.e. at nitrogen concentrations below saturation of the uptake mechanism and/or when growth is not limited by other nutrients, temperature or light: Dugdale, 1967, 1977; Lehninger, 1977; Eppley et al, 1977; Goldman and McCarthy, 1978; Dugdale et al, 1981).

In this work NH_4-N and NO_3-N are assumed to be the only nitrogen sources
available to phytoplankton. Uptake of urea and other organic
nitrogenous compounds (Schell, 1971, 1974a) are disregarded, even
though <5 μM urea-N concentrations may occur in the Bering Sea
(D. M. Schell, R. N. Sambrotto, pers. comm.).

Extracellular release of organic nitrogen and organic carbon by
phytoplankton (Chrost and Faust, 1983; Moller Jensen, 1983) is
neglected.

Maximum specific uptake rates (V_{MAX}) are assumed to be time-invariant.

Transient uptake is considered negligible, compared to total uptake
during the incubation (Brown and Harris, 1978; McCarthy, 1981;
Glibert et al, 1982; Dortch et al, 1982; Collos, 1983).

Nutrient remineralization is assumed negligible during the incubation
period and ^{15}N enrichment in the incubation media was assumed
constant (see Glibert et al, 1982; Paasche and Kristiansen, 1982;
LaRoche, 1983; Garside, 1984; Garside and Glibert, 1984).

It was assumed that alkalinty changes in the incubation media (Brewer
and Goldman, 1976) do not affect primary productivity or nitrogen
uptake measurements.

Isotope effects are considered negligible in ^{15}N experiments.

The following assumptions apply to both carbon and nitrogen tracer
experiments:

Incubation bottles are assumed to simulate *in situ* light conditions.

There is no "bottle effect" (Steemann Nielsen and Kohly, 1956; Pratt
and Berkson, 1959; Verduin, 1960; Vollenweider and Nauwerck,
1961; Soeder and Talling, 1969; Ryther et al, 1971; Qasim et al,
1972; Sheldon et al, 1973; McCarthy et al, 1974; Venrick, et al,
1977).

Daily absolute nitrate and carbon uptake was calculated assuming 13
hours/day to compensate for diel periodicity of carbon and nitrate
productivity and reduced uptake at low irradiances (Doty and Oguri,
1957; Goering et al, 1964; Harding et al, 1981). In late May at
latitudes greater than 60°N, daylight exceeds 16 hours (Nautical
Almanac), but I assumed low solar angles would result in decreased
water column light penetration. Daily ammonium uptake rates were
calculated based on 24 hour days since the NH_4-N uptake mechanism
is not strongly dependent on radiant energy (Goering et al, 1964;
Dugdale and Goering, 1967; Glibert et al, 1982; Harrison, 1983;
Nalewajko and Garside, 1983).

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It was assumed that rates measured at one depth could be used to
calculate mixed-layer primary productivity or nitrogen uptake.
Rate estimates were obtained taking the vertical chlorophyll a
distribution and primary productivity response to irradiance into
consideration. For details see table 9 "Notes".

It is assumed that sampling using Niskin bottles reflects *in situ*
conditions (Calvert and McCartney, 1979).

^{15}N isotope experimental approach:

Samples were collected in the morning. Sampling depths were
standard % surface irradiance depths (100, 50, 25, 10 and 1%) as
determined by Secchi disk or underwater PAR (photosynthetically active
radiation, 400-700 nm) measurements (LI-COR LI-185 meter/LI-192S quantum
sensor, in μEinsteins m^{-2} s^{-1}).

Clear Pyrex reagent bottles (1.05 l) were used as incubation
vessels. *In situ* percent surface light intensities were simulated using
nickel neutral density screens (Perforated Products, Inc.). Samples
were mixed before filling the bottles (Venrick et al, 1977).
Zooplankton was not removed. Autoclaved stock isotopic solutions (2-10
μgat ml^{-1}, 99 atom % K^{15}NO$_3$ or ^{15}NH$_4$Cl) were used for label additions.
Incubation took place on deck in a seawater cooled incubator, at
temperatures 0.5-1°C higher than sea surface temperatures. Integrated
PAR (LI-COR LI-500 integrator/LI-192S quantum sensor) and bath
temperature were recorded. Following incubation for 8-8.5 hours,
samples were filtered through precombusted (4 hours at 500°C) 47 mm
Gelman A/E glass fiber filters (0.3 μm manufacturer's suggested
retention ability), frozen, and later freeze-dried in Fairbanks.
Samples were preserved in desiccators, under vacuum. Samples were not
treated with BaSO$_4$ (Wada et al, 1977). Therefore losses of labile

nitrogenous compounds due to local increases of pH in the filters may have occurred.

At each experimental depth, 1 l seawater was filtered for isotope ratio estimates of unlabeled particulate material. Many isotopic nitrogen uptake studies assume a global, constant, ^{15}N natural abundance = 0.366 atom % ± 1.5% relative (Fiedler and Proksch, 1975), even though great variability in natural ^{15}N abundance has been observed (Wada et al, 1977).

Samples were combusted in a Coleman Nitrogen Analyzer using a modified dry Dumas method (Barsdate and Dugdale, 1965). The final $^{15}N:^{14}N$ isotope ratio was measured on a modified Bendix time-of-flight mass spectrometer (precision: 3.0% error at ^{15}N < 11 atom %, 4.7% error at 15-25 atom %).

Reviews and comments on ^{15}N tracer mass spectrometry principles, techniques, assumptions and calculations can be found in Fiedler and Proksch (1975), Wada et al (1977), Slawyk et al (1977, 1979) and Fisher et al (1979).

The absolute nitrate uptake rates reported below (tables 8, 9) were calculated assuming no strong dependence of nitrate uptake on irradiance. Therefore mixed-layer integrated rates may have been overestimated. $^{15}NO_3$-N incubations were carried out under simulated 10 and 50% surface irradiance, and specific uptake rates were similar at both irradiances or seemed to decrease at the higher irradiance. Sambrotto (1983) discusses the response of open-water Bering Sea phytoplankton to varying irradiance in spring.

Michaelis-Menten equation parameters:

Linear transformations of the information presented in 'substrate (S) vs. substrate:specific uptake rate (S/V) ratio' plots are used to estimate half saturation constants (K_s) and maximum specific uptake rates (V_{max}), as follows:

From the Michaelis-Menten equation:

$$V = (V_{max}*S)/(K_s+S)$$

Dividing both sides by 'S' and rearranging the reciprocal equation, we obtain the linear relationship:

$$S/V = (S/V_{max}) + (K_s/V_{max}),$$

from which the inverse of the slope is V_{max}, and K_s can be calculated from the intercept term in the formula and the value obtained above for V_{max} by linear regression analysis.

Similar transformations are the Lineweaver-Burk equation and the Eadie-Hofstee plots (Lehninger, 1977, p.195). Better estimates may be obtained using hyperbolic algorithms.

Ammonium regeneration by zooplankton:

Data from zooplankton grazing experiments conducted by R. T. Cooney and K. O. Coyle (unp. data) were used to estimate zooplankton excretion rates. Two methods were used:

I.- Using published zooplankton excretion rates (pp. 81-82):

$$E = RNH_4*W/(Z*1000) = (\mu gat\ NH_4\ l^{-1}\ d^{-1})$$

Where:

E = NH₄ excretion rate

RNH₄ = 0.107 µgat NH₄ l⁻¹ mg dwt⁻¹ d⁻¹ (Smith and Whitledge, 1977).

W = zooplankton dry weight 100-1115 mg dwt m⁻² (Cooney and Coyle, unp. data, table 7).

Z = depth of net tow (40-60 m)

1000 = conversion of cubic meters to liters

II.- Zooplankton assimilation efficiency:

Assuming zooplankton assimilation efficiencies of 70-80% of the plant material consumed (Cooney, pers. comm.), and a phytoplankton C:N ratio = 9.0 - 11.0 (at.), the 20-30% nitrogen excreted is obtained:

$$E' = G*A/(Z*12*9) = (\mu gat\ NH_4\ l^{-1}\ d^{-1})$$

In which:

E' = NH₄ excretion rate

G = zooplankton grazing rate (mgC m⁻² d⁻¹)

A = excreted fraction of material consumed (.2 for 80% and .3 for 70% assimilation efficiencies). This value may be approximated by (1-f).

Z = depth of net tow

12 = atomic weight, Carbon

9 = C:N ratio (per atoms) of phytoplankton, 1982 data

Carbon uptake (NaH¹⁴CO₃) experiments:

Marine primary productivity measurements used a modified Steemann Nielsen (1952) NaH¹⁴CO₃ uptake technique (Strickland and Parsons, 1972; Vollenweider, 1974). Alkalinity of the water was estimated according to Strickland and Parsons (1972).

Gieskes and Van Bennekom (1973), Peterson (1980) and Carpenter and Lively (1980) review the historical background, problems and assumptions involved in the application of the radiocarbon technique to aquatic productivity. Assumptions as stated above for the N-uptake experiments apply here as well.

Experimental samples were incubated on deck in 160 ml clear Corning glass milk dilution bottles for 4-5 hours, with radioactive isotope additions of 0.5-1 ml (5 μCi ml^{-1}, Strickland and Parsons, 1972). Labeled material was collected on 25 mm diameter Gelman A/E glass fiber filters (manufacturer's suggested retention ability: 0.3 μm) or Millipore^R filters (0.45 μm suggested retention ability). Both seemed to clear adequately in scintillation cocktail. No dilute HCl solution nor fumes were used to eliminate contaminating radioactive carbonate deposits from the filters, since at the low ambient seawater temperatures a filtered sea water rinse should suffice to eliminate the problem. Sample filters were placed in labelled 7 ml scintillation vials and 6-7 ml wet scintillation fluor added. The sample was not poisoned in any other way.

The fluor was prepared as follows (Donald M. Schell, pers. comm.):

    2 l   Toluene (reagent grade)
    1 l   Triton-X (Kodak)
    10 g   PPO (New England Nuclear)
    1 g   Bis-msb complex (New England Nuclear)

Sample radioactivity was measured in Fairbanks in a Beckman LS-100 scintillation counter (tritium and tritium + ^{14}C windows). Dpm (disintegrations per minute) were estimated by channels and external standard ratio methods.

Working NaH^{14}CO$_3$ solution (5 μCi ml^{-1} in 10 ml glass ampoules) was prepared as in Strickland and Parsons (1972). "Carrier free" (free of non-labelled carbonate) NaH^{14}CO$_3$ stock solution was obtained from New England Nuclear (5 mCi in 5 ml ampoule).

Stock NaH^{14}CO$_3$ nominal radioactivity was measured by injecting 1-2 μl of the 5 μCi ml^{-1} working solution into a mixture of 2 ml methanol and 0.2 ml phenethylamine, to prevent the loss of carbon as CO$_2$ (Weimer et al, 1975; Ilmavirta and Jones, 1977). 4-5 ml scintillation fluor were added. Methanol aids miscibility of the aqueous label solution and phenethylamine.

Experiments with seawater containing natural phytoplankton assemblages from a particular depth were performed at various simulated light intensities. For each sample, two dark carbon uptake replicates and three replicate subsamples at each simulated light intensity were incubated. The replicates were averaged, and dark carbon uptake subtracted from the light averages. I assumed uptake of carbon in the dark represents heterotrophic activity not associated with photosynthesis.

The values presented below (carbon uptake in the light minus dark bottle measurements) are assumed to estimate net primary productivity (P$_{NET}$). The validity of applying a respiration correction to ^{14}C data to calculate gross photosynthesis has not yet been resolved (McAllister et al, 1964; Bunt, 1965; Morris and Beardall, 1975; Laws, 1975; Peterson, 1980). Photorespiratory carbon losses in the phytoplankton seem to be of potential importance, but there still is no quantitative verification of actual photorespiration of phytoplankton in natural aquatic environments (Parsons et al, 1977). Epontic (under-ice) algae may have evolved an efficient strategy for reducing respiratory losses, namely growing in the underside of the ice platform and avoiding stresses due to water column mixing deeper than the critical depth. The

ecological significance of photorespiration and photoinhibition in estimates of carbon flow in planktonic systems is difficult to assess.

The question of over- or underestimation of productivity by the $H^{14}CO_3$ method is still unsettled. Morris (1980) suggests that due to the production of storage products in eutrophic waters, the radiocarbon method may overestimate primary productivity. Peterson (1980) and Legendre et al (1983) suggest that the method underestimates P if dark carbon uptake is subtracted from light uptake. In general, the problem of underestimating productivity by using the radiocarbon method seems to be most pronounced in oligotrophic marine (Sheldon et al, 1973; Sheldon and Sutcliffe, 1978) or limnological waters (Verduin, 1975). The problem may not affect carbon uptake measurements of the ice edge production regime during the late winter and spring, when the region behaves as an eutrophic system.

Guidelines for treatment of irradiance vs. productivity data can be found in Platt et al (1980), Gallegos and Platt (1981) and Cote and Platt (1983). Vollenweider (1966) also suggests a family of functional relationships to describe the resulting 'irradiance vs photosynthetic rate' curves. Here the approach of Steele (1962) is used, as in Kremer and Nixon (1978):

$$G = G_{MAX}*(I/I_{OPT})*exp(1-(I/I_{OPT})),$$

where G = production rate (mg C m^{-3} h^{-1})
  G_{MAX} = maximum productivity
  I = irradiance (μEinsteins m^{-2} s^{-1})
  I_{OPT} = optimum irradiance

The model curves (dotted or continuous lines) in figures 12-21 stop at on-deck irradiance (100% surface light intensity) for each

experiment. This was the highest irradiance to which a particular
sample was exposed.

All the above are empirical models. A mechanistic description of
the natural process has not been accomplished yet.

As mentioned in the assumptions, daily production rates were
estimated assuming 13 hour days.

Epontic algae ^{15}N and ^{14}C incubations:

Epontic (under-ice) algae were also subjected to ^{15}NH$_4$-N, ^{15}NO$_3$-N
and H^{14}CO$_3$ uptake measurements. Ice samples were collected with buckets
from slush surrounding the ship.

In one instance a floe (approximately 1x1.5x1.5 m^3) was brought on
board with a hydraulic crane. This was an opportunity to observe the
"spongy" underside of spring ice, where a brown algal layer (bottom 3-25
cm) develops. Part of this colored layer was shaved into a bucket and
left to melt at ambient temperature and subdued light. The slush was
stirred occasionally, and after 4-5 hours, bottles for nitrogen and
carbon uptake experiments were filled. The temperature of the ice-water
did not change over the thawing period. Samples for chlorophyll a,
nutrient concentration, alkalinity (see Jones et al, 1983), particulate
C:N ratio, algal species composition and ^{15}N abundance in unlabeled
particulate N were collected.

Measurements of N and C assimilation in the ice environment are
riddled with problems, as witnessed by Clasby et al (1976), and should
be regarded as gross approximations. I consider the epontic carbon and
nitrogen uptake rates presented in this thesis to underestimate *in situ*

activity, mainly due to previous brown ice decay, washout of cells while the floe is hauled on board, the poor chances of uniform label distribution in the incubation bottles, and the potentially adverse conditions arising from salinity and temperature changes as the ice thaws during the incubation. Conversely, heterogeneous label distribution in the incubation vessels can lead to high label activity pockets in which the algae assimilate large amounts of an isotope (^{15}N, ^{14}C), resulting in an overestimate of productivity (D. Schell, pers. comm.).

C:N ratios (plankton elemental composition):

Samples for particulate elemental composition were collected on precombusted 25 mm Gelman A/E glass fiber filters. Water volume filtered varied depending on particulate matter concentration in the water.

Particulate nitrogen was estimated by Micro Dumas combustion in a Coleman Nitrogen Analyzer, by a modified Solórzano and Sharp (1980) technique, or by combustion in a Perkin-Elmer 240C Elemental Analyzer (PN, PC). Banse (1974, 1977) discusses possible errors involved in C:N and C:chlorophyll a determinations.

Phytoplankton species identification and enumeration:

Water for phytoplankton identification was preserved in 100 ml jars with modified Lugol's solution (Rodhe, Vollenweider and Nauwerck, 1956; Vollenweider, 1974). Approximately 1 ml per 100 ml of sample was used to produce a moderate tea color.

Standing stock determinations were made by cell counts under a
Zeiss inverted phase contrast microscope (Utermöhl, 1931, 1958).
Each preserved sample was agitated, poured into a 5 ml Zeiss settling
chamber and left to settle overnight. Bubbles were removed from the
chamber with a thin wire an hour before counting. The volume in the
chamber was brought back to 5 ml with deionized water, and the chamber
covered again before counting. Phytoplankton were identified and
counted at 40X and 100X magnification using the following keys:
Rabenhorst (1930, 1933, 1959 and 1961-1966), Cupp (1943), Yamaji (1966)
and Takahashi (1981).

Depending on the concentration of cells in the sample, 1/2, 1/4 or
1/8 of the bottom plate was counted. Theoretically, a statistically
correct count has been accomplished after counting between 100 - 300
cells (K. O. Coyle and L. Schandelmeier, pers. comm.). Counts are
reported as cells l^{-1}.

RESULTS AND DISCUSSION

I. Fall ice-edge primary productivity:

Solar heating of the Earth's surface is strongly dependent on latitude, decreasing toward the poles, with a minimum in December in the northern hemisphere. In late October in the Chukchi Sea, high storm frequency contributes to reduced insolation as cloud cover increases, and low temperatures induce southward sea-ice advance (Pease, 1981). Winter ice-edge primary productivity is likely to be limited by light, temperature and sometimes nutrient availability. Under similar conditions phytoplankters are known to lower their metabolic rate, become dormant (Slagstad, 1982) or produce spores (Doucette and Fryxell, 1984). During the ice-advance period some phytoplankton cells are probably incorporated in forming ice (Meguro et al, 1966; Hoshiai, 1977; Palmisano and Sullivan, 1982). Thus, part of the phytoplankton community may overwinter (Buinitsky, 1977).

Specific nitrogen uptake rates ($V(NH_4)$, $V(NO_3)$) measured in the Chukchi Sea ice-edge water column on October 23, 1981 (table 2), are comparable to rates measured during June and July 1981 in the open water over the Bering Sea shelf (Müller-Karger, unpubl. data; Sambrotto, 1983), but are an order of magnitude less than rates measured at the spring ice edge in 1982 and 1983.

A hyperbolic $V(NH_4-N)$ response to incremental ammonium additions

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was found associated with undetectable NH_4-N levels in the water along the ice edge (table 2, figure 2). The slower ammonium specific uptake rates of the community living at 2 m (*in situ* rates estimated by label additions <1 µgat l^{-1}, table 2) may be caused by stress imposed by ice formation and low temperatures at the surface (-0.75°C *vs.* 0°C at 8 m). V_{max}(NH_4-N) estimates were 2.33×10^{-3} h^{-1} at 2 m and 1.29×10^{-3} h^{-1} at the 50% light depth. Half saturation constants at 2 and 8 m were $K_s = 1.77$ and 0.06 µgat NH_4-N l^{-1}, respectively.

Table 2. Inorganic nitrogen specific uptake rates (V_t). Station occupied at 71°21'N, 166°11'W on October 23, 1981, 0900 local time.

Inorganic ^{15}N added µgat l^{-1}	Depth: 2 m Chla: 1.03 mg l^{-1} Ambient nutrient: NH_4: 0.00 µgat l^{-1} NO_3: 5.80 µgat l^{-1} V_t(NH_4) $\times 10^{-3}$ h^{-1}	V_t(NO_3)	Depth: 8 m Chla: 1.16 mg l^{-1} Ambient nutrient: NH_4: 0.00 µgat l^{-1} NO_3: 0.00 µgat l^{-1} V_t(NH_4) $\times 10^{-3}$ h^{-1}	V_t(NO_3)
0.5	0.7372	1.8922	0.8239	0.0809
1.0	0.7139	1.8084	1.1773	0.0647
2.0	1.1049	1.8034	1.5792	0.2060
4.0	1.6953	1.5362	1.2148	0.2198
V_{max}	2.33		1.29	
K_s	1.77		0.06 µgat l^{-1}	

The difference between average nitrate specific uptake rates at 2 m (1.76×10^{-3} h^{-1}) and 8 m rates (0.14×10^{-3} h^{-1}) was probably associated with different ambient nutrient and light levels at the two depths (table 2). Algae at 2 m may have been taking up NO_3-N at V_{max} (figure 3). Because of the non-limiting status of nitrate in the shallow sample and the low uptake rates in the deeper sample, it was not possible to estimate K_s for nitrate.
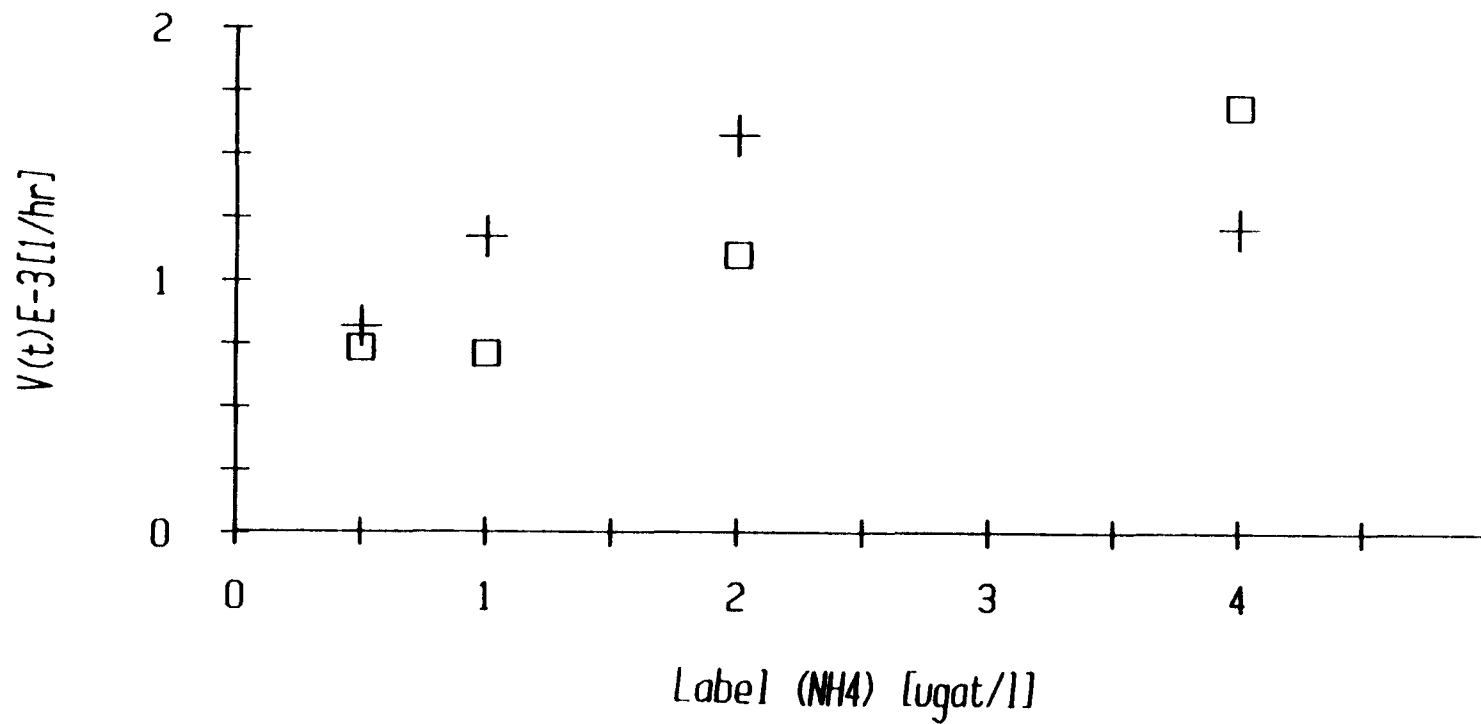
Figure 2. October 1981 serial concentration ammonium uptake rates at the Chukchi Sea ice edge. Squares: 2 m samples incubated at 100% surface irradiance (ambient NH_4-N = 0.0 µM). Crosses: 8 m samples incubated at 50% surface irradiance (ambient NH_4-N = 0.0 µM).
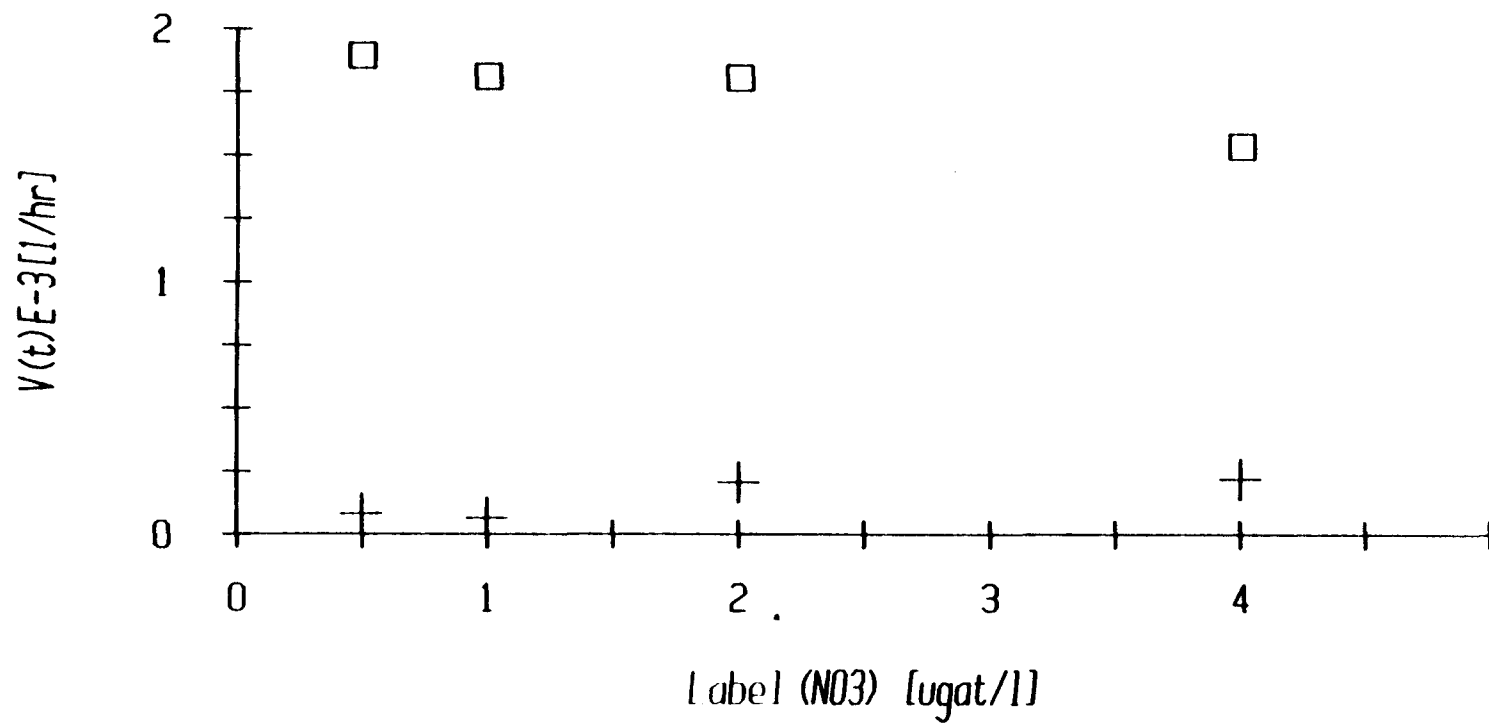
Figure 3.   October 1981 serial concentration nitrate uptake rates at the
Chukchi Sea ice edge.   Squares: 2 m samples incubated at 100% surface
irradiance (ambient NO_3-N = 5.8 µM).   Crosses: 8 m samples incubated
at 50% surface irradiance (ambient NO_3-N = 0.0 µM).

The f-ratio (NO_3-N uptake rate divided by NH_4-N + NO_3-N uptake rates, Dugdale and Goering, 1967) was 0.72 at the surface. Upon addition of 4 μgat $^{15}NH_4$-N l^{-1} the f-ratio fell to 0.48. This is unlikely to occur in situ except as a transient event, or perhaps in waters close to the benthos. Coyle (1981) analyzed fall (September-October, 1980) zooplankton samples from the Siberian Chukchi Sea and found small animals dominant. Grazing pressure may have been less than 1% of primary productivity (Coyle, pers. comm.). Low ammonium levels in the water and low NH_4-N uptake rates also suggest limited grazing in the central Chukchi Sea occurs in the fall.

Phytoplankton cells numbered approximately 5.79×10^9 m^{-2} (in a 40 m mixed layer). Ice 0.08 m in thickness contained 9.10×10^6 cells m^{-2}. The Shannon-Weaver diversity index (Peet, 1974) of the ice community was higher on a per volume basis than that of the water column community, while the equitability (Lloyd and Ghelardi, 1964) of both communities was similar (tables 3, 4). Twenty seven species (lumping all *Chaetoceros* into one group and using it as one species in diversity calculations, since classification to species level was not possible) comprised the ice assemblage as compared to 17 species in the water column. *Nitzschia seriata*, *N. pungens*, *Rhizosolenia delicatula* and *Chaetoceros* sp. dominated the water column and few flagellates were present. Many cells trapped in ice appeared intact, but the fraction of apparently non-viable cells was not quantified. In the ice *Chaetoceros* spp. dominated but *Cylindrotheca closterium* was also common. The concentration of flagellates in ice was twice that found in the water column.

Table 3. Station 006, 5m phytoplankton species counts and community diversity.

Taxa	Cells/l
CENTRIC DIATOMS	
Coscinodiscus perforatus	400
Rhizosolenia delicatula	22,400
alata (auxospore formation)	800
Chaetoceros spp.	21,600
PENNATE DIATOMS	
Thalassionema nitzschioides	2,800
Thalassiothrix delicatula	4,000
longissima	1,200
Asterionella (glacialis) japonica	4,000
Cylindrotheca closterium	8,400
Nitzschia seriata	30,800
frigida	2,800
longissima	10,800
pacifica	400
pungens	22,000
Surirella norwegica	400
DINOFLAGELLATES	
Ceratium sp.	400
Unidentified flagellates (< 9 µm)	7,600
Total cells	144,800
Shannon-Weaver Diversity index	
(Shannon and Weaver, 1963)	3.25
Equitability	
(Lloyd and Ghelardi, 1964)	0.78
Maximum diversity	4.17

NOTE: At least five different species of *Chaetoceros* were lumped under *Chaetoceros* spp.

Table 4. Station 006, ice sample (n=3) species counts and community diversity.

Taxa	Cells/l
CENTRIC DIATOMS	
Coscinodiscus perforatus	400
Corethron Hystrix	400
Leptocylindrus danicus	1,600
Rhizosolenia hebetata	1,600
alata	3,600
styliformis	800
Chaetoceros spp.	34,267
Biddulphia aurita	1,200
Eucampia zoodiacus	1,200
PENNATE DIATOMS	
Campyloneis grevillei	400
Thalassionema nitzschioides	4,400
Thalassiothrix frauenfeldii	400
longissima	2,800
delicatula	3,600
Grammatophora sp.	1,200
Asterionella (glacialis) japonica	7,200
Navicula sp.	400
Cylindrotheca closterium	10,667
Nitzschia section *fragilariopsis*	1,600
seriata	3,067
bilobata	400
longissima	5,467
pungens	5,467
Unidentified diatoms	6,000
DINOFLAGELLATES	
Ceratium sp.	400
Distephanus speculum (Chrysophyta)	400
Unidentified flagellates (< 9 µm)	14,800
Total cells	113,735
Shannon-Weaver Diversity index	
(Shannon and Weaver, 1963)	3.64
Equitability	
(Lloyd and Ghelardi, 1964)	0.77
Maximum diversity	4.75

NOTE: At least five different species of *Chaetoceros* were lumped under *Chaetoceros* spp.

In October 1981, chlorophyll $\underline{a}$ concentration in the northern Bering and Chukchi Seas ranged from .90 to 9.00 mg Chl.$\underline{a}$ m^{-3}. Patchy maxima were seen in the Bering Strait. The information available is not sufficient to establish whether this is a local phenomenon. Higher phytoplankton biomass in the Strait is reported previously (Dawson, 1965; Arsenyev and Voytov, 1968; Taniguchi, 1969; McRoy, Goering and Shiels, 1972; McRoy and Goering, 1974a, 1974b), and may be related to local hydrology (Aagard and Coachman, 1975).

Along the ice edge, chlorophyll $\underline{a}$ ranged from 1.0 to 3.0 mg m^{-3}. Assuming a C:Chl$\underline{a}$ ratio of 35:1 for relatively unhealthy phytoplankton (Parsons et al, 1977) and a C:N ratio of 8:1 (atoms, Banse, 1974), absolute nitrogen uptake was 0.2 µgat NH$_4$-N l^{-1} d^{-1} and 8x10^{-2} µg-at NO$_3$-N l^{-1} d^{-1}. At these rates, it would take about 71 days to deplete surface nitrate and over 20 days to double cellular nitrogen.

II. Spring oceanographic observations in the ice-edge habitat:

The distribution of physical-, biological- and chemical-oceanographic variables in the spring 1982 Bering Sea ice edge was generally similar to that observed previously (figures 4, 5, 6), even though climatic differences between 1982 and 1975-1977 were great (Alexander and Cooney, 1979; Alexander and Niebauer, 1981; Niebauer et al, 1981). Niebauer and Alexander (in prep.) discuss the 1982 ice-edge zone. However, physical oceanographic and meteorological conditions at the Bering Sea ice edge differed drastically between spring 1982 and spring 1983. In late April 1983 the ice edge was over 380 Km further north than in early May 1982 at the longitude of Nunivak island (166°W,

figure 1). Large interannual (1976-1979) variations in maximum ice
extent have been noted before (Niebauer and Alexander, in prep.).

Between March 30 and May 1, 1982, the ice edge was relatively
stationary and near normal maximum (Navy-NOAA Joint Ice Center, Naval
Polar Oceanography Center, Suitland facsimiles). Around 27 April 1982
large polynyas formed in the southeastern Bering Sea-Bristol Bay area
under 15-25 Kn winds from the NNW. On May 1 air temperature was between
-5 and -2°C with a high wind chill factor, and grease ice (a thin layer
of new ice slush) formed in the sampling area. By May 3, 1982,
north-central Bering ice cover was less than 4/10 (areal coverage) and
Bristol Bay coasts became partially ice-free (polynyas not shown in
figure 1). Between May 7-11 wind direction changed to SSW (0-7 Kn,
0.5°C). The 18 May 1982 ice-edge position was similar to that of late
April, 1983 (figure 1).

Maximum ice extent in January - March, 1983, approximated the May
4, 1982, ice-edge contour of figure 1 (normal maximum extent, Overland
and Pease, 1982). An early retreat occurred between April 1 and April
26, 1983, to north of Nunivak island (figure 1). Soon after May 3,
1983, the Bering Sea coasts including Norton Sound became almost
ice-free (less than 3/10 cover), and the ice edge became extremely
irregular.

Late April 1983 cross sections frequently showed homogeneous
vertical density profiles related to tidal upwelling close to the 60 m
isobath (figures 7, 8c). Density decreased towards the north with water
column depth (figure 11c). Low shallow-water-column sigma-t (<80 m
depth; <25.0 sigma-t units E of St. Matthew Island: figure 8c; <25.6

sigma-t units N and W of St. Matthew Island, figures 9c, 10c) compared
to deep (bottom depth >80 m) Bering sigma-t values (>26.0 sigma-t units,
figures 9c, 10c, 11c) suggest that the early 1983 ice retreat was caused
by a rapid, massive, ice thaw. Ice retreat and continuous high winds
precluded stabilization as strong as seen in 1982 (average mixed-layer
depth at all stations was 32 m in 1983, compared to 22 m in spring 1982,
assuming that both sampling areas and periods are similar - see figure
1). The uniform salinity/density gradient with depth in the 1983
sections (figures 8c, 9c, 10c, 11c) suggests that late April - early
May, 1983, stable meltwater structures (cf. figure 6c, 1982, but at a
smaller scale) were transient, and that breakup of the ice-meltwater
layer diluted the more saline deeper waters. Chlorophyll $\underline{a}$
concentration increases were associated with the gradual density changes
with depth (figures 8d, 9d, 10d). The chlorophyll $\underline{a}$ concentrations seen
in late April 1983 (1-10 mg Chl$\underline{a}$ m^{-3}) were, however, not of bloom
proportion (>20 mg Chl$\underline{a}$ m^{-3}, cf. figures 6d, 11d). Fast plant growth
may have occurred in the transient surface meltwater structures, and the
cells mixed deeper by wind action. The phytoplankton would thus
experience lower irradiances and net productivity would decrease. Low
water-column chlorophyll $\underline{a}$ may have also been the result of
light-limited phytoplankton growth independent of prior development of a
stable upper-water-column structure.

Continuous surface chlorophyll $\underline{a}$ measurements conducted in 1982
(figure 4) show the ice-edge bloom in relation to ice position. The
wind reversal of May 7-10, 1982, pushed the ice edge 100 Km shoreward
without disturbing the bloom or the meltwater structure (figures 4, 6d,

May 11 transect). In such a situation, shallow meltwater structures (figures 6b, 6c) may not last more than a week, unless a new ice advance/thaw occurs, or insolation is strong enough in May, in which case temperature stratification will ensue. Otherwise the mixed layer depth will increase.

Epontic algal communities were rare in 1982 but ubiquitous in 1983. The colored ice layer varied in thickness from 1 to about 35 cm in 1983. Pigment concentration in the ice ranged from 5-130 mgChla m^{-3}. Slush ice and ice floes may contain over 4×10^3 mgChla m^{-3} (Whitaker, 1977; Alexander and Chapman, 1981; Hoshiai, 1981, 1977). Brown ice is fragile (Buinitsky, 1977), and is probably the first ice to melt or be shaved off in ice floe collisions. The epontic algal community thus released to the water column, and the lower degree of vertical water-column stability in 1983 as compared to 1982, may explain the chlorophyll a patches found on the bottom, at depths ranging from 60 m to 110 m (figures 9d, 10d, 11d).

Shelf nitrate levels were lower in 1983 than in 1982. However, it is not clear if this difference is due to geographical separation of the sampling areas (figure 1). In 1983, NO_3-N concentration exceeded 17 µgat l^{-1} seaward of the 80 m isobath, from 10-12 µgat l^{-1} between the 60 m and 80 m isobaths, but was less than 6 µgat l^{-1} shoreward of the 60 m isobath (figures 8f, 9f, 10f, 11f). This may be normal at the end of winter over the shallow (40-60 m) central Bering Sea (Niebauer et al, 1981), and is probably the result of limited water exchange between the deeper Bering Sea and the shallow shelf, as well as slow nitrification rates due to low winter temperatures. The nitrate

gradient with depth across the shelf was probably accentuated by slow

plant growth throughout the water column in spring 1983. NO_3-N

isopleths reflected sigma-t structure and indicated a deep (>60 m) water

invasion of the shallower shelf along the bottom (figures 8f, 9f, 10f,

11f).

Ammonium distribution did not seem to follow density patterns but

could reflect weak physical mixing (figures 8e, 9e, 10e, 11e). NH_4-N

isopleths intersect the sediments at two points in figure 9e (station

39), figure 10e (station 57, 58) and figure 11e (stations 70-74). This

indicates that shallow shelf (<60 m) NH_4-N may have resulted from

remineralization of recently settled out plant cells in or close to the

sediment. Niebauer *et al* (1981) noticed a tendency of ammonium to

increase in the ice-edge zone after the onset of stratification and

suggest that *in situ* ammonification may be the mechanism.

Stations 2, 7 and 17 (figure 8d) were occupied successively in the

same area during early development of the spring 1983 bloom.

Chlorophyll a rose from less than 1 mg m^{-3} to about 6 mg m^{-3} in 5 days.

Station 72 (figure 11d) was occupied at the same location on 5 May 1983.

The slow chlorophyll a increase (compare with 1982 data: table 9) is

probably associated with higher frequency of mixing events in April-May

1983 as compared to the same period in 1982. Stations (18, 33, 71),

(19, 32, 70) and (20, 31, 69, see Appendix) represent other time series

showing little plant growth between the last days of April and May 5,

1983. These stations were continuously affected by both tidal and wind

mixing since they were close to or shallower than the 60 m isobath (cf.

figure 11d).

Between April 30 (station 41, figure 9d) and May 1, 1983 (stations

45-46, not shown), subsurface (15-20 m) chloropyll $\underline{a}$ levels rose from 6

to 8-11 mg m^{-3} over deep (>100 m) waters. A mixed-layer temperature

increase (approximately 0.3°C) was in part responsible for stability,

suggesting that the developing bloom was in a transitory stage between

ice-edge blooms and open Bering shelf blooms.

A transect parallel to the ice was occupied west of St. Matthew

Island on 2 May 1983 (figure 10). Stations 54, 55 and 56 had less than

1/10 ice cover, stations 57 and 58 had no ice and station 59 had

(4-6)/10 cover. Clorophyll $\underline{a}$ levels were less than 5 mg m^{-3} except at

stations 54 and 55. Looking north (into figure 10d) a 2.0 mgChl$\underline{a}$ m^{-3}

isopleth was found between 20 and 60 m depth. The intrusion over the

shelf of deep Bering Sea water, rich in NO_3-N, is evident from the

sigma-t and NO_3-N + NO_2-N profiles (figure 10f). Waters west of St.

Matthew Island were more saline below 60 m (>32.20 °/∞, figure 10b).

This indicates the relative proximity of these stations (figure 7) to

the shelf break (170 m). Further west of St. Matthew Island the ice

edge extends over still deeper waters (figure 1).

On May 5, 1983, the water column east of St. Matthew Island showed

a weak, relatively uniform, cross-shelf horizontal density gradient

(0.0026 sigma-t units Km^{-1}) with increasing depth (figure 11c). A mixed

layer was present at 15-25 m in this section (differences of 0.05

sigma-t units or 50 g m^{-3} across the MLD), but is masked in figure 11c

by large scale horizontal gradients (vertical exaggeration: X4600).

The effect of insolation on upper water column temperature is apparent

in the 5 May, 1983, transect, where vertical stability was due to both

vertical temperature gradients and salinity differences (figures 11a, b, c). A bloom developed in the period between 22 April and 5 May, 1983, across the shelf east of St. Matthew Island (figure 11d), reducing surface NO_3-N (figure 11f). Phytoplankton must have grown faster than vertical mixing rates to develop the 15-26 mgChl$\underline{a}$ m^{-3} maximum present between 5-30 m, but high concentrations of pigments were seen all the way to the bottom at stations 74 and 75.

Average MLD (NH_4-N + NO_3-N):(PO_4-P) (atoms) for all April-May 1983 stations was 5.3; for February 1983 it was 9.9 (Muench, unp. data.). These ratios suggest that phosphorus was in excess in the mixed layer relative to the average deep oceanic N:P ratio (15:1 at, Redfield et al, 1963), and was not a limiting nutrient at the onset of the ice-edge bloom. Dissolved silica levels were also high.
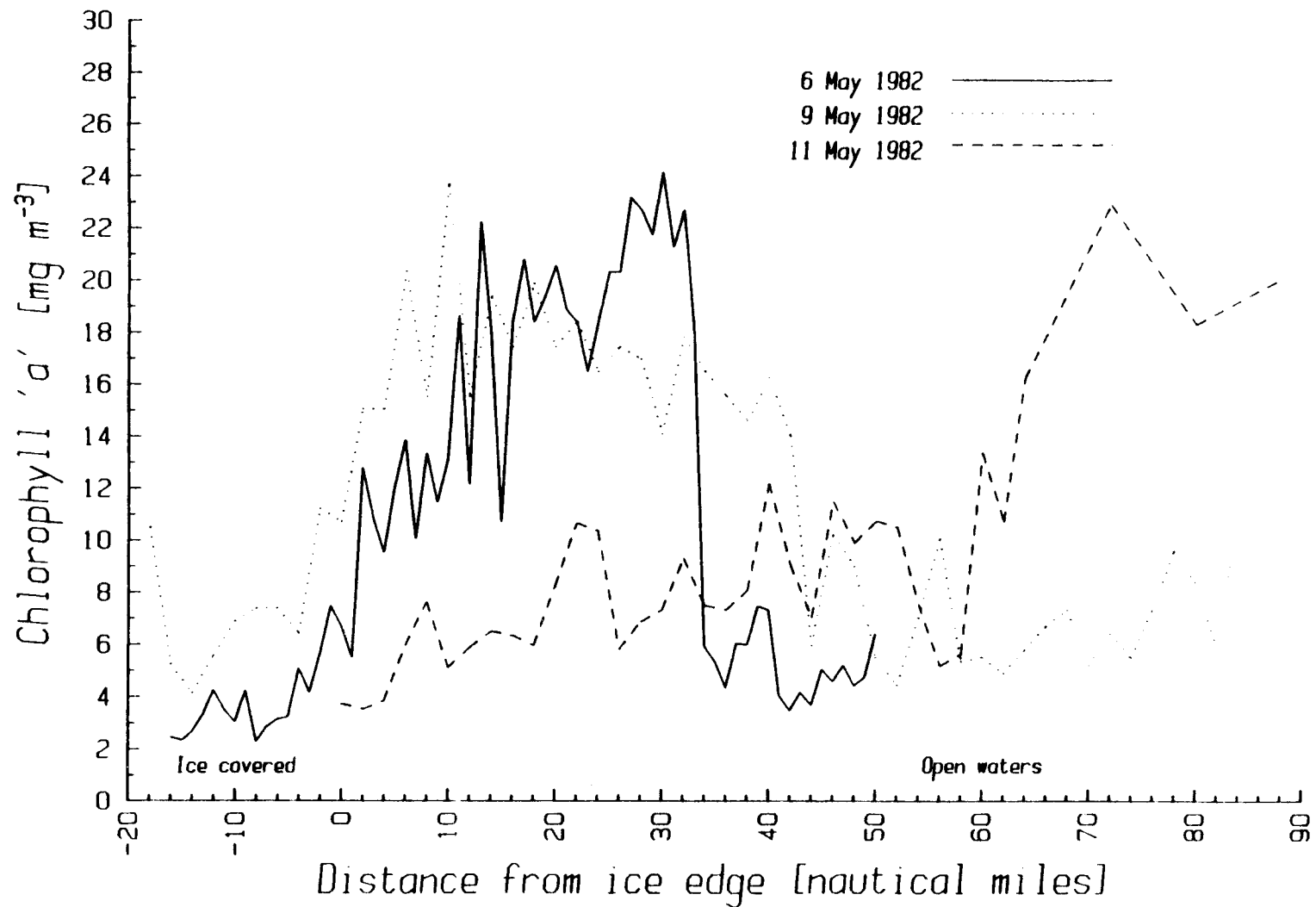
Figure 4. Spring 1982 surface chlorophyll a concentration relative to ice position.
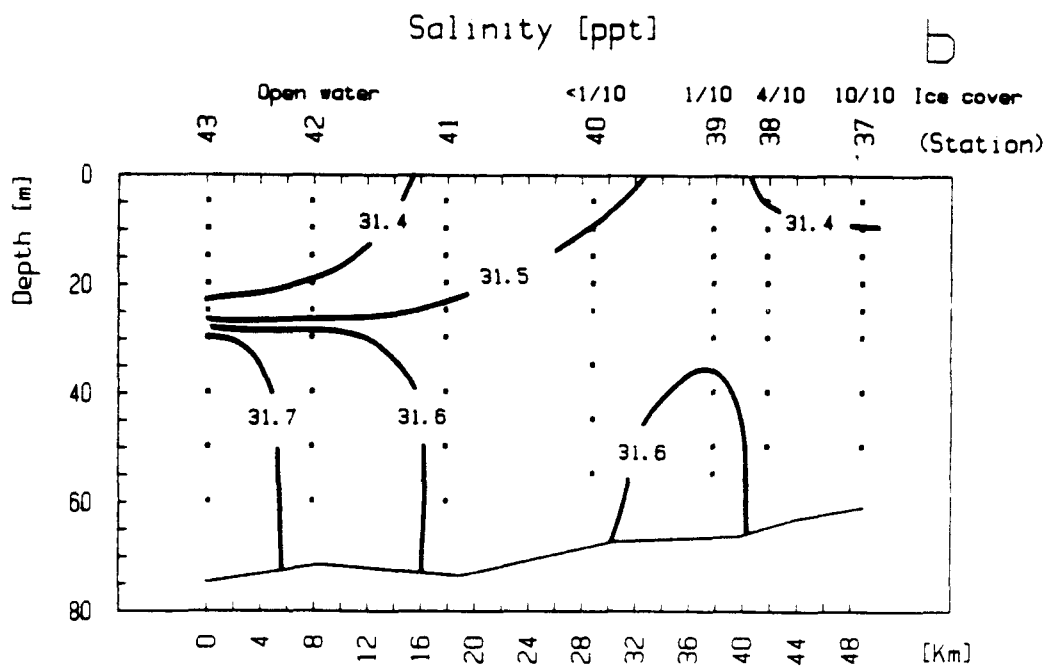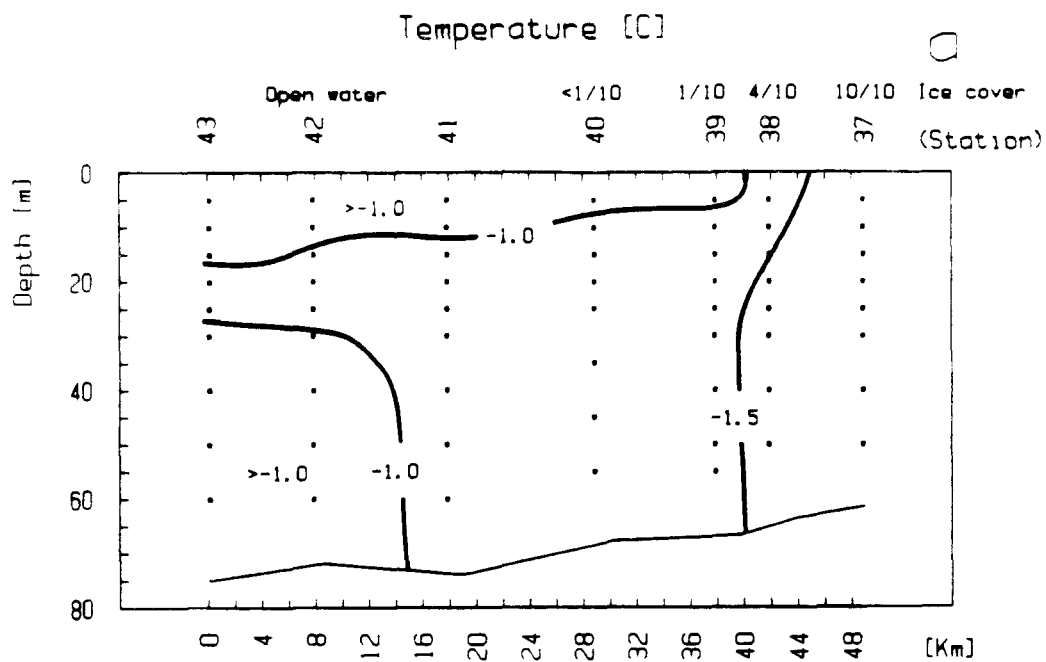
Figure 5a. 4 May 1982 ice-edge cross section:
Temperature (°C); b. Salinity (°/oo).

Sigma-t

C

| Open water | | | <1/10 | 1/10 | 4/10 | 10/10 | Ice cover |
| 43 | 42 | 41 | 40 | 39 | 38 | 37 | (Station) |

Chlorophyll a [ug/l]

d

| Open water | | | <1/10 | 1/10 | 4/10 | 10/10 | Ice cover |
| 43 | 42 | 41 | 40 | 39 | 38 | 37 | (Station) |
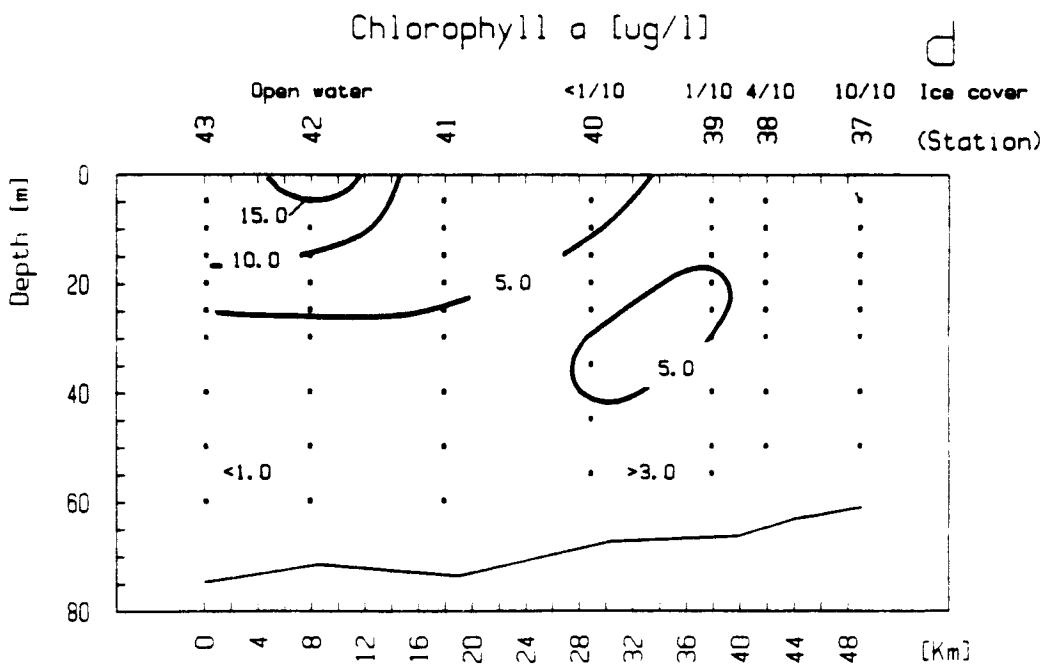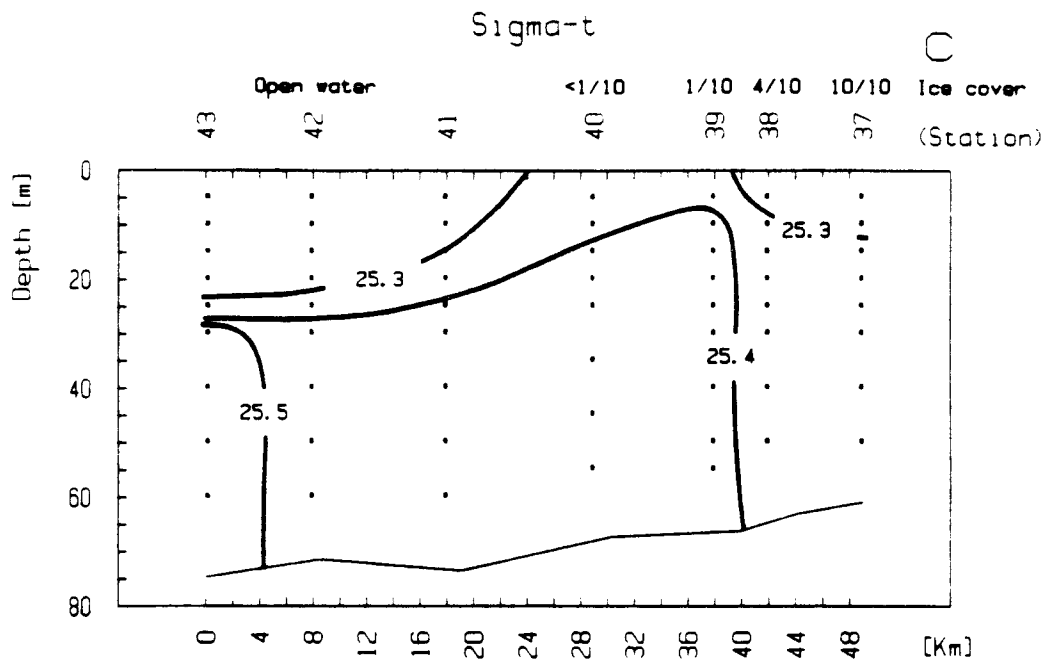
Figure 5c. 4 May 1982 ice-edge cross section:
Sigma-t; d. Chlorophyll a (mg Chl m⁻³).

Ammonium [uM]   e

Figure 5e. 4 May 1982 ice-edge cross section:
Ammonium (ugat N l⁻¹); f. Nitrate (ugat N l⁻¹).
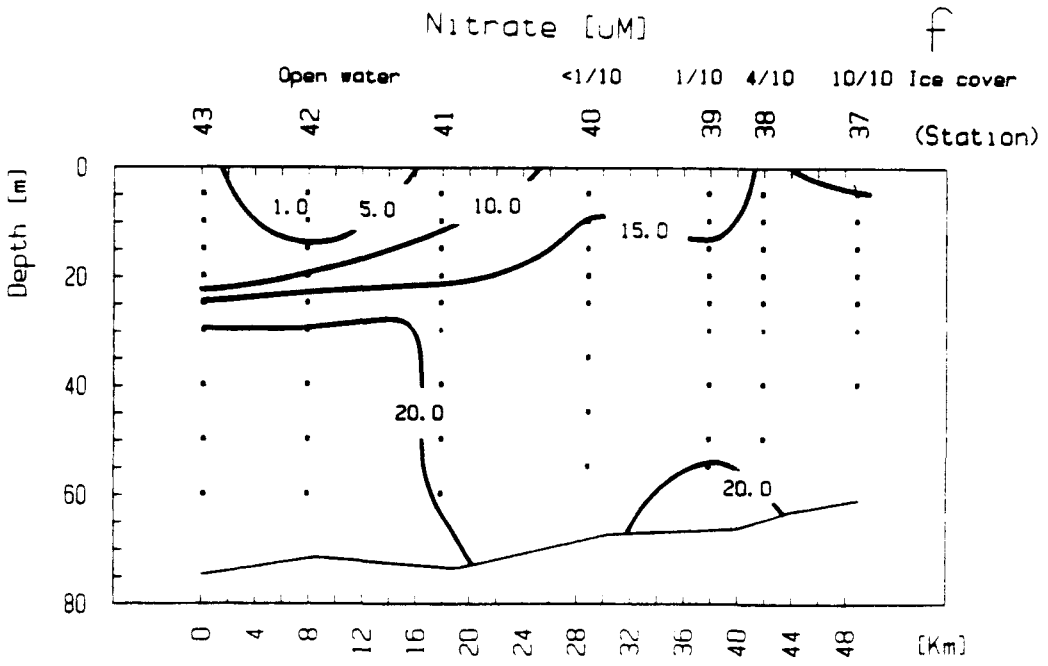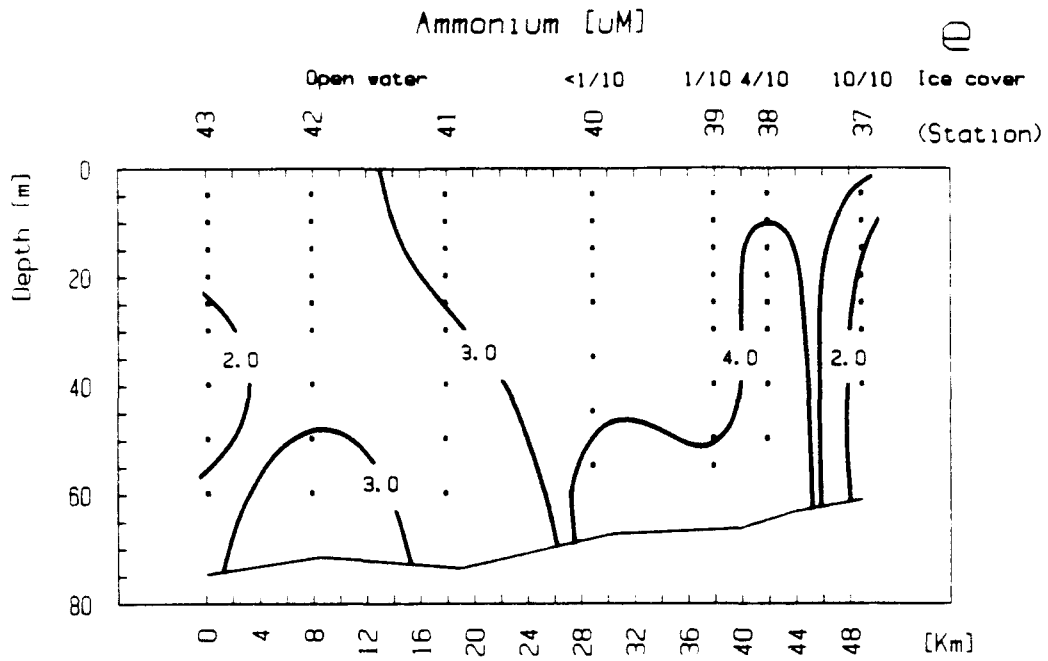
Figure 5e. 4 May 1982 ice-edge cross section:
Ammonium (ugat N l⁻¹); f. Nitrate (ugat N l⁻¹).
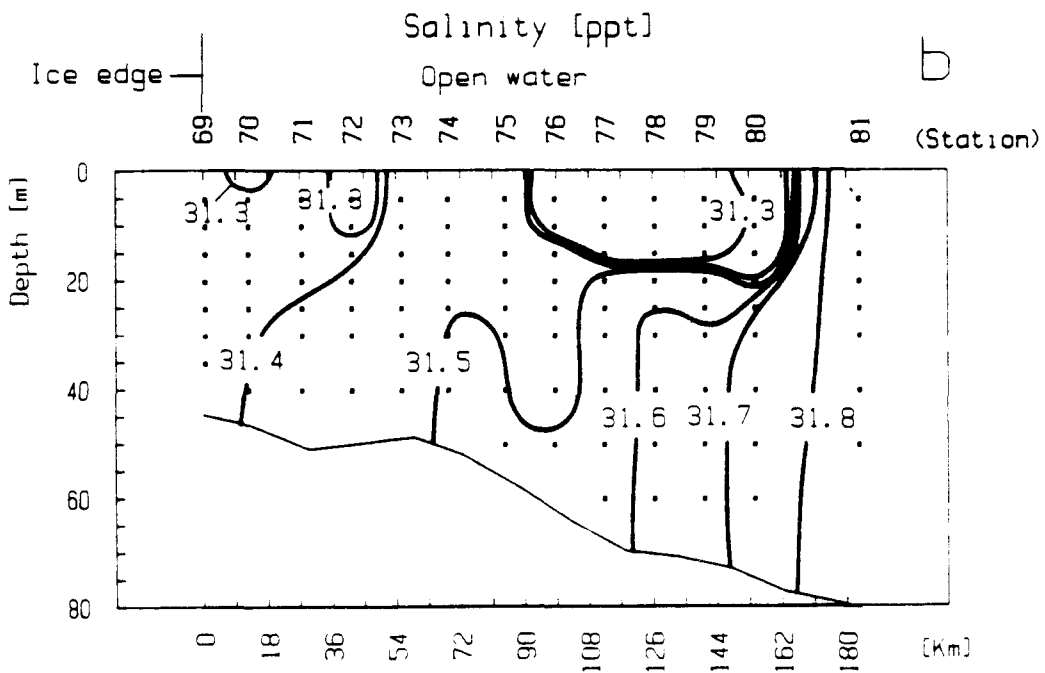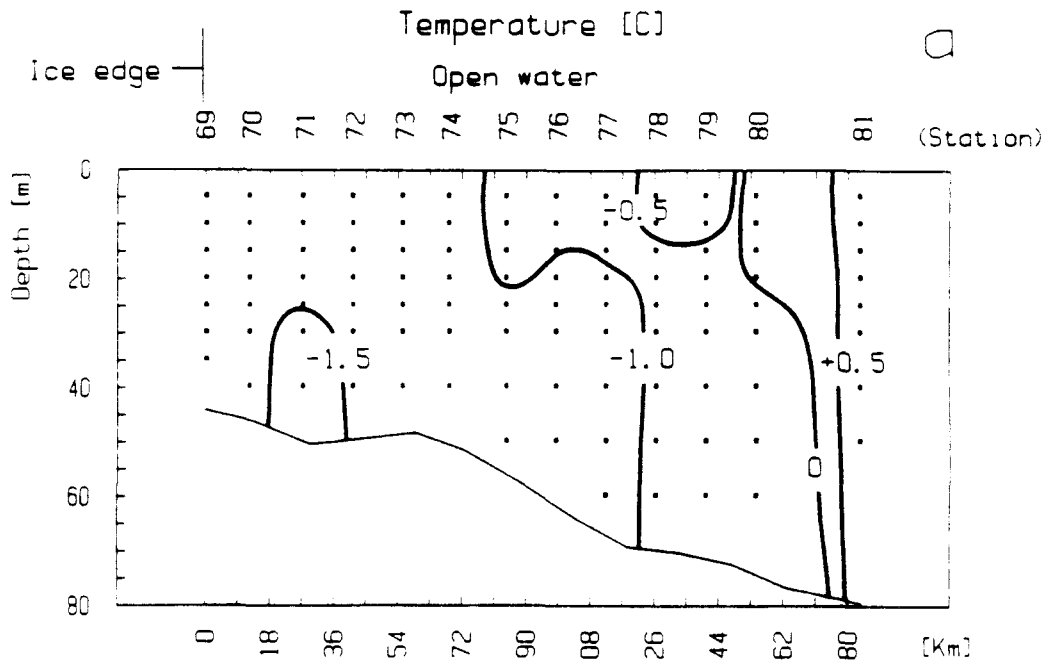
Figure 6a. 11 May 1982 ice-edge cross section:
Temperature (°C); b. Salinity (°/oo).
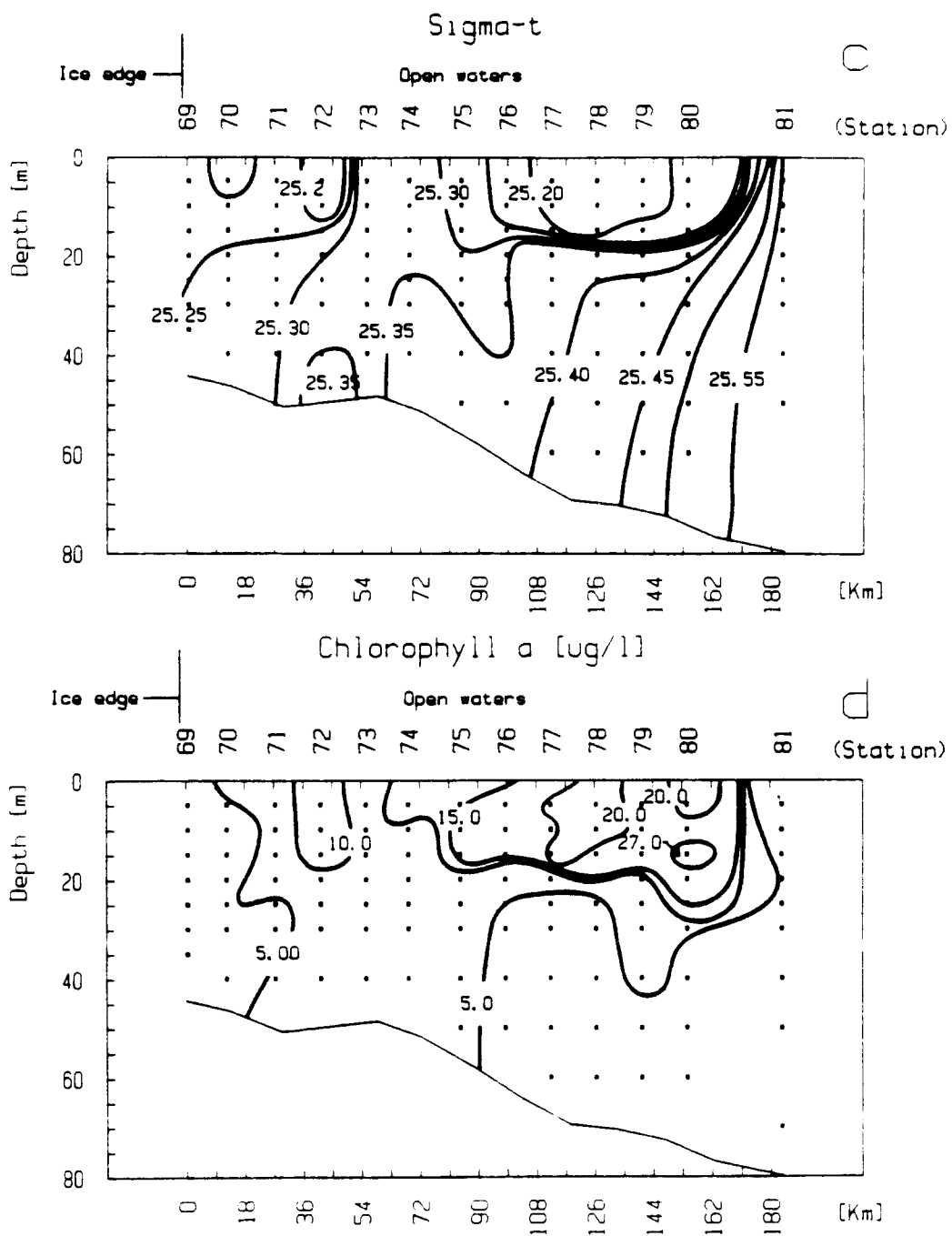
Figure 6c. 11 May 1982 ice-edge cross section:
Sigma-t; d. Chlorophyll a (mg Chl m⁻³).
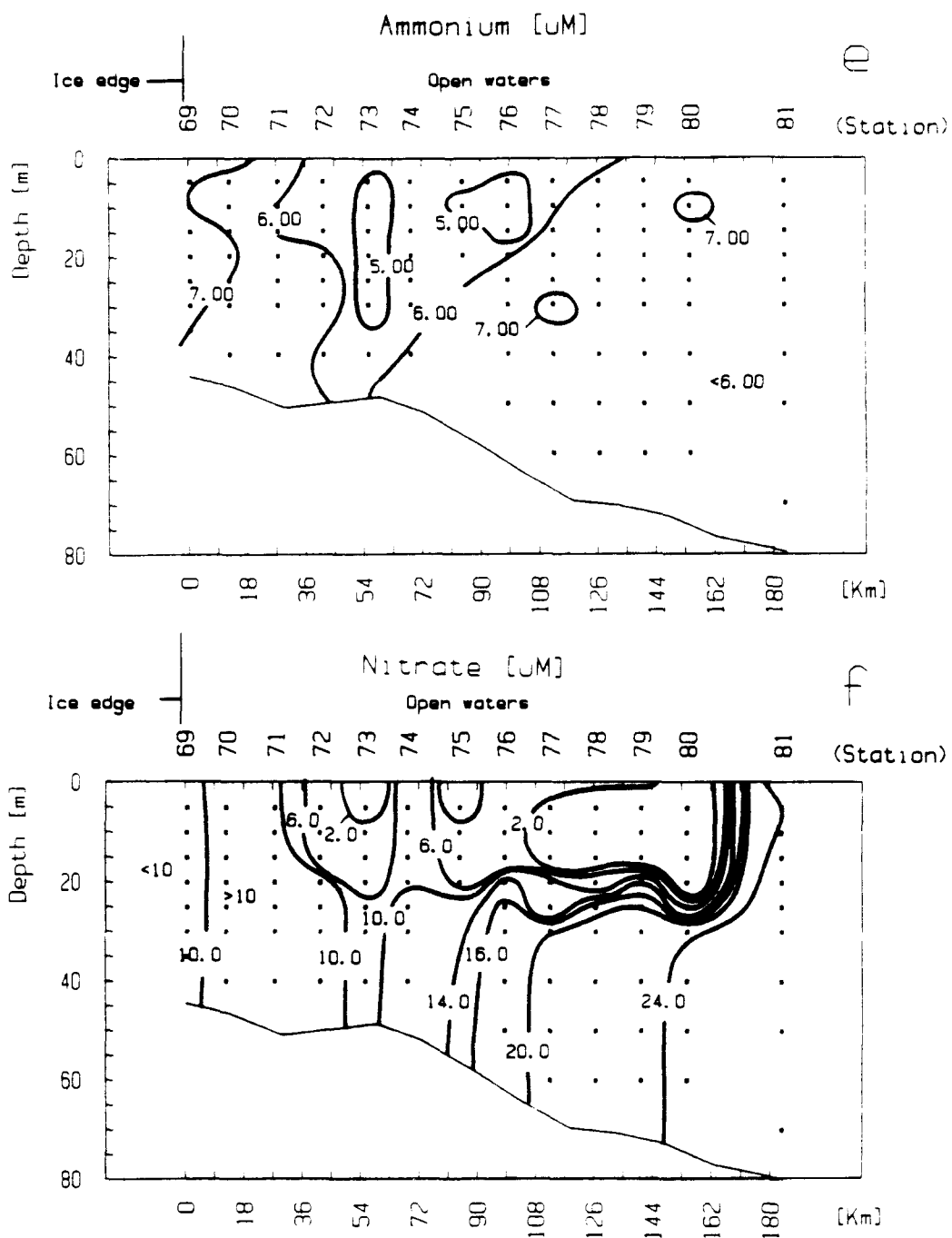
Figure 6e. 11 May 1982 ice-edge cross section:
Ammonium (μgat N $]^{-1}$); f. Nitrate (μgat N $]^{-1}$).
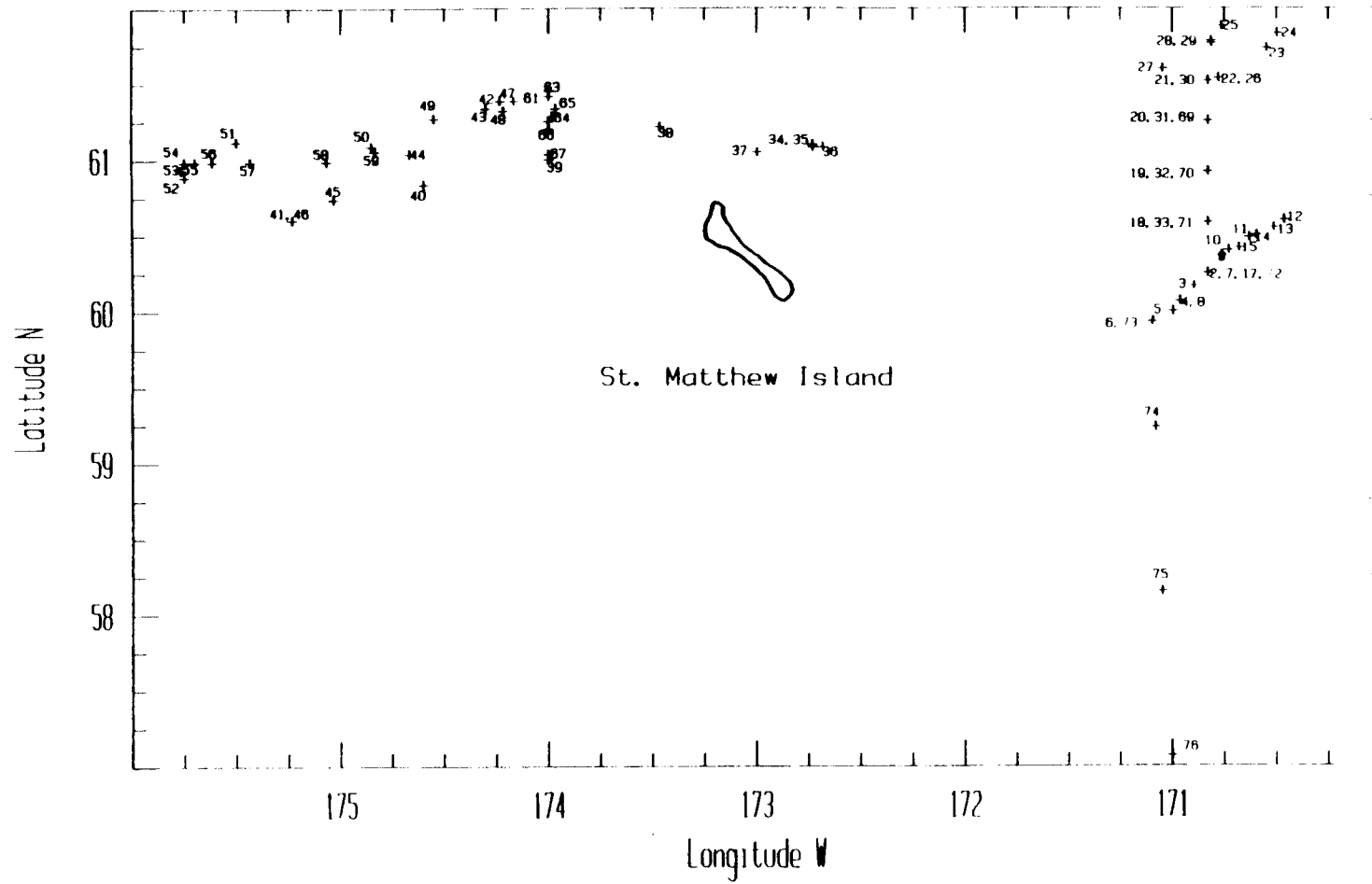
Figure 7. April-May 1983 ice-edge cruise track (referr to following
figures).

Temperature [C]

a

| 0 | 0 | 0 | 0 | 5/10 | Ice cover |
| 17 | 18 | 19 | 20 | 21 22 | 23 24 (Station) |

Depth [m]

-1.3

-1.4 -1.5 -1.6

<-1.6

-1.6

0 17 34 51 68 85 102 119 136 153 170 [Km]

Salinity [ppt]

b

| 0 | 0 | 0 | 0 | 5/10 | Ice cover |
| 17 | 18 | 19 | 20 | 21 22 | 23 24 (Station) |

Depth [m]

31.1

31.0

<30.9

31.0 >30.9

30.9

31.2 30.9

31.3

0 17 34 51 68 85 102 119 136 153 170 [Km]
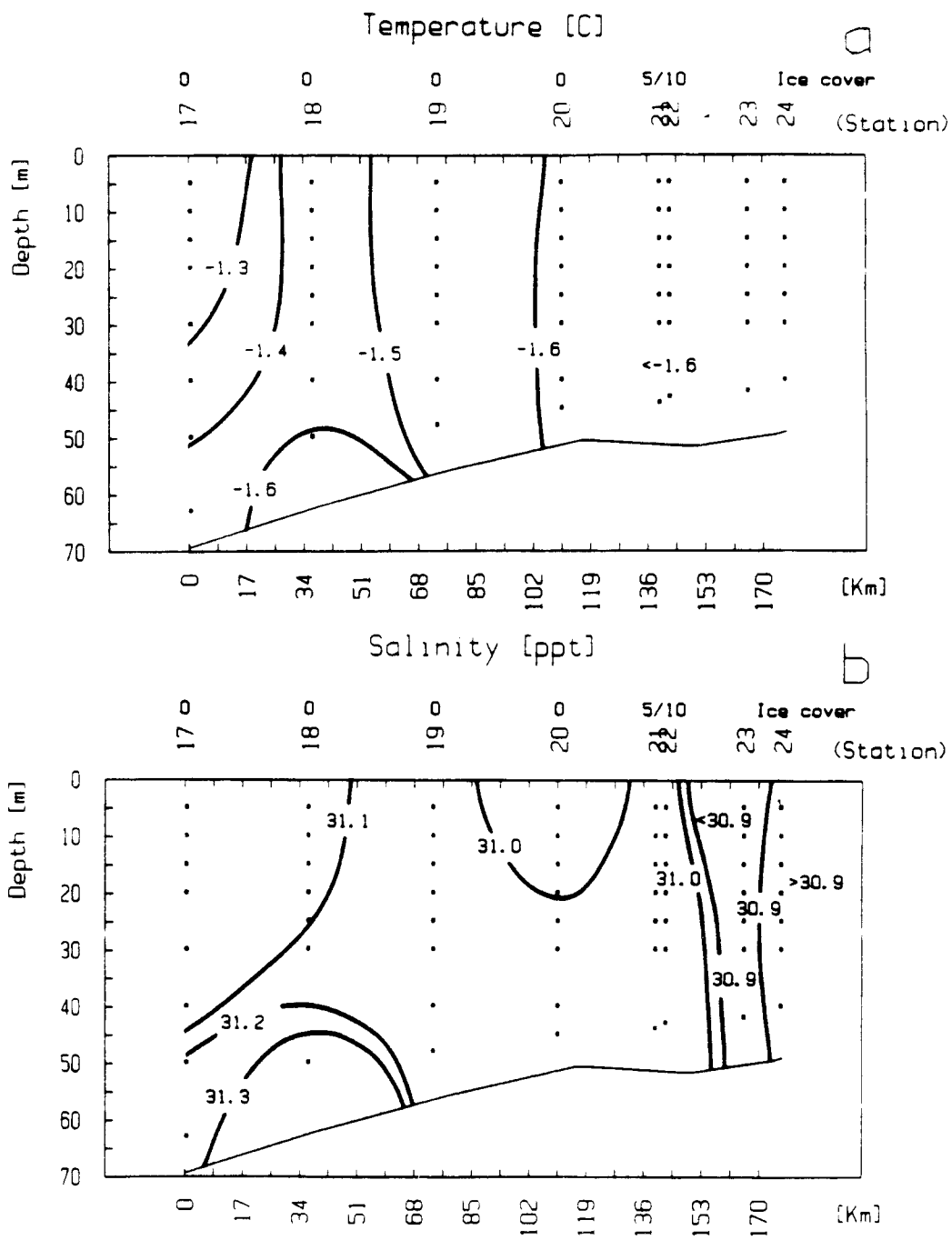
Figure 8a. 27-28 April 1983 ice-edge cross section E of St. Matthew
Island:
Temperature (°C); b. Salinity (°/oo).

Sigma-t
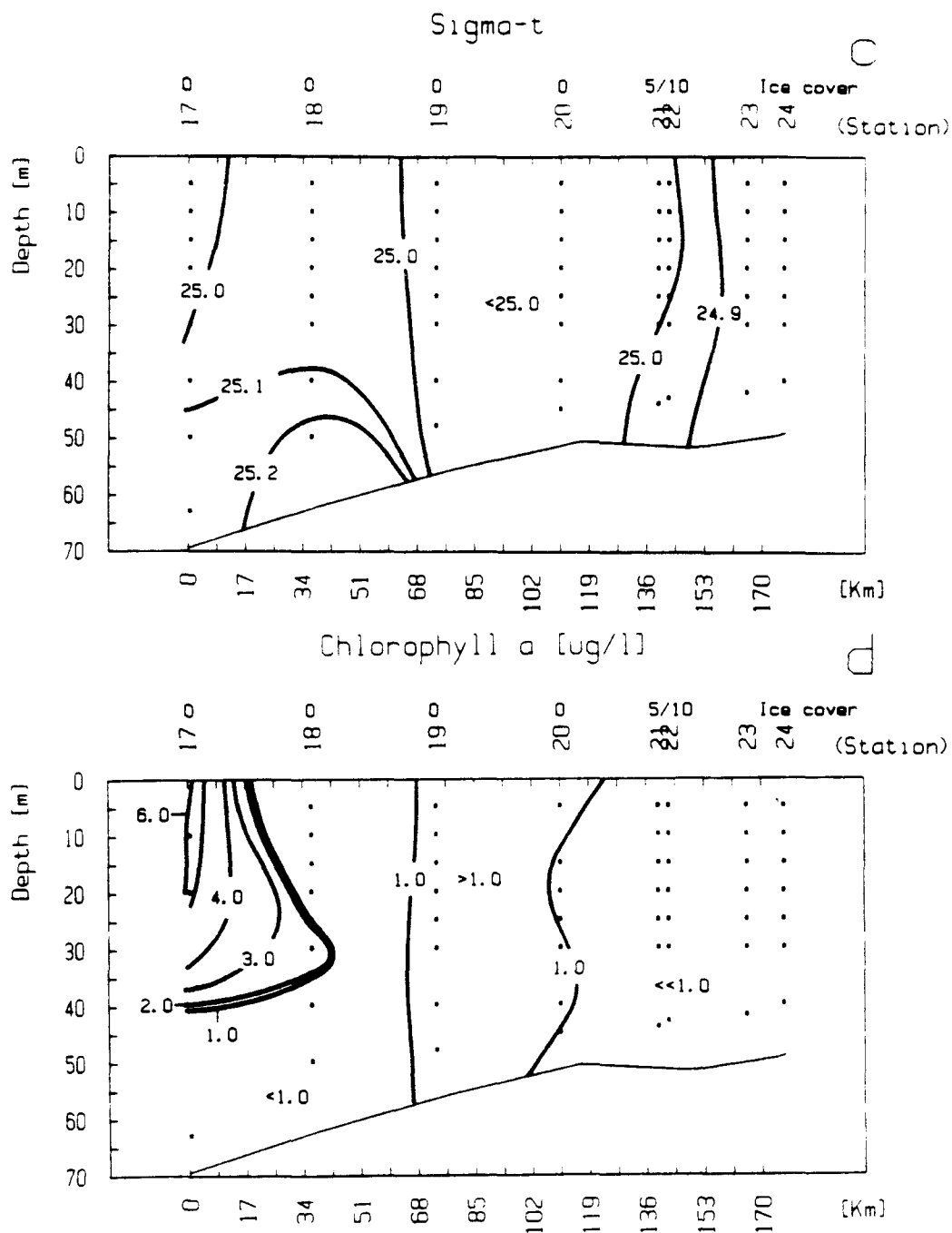
Chlorophyll a [ug/l]

Figure 8c.   27-28 April 1983 ice-edge cross section E of St. Matthew
Island:
Sigma-t;   d.   Chlorophyll a (mg Chl m^{-3}).
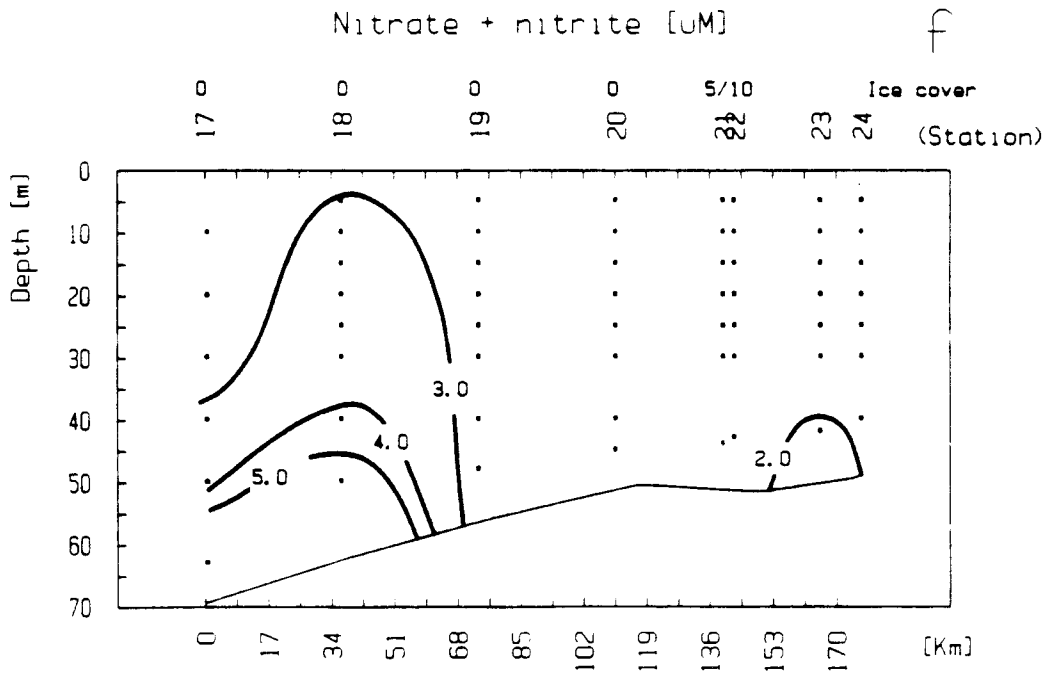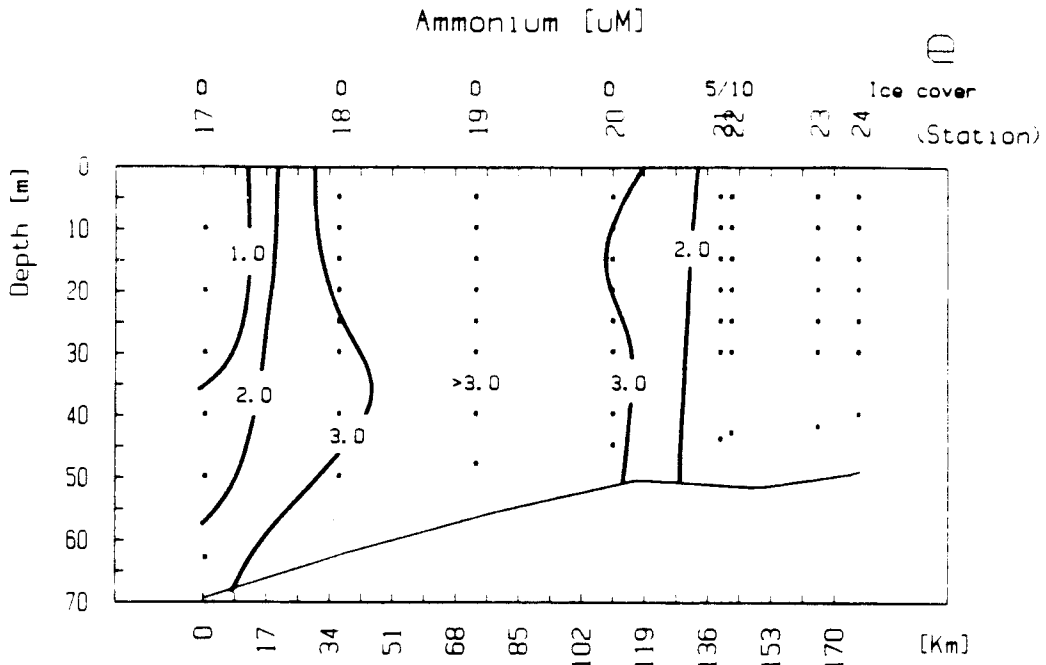
Figure 8e. 27-28 April 1983 ice-edge cross section E of St. Matthew
Island:
Ammonium (ugat N l⁻¹); f. Nitrate + nitrite (ugat N l⁻¹).
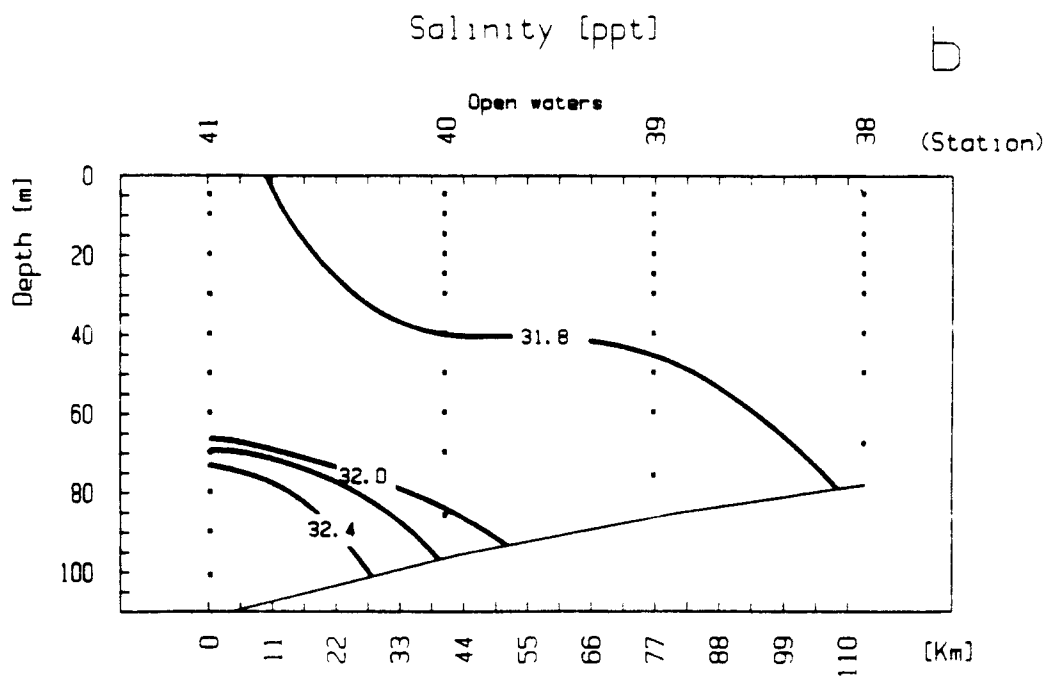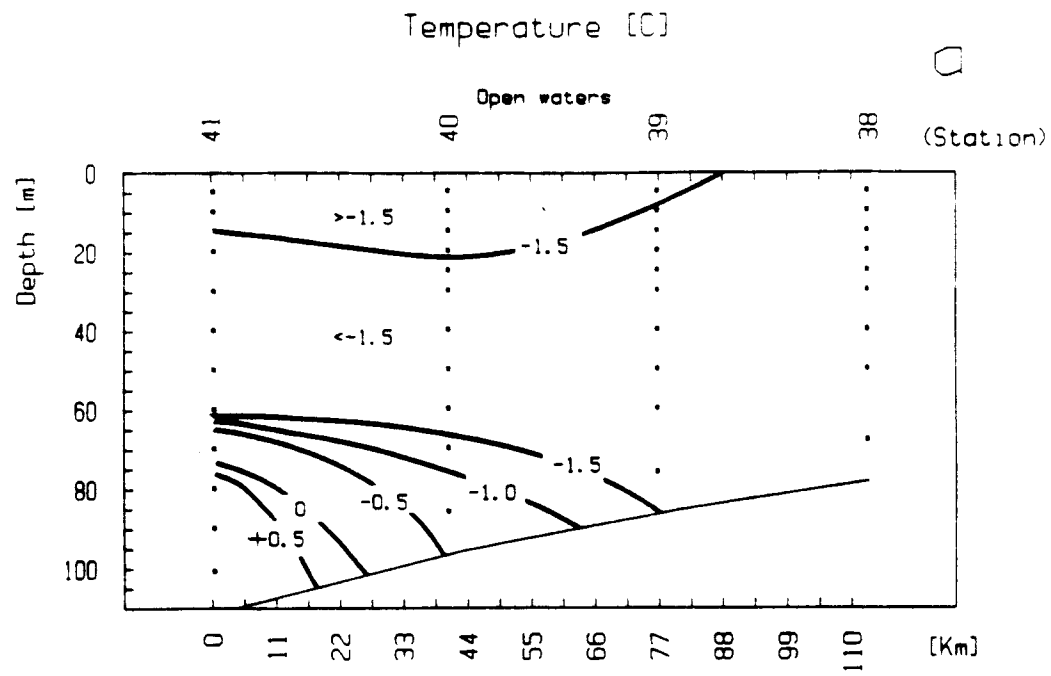
Temperature [C]

Figure 9a. 30 April 1983 ice-edge cross section NW of St. Matthew Island:
Temperature (°C); b. Salinity (°/oo).
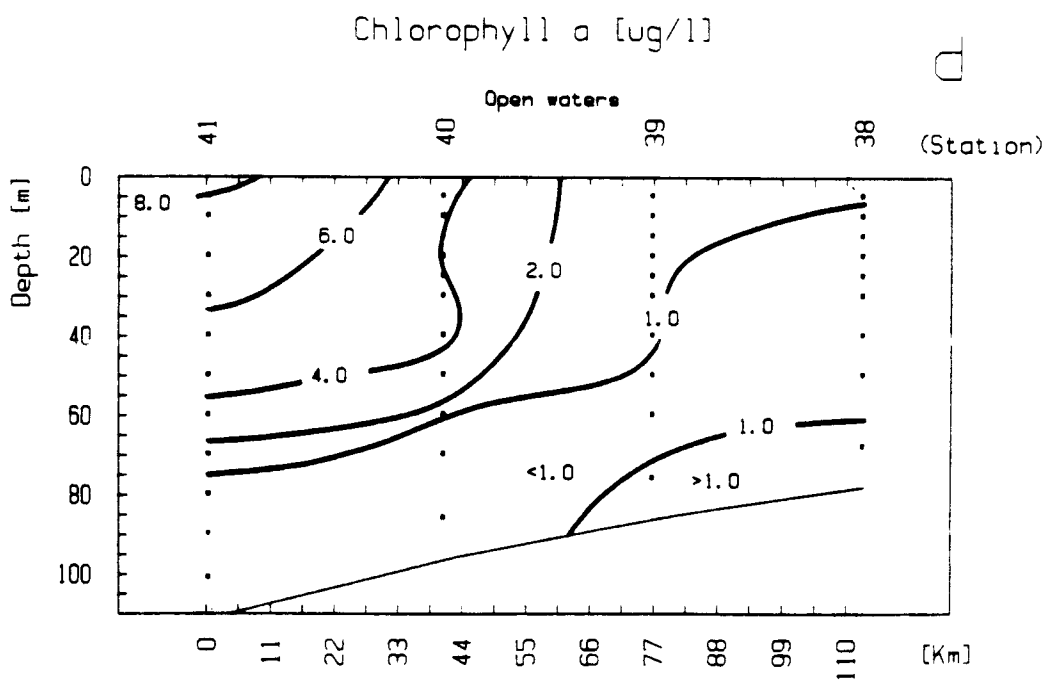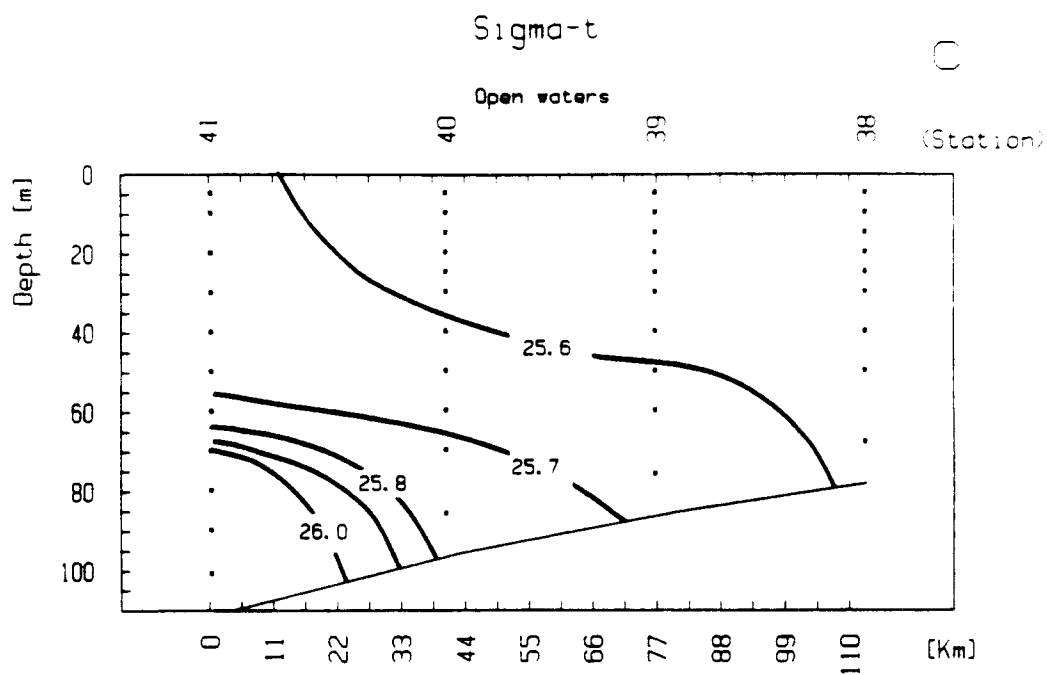
Figure 9c. 30 April 1983 ice-edge cross section NW of St. Matthew
Island:
Sigma-t; d. Chlorophyll a (mg Chl m⁻³).

Ammonium [uM]

Open waters

41   40   39   38   (Station)

Nitrate + nitrite [uM]

Open waters

41   40   39   38   (Station)
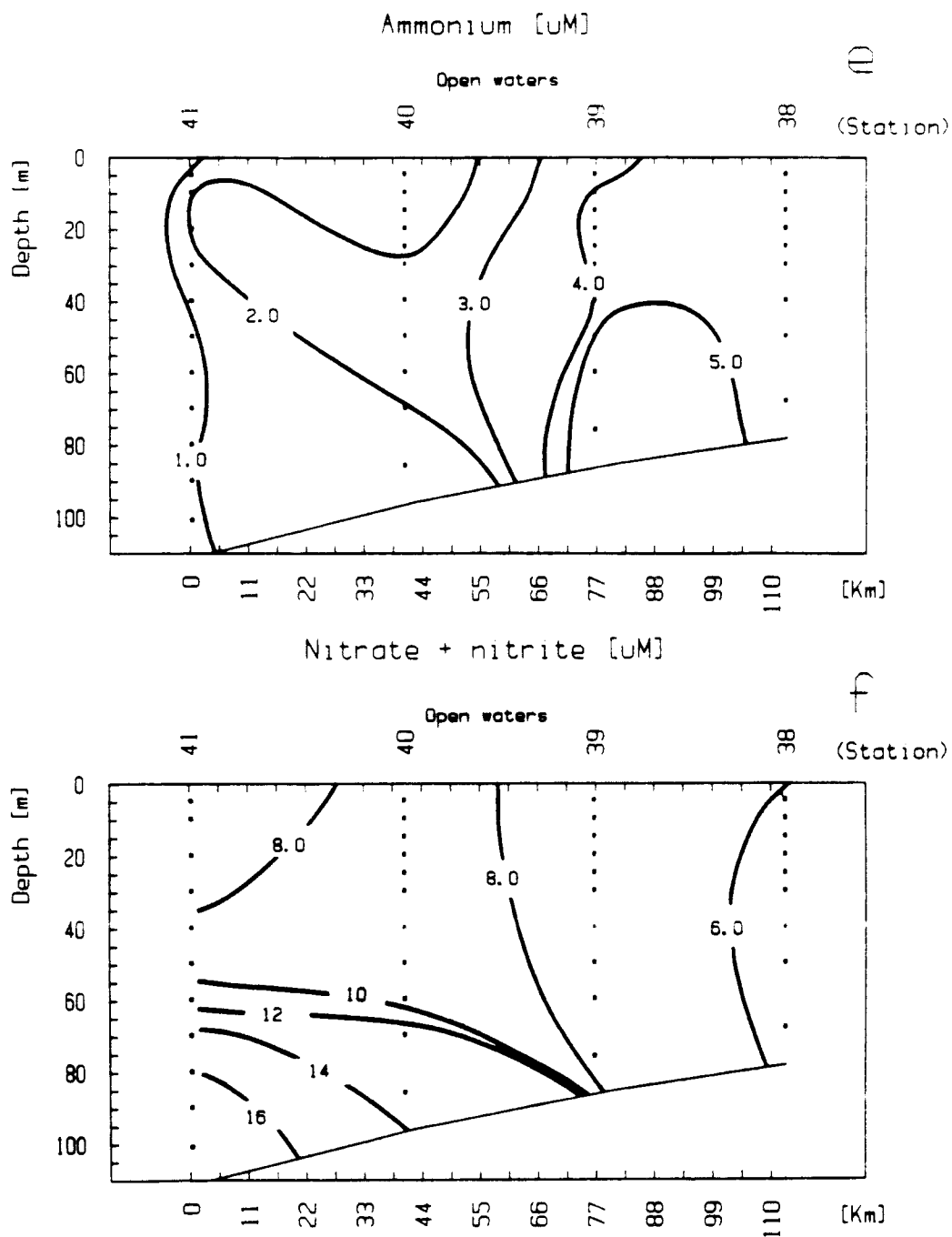
Figure 9e. 30 April 1983 ice-edge cross section NW of St. Matthew
Island;
Ammonium (µgat N l⁻¹); f. Nitrate + nitrite (µgat N l⁻¹).

49
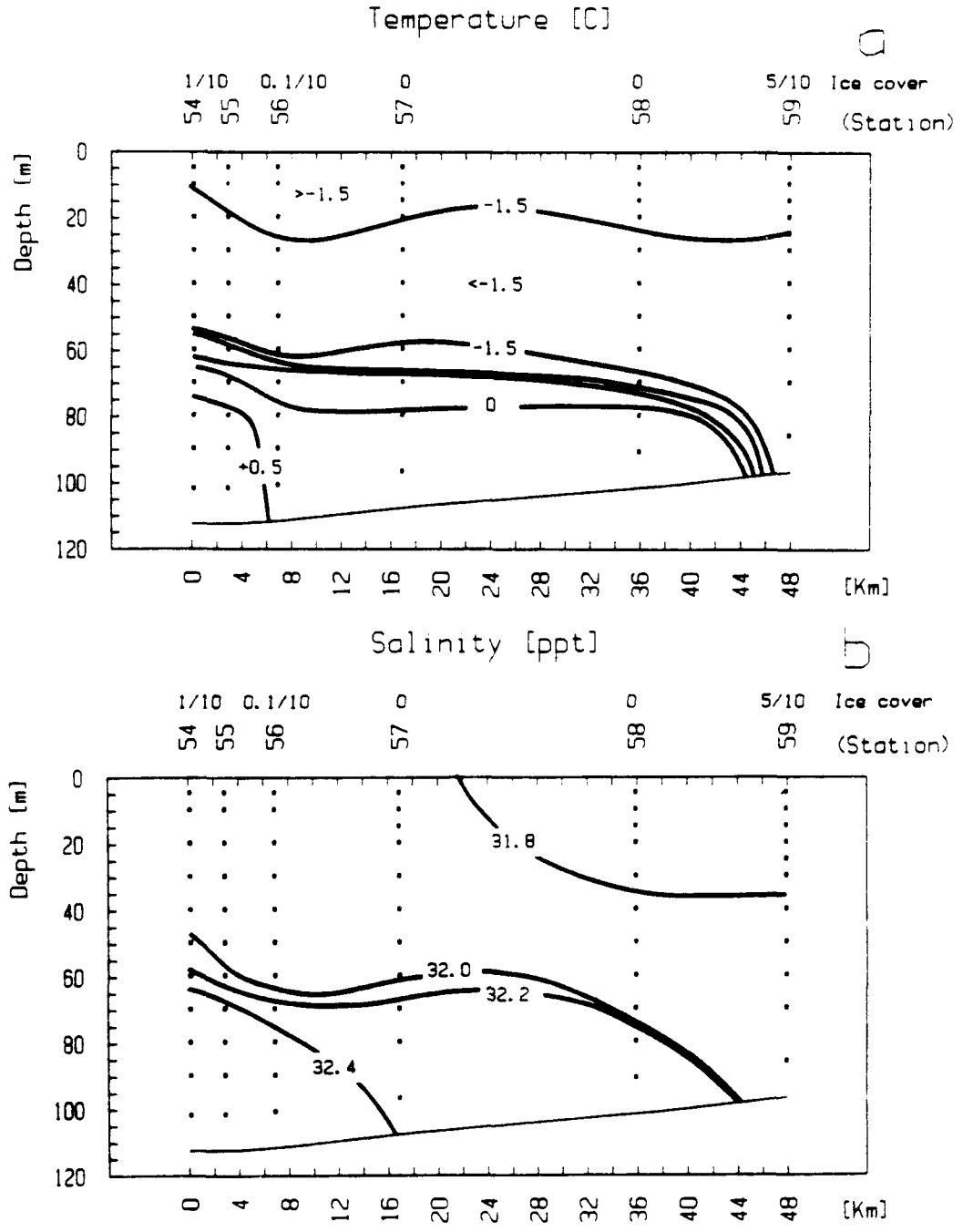
Figure 10a. 2 May 1983 ice-edge cross section W of St. Matthew Island:
Temperature (°C); b. Salinity (°/oo).

Sigma-t
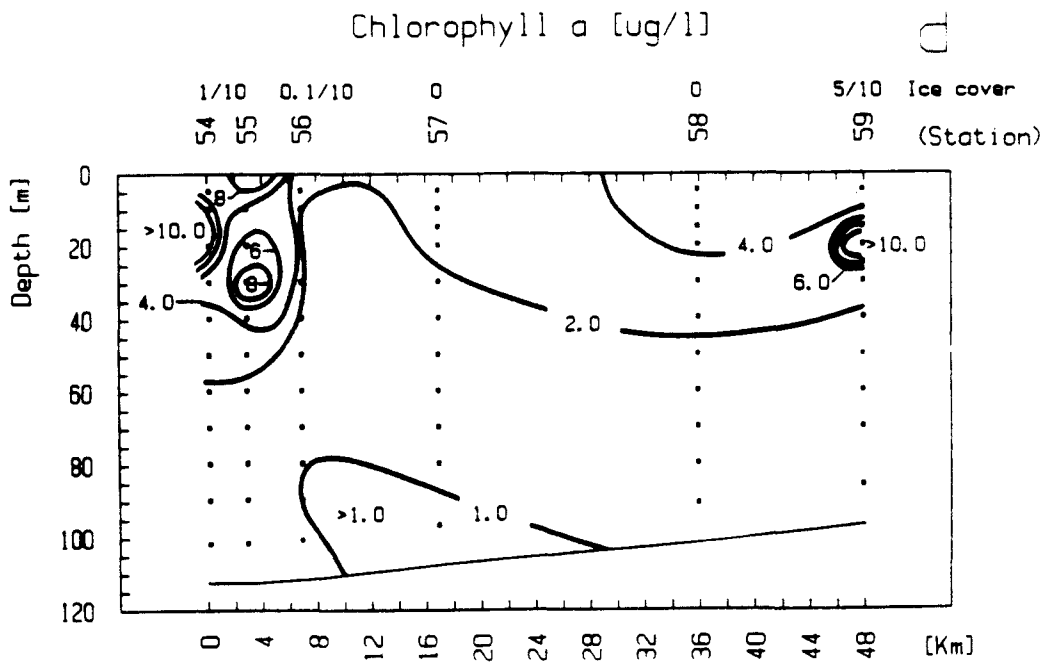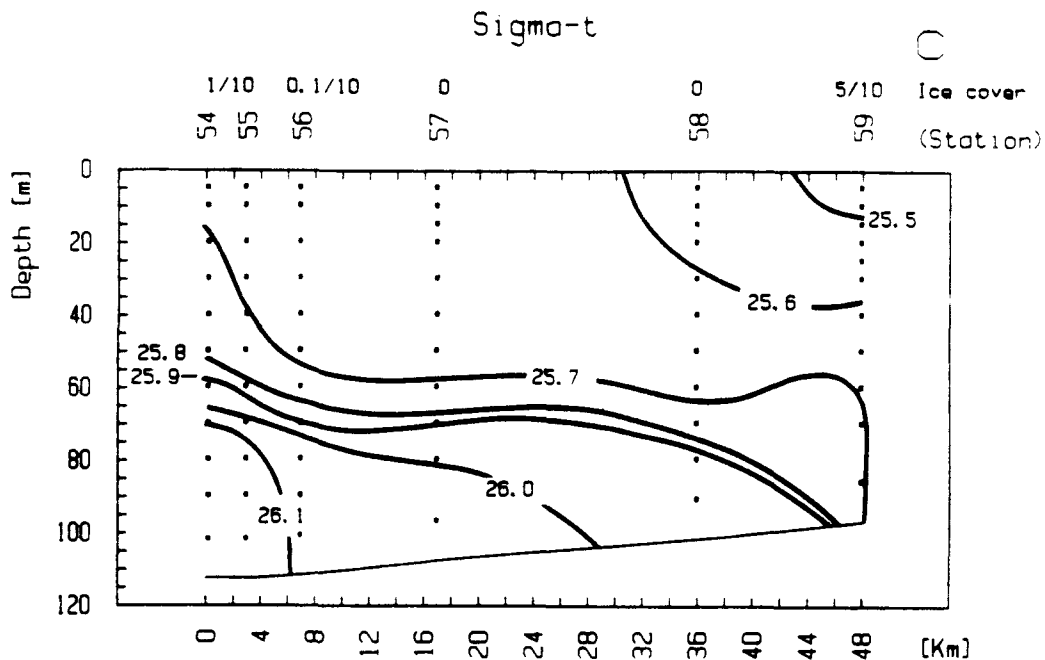
Chlorophyll a [ug/l]

Figure 10c. 2 May 1983 ice-edge cross section W of St. Matthew Island: Sigma-t; d. Chlorophyll a (mg Chl a⁻³).
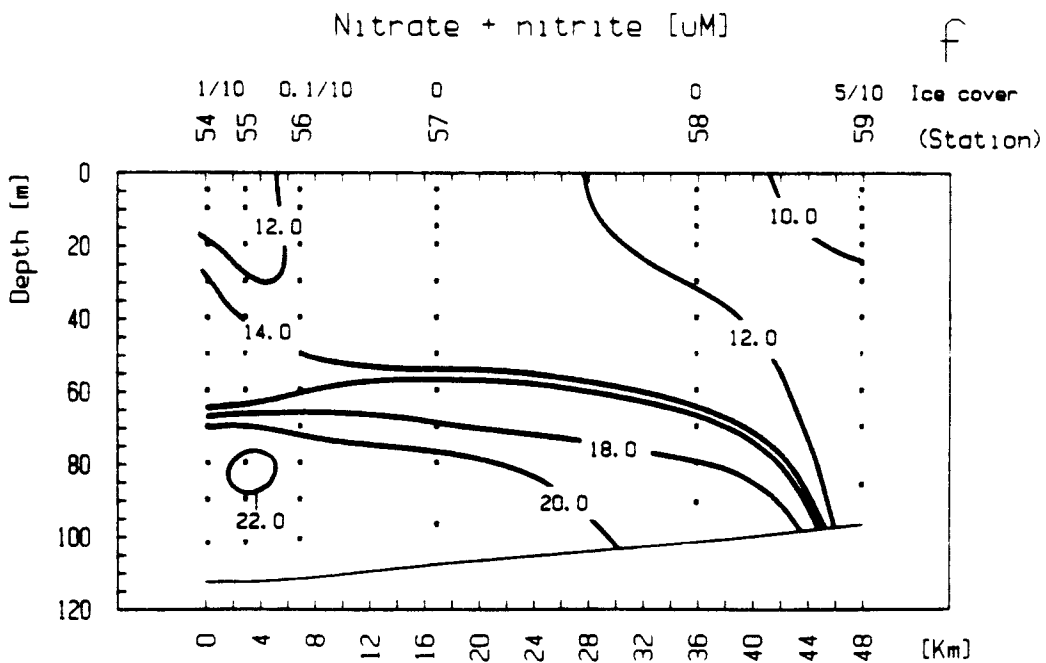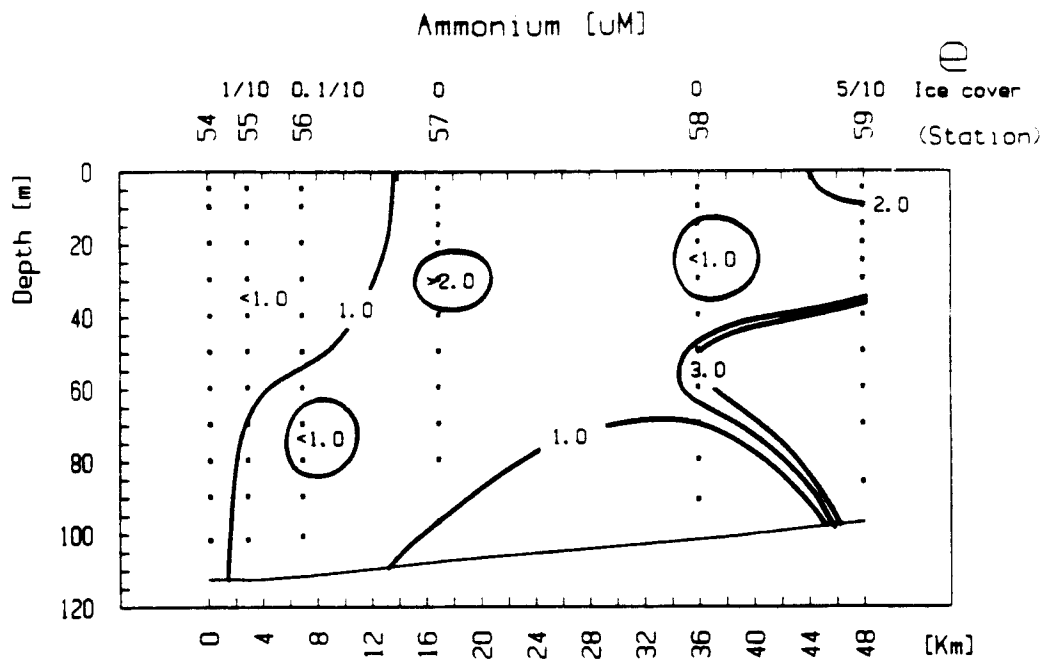
Figure 10e. 2 May 1983 ice-edge cross section W of St. Matthew Island;
Ammonium (µgat N l⁻¹); f. Nitrate + nitrite (µgat N l⁻¹).
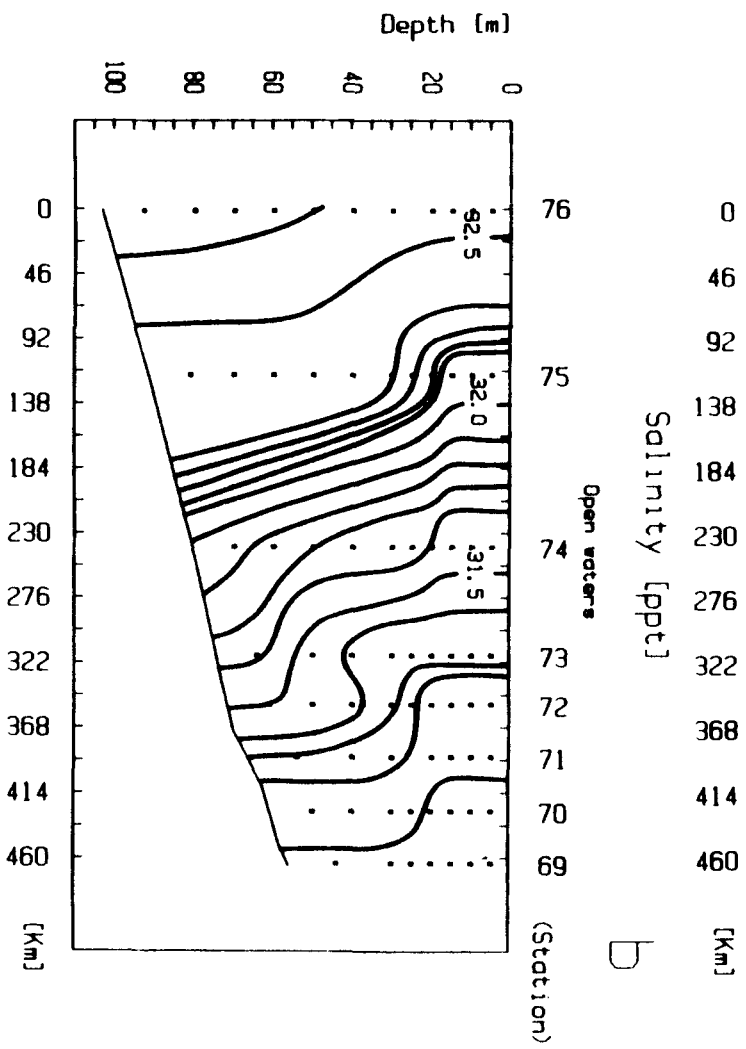
Figure 11a. 5 May 1983 ice-edge cross section E of St. Matthew Island: Temperature (°C); b. Salinity (°/oo).

Temperature [C]

Sigma-t

c

(Station)

Open waters

Chlorophyll a [ug/l]

d

(Station)

Open waters
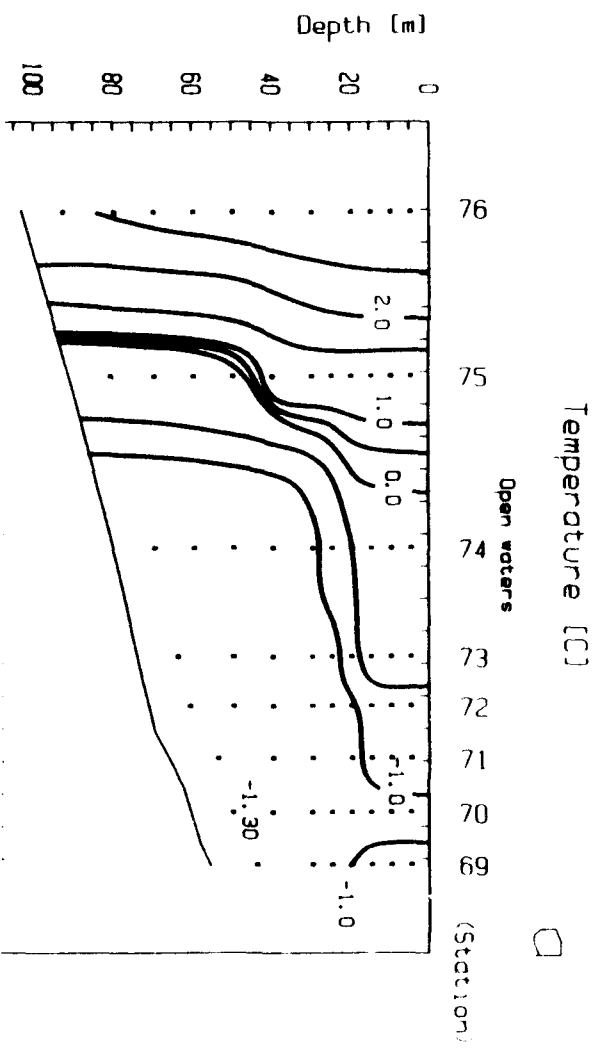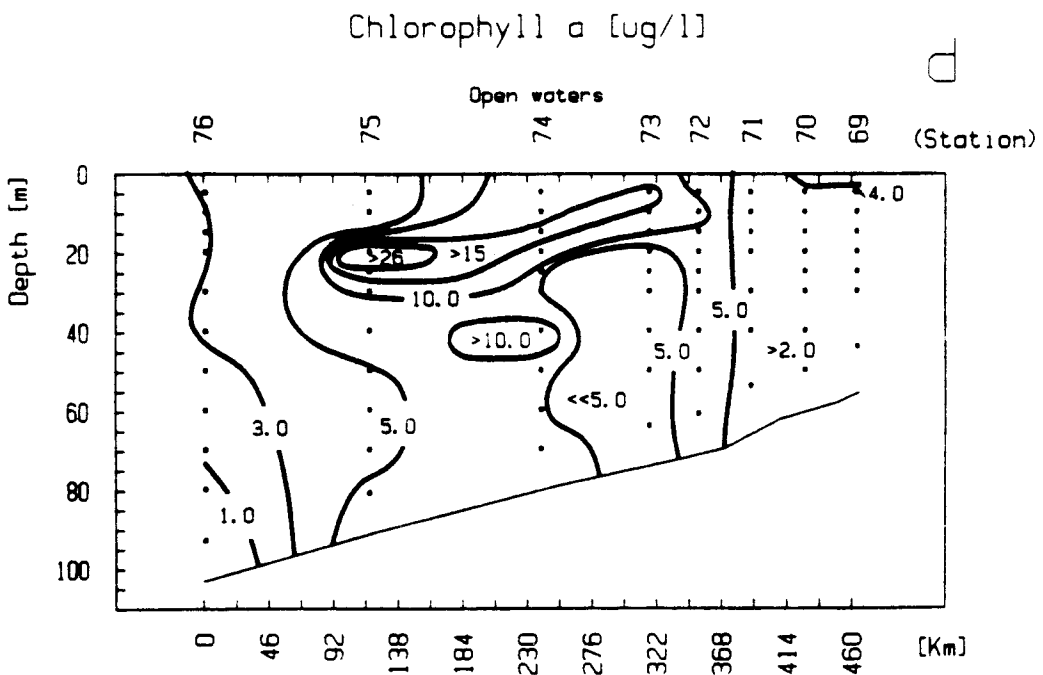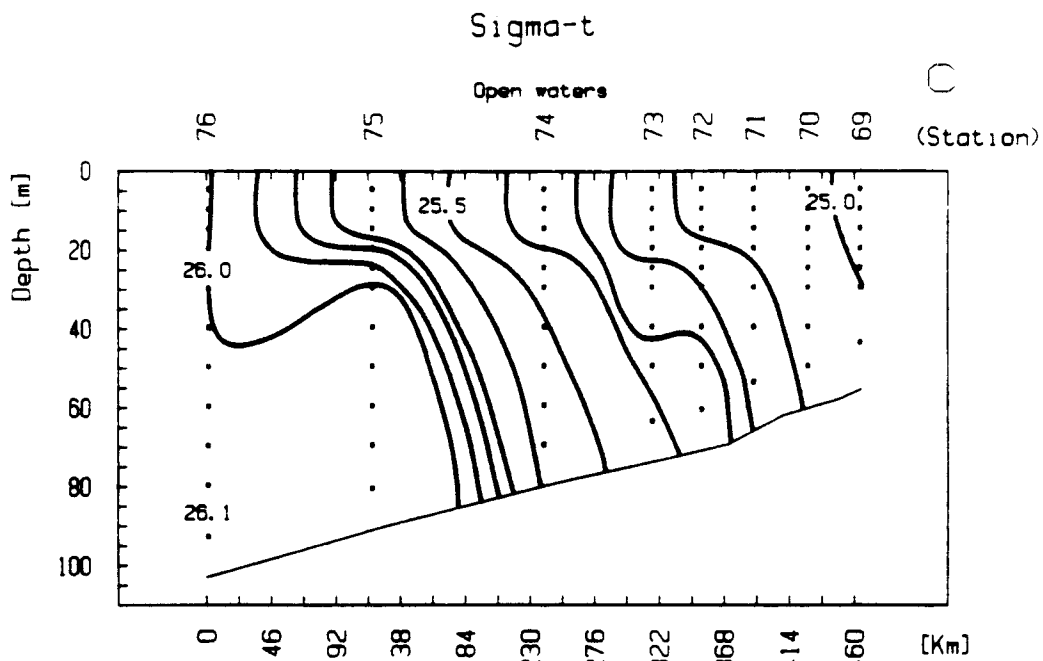
Figure 11c. 5 May 1983 ice-edge cross section E of St. Matthew Island;
Sigma-t; d. Chlorophyll a (mg Chl m⁻³).
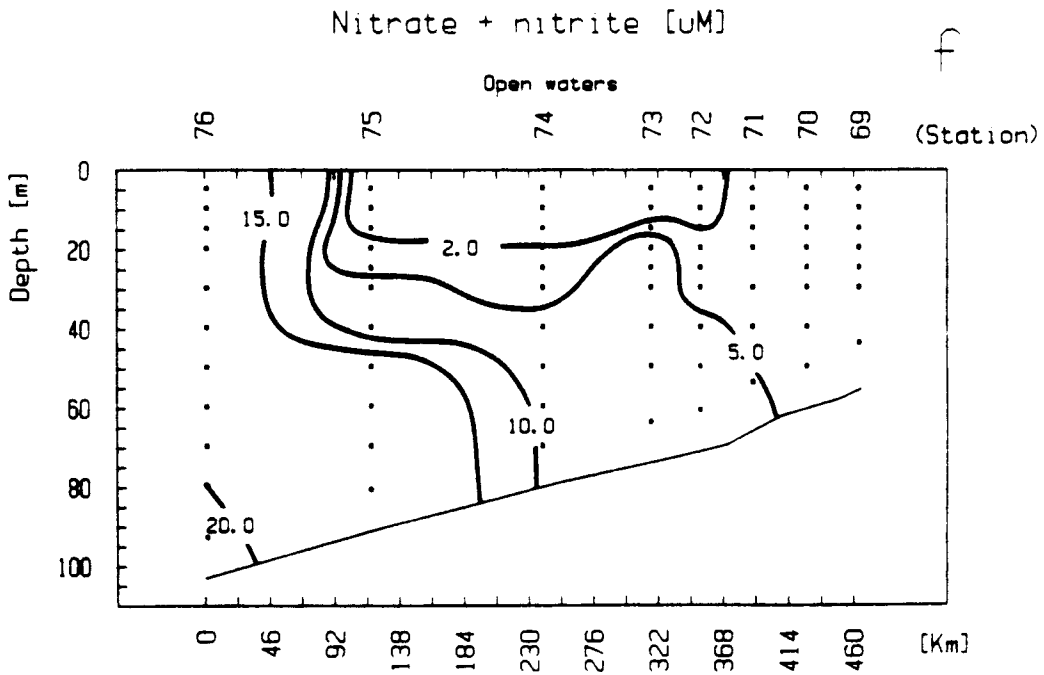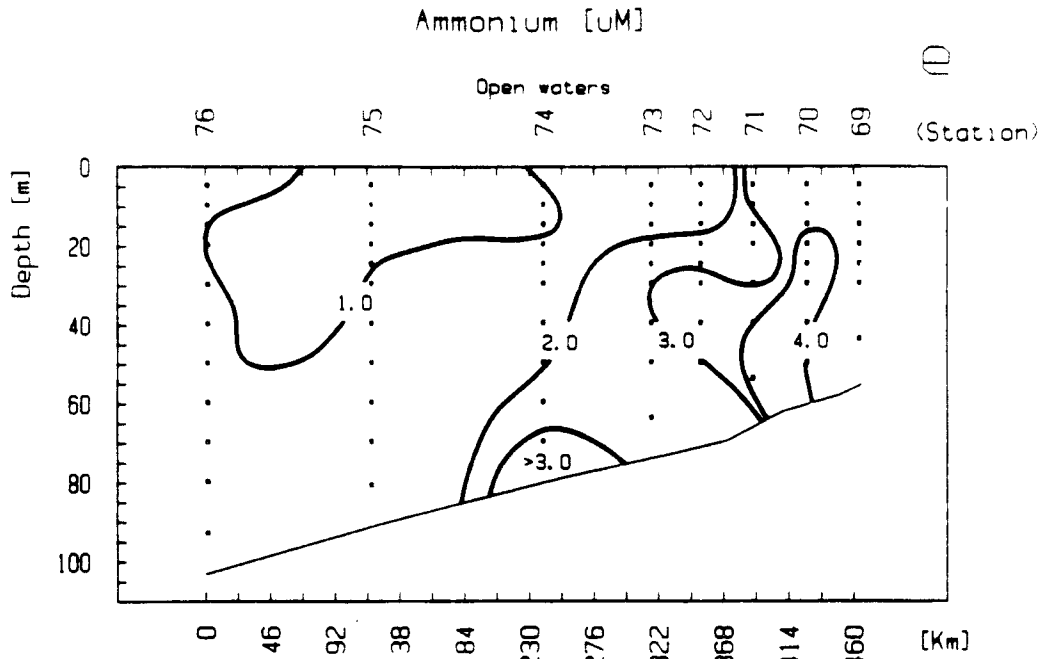
Figure 11e. 5 May 1983 ice-edge cross section E of St. Matthew Island:
Ammonium (μgat N l⁻¹); f. Nitrate + nitrite (μgat N l⁻¹).

Bering Sea spring ice-edge primary productivity:

High storm frequency and ice cover resulted in low subsurface light intensity at the ice edge in April and part of May, 1983. Under relatively calm conditions (winds < 20 Kn), surface irradiance averaged 0.4 times on-deck irradiance in 1982 and 0.7 in 1983. Extinction coefficients increased with water-column productivity (k=.11-.56 m^{-1}, ave.=0.33 m^{-1}, 1982; k=0.15-0.33, ave.=0.21 m^{-1}, 1983). Euphotic zone depth (0.1% surface light intensity) was reduced to less than 15 m on May 5, 1982, in a water column with 176 mgChla m^{-2} (MLD integrated). Euphotic depths in 1983 were less than 35 m in several cases (stations 7, 42, 50, 56 and 74) due to high cloud coverage or/and ice presence (station 42, 56). High plant concentration in the water column also decreased the euphotic depth in 1983 (station 42: 14 mgChla m^{-2}; station 74: 243 mgChla m^{-2} in MLD). As mentioned above, it is not clear if the information collected at the Bering Sea ice edge in 1982 is directly comparable to 1983 data, due to differences in geographical location and time of collection between the two years. Nevertheless, this information suggests that primary productivity in 1983 was less than in 1982.

Ice-edge phytoplankton are adapted to a low-light environment. Epontic algae adaptation to low light has been reported by Clasby et al (1973). Steemann Nielsen (1975) and Falkowsky (1980) observe that shade adaptation is important in a stratified water column. Beardall and Morris (1976) show that growth at low irradiances leads to enhanced ability to use low light levels. The higher photosynthetic capacity of deeper phytoplankton would increase water-column integrated

productivity.

In the ice-edge bloom, maximum photosynthetic rates occurred at a fraction (17% - 50%) of surface irradiance (figures 12-21, also see Methods). Photoinhibition took place at irradiances found in the upper 0-1.5 meters (>100 μE m^{-2} s^{-1} in 1982, >200 μE m^{-2} s^{-1} in 1983) while the optimum light intensity for photosynthesis occurred at around the bottom of the mixed layer (<200 μE m^{-2} s^{-1}, both in 1982 and 1983). Photoinhibition may be a consequence of chlorosis (i.e. the yellowing, bleaching or decay of chlorophyll; Falkowski, 1980; Slagstad, 1982), and may depend on the light history of the plants and degree of mixing in the mixed layer (Denman and Gargett, 1983; Falkowski, 1983). Gallegos et al (1983) discuss the susceptibility to photoinhibition and subsequent adaptation to high irradiances in phytoplankton of the Canadian Arctic.

Steele's (1962) equation (see Methods) projected optimum irradiances (I_{OPT}) between 17-40% surface (on deck) light intensity in 1982 and from 30 to 50% in 1983. Such response to light variation was evident in 1982 and 1983 phytoplankton (figures 12-21) and ice algae, suggesting that all these communities were similar.

Steele's equation cannot predict absolute carbon fixation rates unless P_{MAX} (maximum photosynthetic rate) and I_{OPT} are known. The relationship held at all surface light intensities at which experiments were conducted, except at station 74 in 1983. Samples collected at different depths at any station had similar responses to irradiance but different P_{MAX} (figures 12-15). This suggests that the mixed layer phytoplankton community is adapted to a particular relative irradiance

(I/I_{SURF} = 17-50% surface irradiance during mid-day). It also suggests
that the period of photoadaptation to a new I_{OPT} is longer than the 4-5
h incubation period. Lewis et al (1984) explore the theoretical
background and review the literature on the time scale of
photoadaptation. Lewis et al stress that the I vs. P relationship is
time-dependent and Falkowsky (1980) suggests that adaptation occurs in
less than 24 h. In general, in the ice-edge zone the same response was
always observed on a relative (P/P_{MAX}, I/I_{OPT}) basis as in Goldman
(1980).

Platt et al (1982) were able to differentiate between deep and
mixed layer phytoplankton communities based on their light response
characteristics, but at the Bering Sea ice edge the vertical separation
of communities is not as strong due to relatively weaker water-column
stability. Sambrotto (1983) discusses the vertical separation of SE
Bering Sea communities during late spring to summer stability as
reflected in nitrogen uptake measurements. The high potential
productivity of deeper ice-edge zone phytoplankton may be partially a
consequence of depressed compensation light intensities of temperate and
arctic phytoplankton at low temperatures and low insolation (Platt and
Jassby, 1976; Platt et al, 1982).

The depth at which I_{OPT} occurred was usually also dominated by a
subsurface chlorophyll a maximum. It would seem therefore that
phytoplankton are able to adjust their physiology to occupy this
particular light (and nutrient) level by actively adjusting their
buoyancy, as suggested by Jamart et al (1977), Bienfang (1981) and
Bienfang et al (1983). Maximum absolute photosynthetic rates varied

directly with biomass or chlorophyll $\underline{a}$ (P=0.60*Chl$\underline{a}$+1.55, n=17, r=0.65,
figure 22). An increasing trend in P with incubation temperature was
also noticed.

Photosynthetic rate was low in samples collected at the ice edge
proper or ice covered waters (stations 37, 48, 49, 50, in 1982) but
higher in the ice meltwater layer where the bloom was underway (stations
45, 56, 57, in 1982). In general, primary productivity measured in 1982
was higher than in 1983. Assimilation numbers were similar in both
years (<<3.0 mgC mgChl$\underline{a}^{-1}$ h^{-1}) but biomass was usually higher in 1982.
Vedernikov (1975) and Platt et al (1982) also find low assimilation
numbers for arctic phytoplankton. Platt et al suggest that arctic
phytoplankton in general may not utilize light very efficiently,
whatever the mechanism of adaptation. At station 74, in the transect
with highest biomass in 1983 (figure 11d), 10 m productivity was low
(about 6 mgC m^{-3} h^{-1} by 10.5 mgChl$\underline{a}$ m^{-3}, figure 21) compared to 1982
productivity (up to 18 mgC m^{-3} h^{-1} by 9.3 mgChl$\underline{a}$ m^{-3}, station 45, figure
13 and possibly station 57 by 17.8 mg Chl$\underline{a}$ m^{-3}, figure 14). Plants at
station 74 (1983) did not show photoinhibition even at irradiances over
700 μE m^{-2} s^{-1} and showed sustained photosynthetic rates between 10%
and 100% surface light intensity. Alexander (pers. comm.), in a
previous study, did not find photoinhibition in the Bering Sea spring
ice-edge bloom.

The different shape of the irradiance $vs.$ carbon uptake curve at
station 74 (1983, figure 21) suggests the presence of a species
assemblage different from ice-edge communities. Phytoplankton species
counts show that at all other 1983 stations either $Thalassiosira$ spp.

(see below), *Nitzschia* section *fragilariopsis* or unidentified flagellates numerically dominated the phytoplankton. These were also the species that were most abundant in brown ice samples. At station 74 these species were still present in the water column (very few *Thalassiosira* spp. were counted), but *Chaetoceros* spp. comprised over 30% of the phytoplankton. In particular *C. debilis* was found in great numbers ($>2.4 \times 10^5$ cells l^{-1}).

No animals (crustaceans, polychaetes or fishes: Horner and Alexander, 1972; Alexander, 1974, 1981) were seen in the brown layer of the underside of ice floes. Alexander and Chapman (1981) conclude that Bering Sea ice-edge blooms can be seeded by epontic species but point out conflicting reports (Horner and Alexander, 1972; Saito and Taniguchi, 1978; Hameedi, 1978; Schandelmeier and Alexander, 1981). The taxonomic data collected during 1982 and 1983 is not enough to describe in detail the succession (Odum, 1969) of species following the ice-edge bloom, and the problem is further complicated by the presence of flagellates (Bonin *et al*, 1981). Epontic species and ice-edge bloom species seem to be similar and *Nitzschia* section *fragilariopsis*, *N. seriata*, *N. frigida*, *Pleuro-* or *Gyrosygma* and several *Thalassiosira* species (*T. decipiens, T. gravida, T. rotula, T. aestivalis*) were common in both habitats.

Productivity of the epontic community ranged from 38-145 mgC m^{-3} h^{-1} with pronounced photosynthetic inhibition at high irradiances. Alexander and Chapman report no photoinhibition and rates ranging from less than 80 mgC m^{-3} d^{-1} to 200-396 mg m^{-3} d^{-1}, at much higher chlorophyll levels than seen in 1982 or 1983 (see above). These

physiological differences indicate great variability in community composition from year to year.

After the ice-edge bloom, *Chaetoceros debilis*, *C. compressus* and *C. socialis* may be dominant transient species in the early open-shelf blooms leading to the *Phaeocystis* bloom described by Goering and Iverson (1980) and Kokur and Iverson (1980). *Chaetoceros* spp., including *C. debilis*, were found in epontic algal samples, but in very low numbers. The apparent dominance of pennate diatoms in the ice-edge bloom suggests that these species are healthy and able to maintain buoyancy, since they do not sink out fast. Dinoflagellates were present in the ice and the ice-edge zone as a minor fraction of the phytoplankton community.

Ice-edge phytoplankton nitrogen uptake:

At the Bering Sea ice edge, nitrogen is available to algae as nitrate, ammonia, and dissolved organic nitrogen. A phytoplankton bloom may become nitrogen limited if isolated from nitrogen supplies. Whether this occurs at the ice edge is discussed below in a nitrogen budget treating nitrogen supply mechanisms.

Results of $^{15}NH_4$-N and $^{15}NO_3$-N uptake measurements carried out in 1982 and 1983 indicate that phytoplankton at the ice edge were not nitrogen limited (figures 23, 24, 25). Rates measured under a range of nutrient concentrations did not vary, suggesting saturation of the nitrogen uptake mechanisms. The ratio of carbon uptake to total absolute nitrogen uptake rate was greater than 1 in all samples treated with both isotopes suggesting N-unlimited growth (Slawyk, Collos and Auclair, 1977, 1979; Collos and Slawyk, 1980). Inhibition of ρNO_3-N

by the presence of NH_4-N, as observed by Syrett and Morris (1963),
MacIsaac and Dugdale (1972), Thacker and Syrett (1972a), Morris (1974),
Syrett and Leftley (1976), McCarthy et al (1977) and Olson (1980) in a
carbon rich environment was not seen.

NH$_4$-N levels were high (<1.0 to >4.0 μgat l^{-1}) and remained high
during the 1982 and 1983 sampling periods. NO$_3$-N decreased rapidly with
plant growth but was never undetectable (figures 6-11, 23-25). At
station 68, in 1982, upper 15 m nitrate concentration was about 2 μgat
l^{-1} and serial ^{15}NO$_3$-N additions induced a hyperbolic uptake response by
phytoplankton (figure 25). Station 68 was occupied in the stable ice
meltwater layer where the ice-edge bloom was under development.
Potential specific uptake rates at this station were higher than those
observed at station 30, even under decreased nitrate conditions (figures
23-25).

Community nitrate specific uptake rates may change along the
successional species gradient mentioned above. ^{15}NO$_3$-N uptake by early
spring communities incubated at different light intensities shows
depression of the rates at high irradiances in high nitrate levels. The
ratio of the specific uptake rates at 50% surface light intensity (SLI)
to V(10%SLI) approached 0.5 at >9.0 μgat NO$_3$-N l^{-1}. As ambient NO$_3$-N
decreased to 2 μgat l^{-1} the ratio V(50%SLI):V(10%SLI) approached 1.0
(station 74, 1983), possibly due to a shift in species composition
towards the end of the ice-edge bloom. The relationship between carbon
fixation and nitrate uptake mechanisms is discussed by Hipkin et al
(1983). Nitrate uptake inhibition by high irradiance may be related to
photoinhibition of carbon uptake in early bloom and epontic species. To

my knowledge this is the first report of possible nitrate uptake

photoinhibition.

The mechanisms controlling phytoplankton succession or community

structure have not been elucidated. For example, Turpin et al (1981)

suggest that small-scale nutrient patchiness can affect individual

growth rates (μ) or community structure, even though there is no

change in the average nutrient concentration in the water. Succession

is probably controlled by the light and mixing history of the water

column as well.

In the ice-edge habitat, the distinction between new and

regenerated nutrients (Dugdale and Goering, 1967) is unclear due to the

availability of nutrients to the plants growing in the ice meltwater

layer (see below). Dugdale and Goering's model only applies to the deep

ocean with a stable mixed layer. At the ice edge, the proportion of

nitrate uptake to combined NH_4-N + NO_3-N uptake (f-factor, Dugdale and

Goering, 1967) is consistently above 0.65, reflecting the initial high

concentration and high NO_3-N supply rates to the upper 20 m. The

relative preference indices (RPI, McCarthy et al, 1977) suggest that

ammonium tends to be the preferred nutrient form used by ice-edge

phytoplankton (RPI = 1.06-1.3 for ammonia as compared to 0.93-1.06 for

nitrate).

Nitrogen uptake rates of the epontic ice-algal community suggest

that nitrogen turnover is important in the ice. The nitrogen turnover

index (Eppley, 1981; Harrison et al, 1983) in the brown algal layer was

1.3-1.4 (station 043028). The f-factor was 0.41 and the relative

preference indices for ammonium and nitrate suggested preference for

ammonium. High concentration of NH_4-N is reported for Arctic sea ice (1-22 μgat l^{-1}, Alexander and Chapman, 1981). The high abundance of flagellates in the present study supports the idea of high nitrogen cycling rates in the ice (Azam *et al*, 1983). Individual nitrogen and carbon uptake rates and relevant observations for 1982 and 1983 are presented in the Appendix.

Absolute Carbon uptake [mgC m^{-3} h^{-1}]

20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0

25 50 75 100 125 150 175 200 225 250 275

Absolute Light intensity [uE m^{-2} s^{-1}]
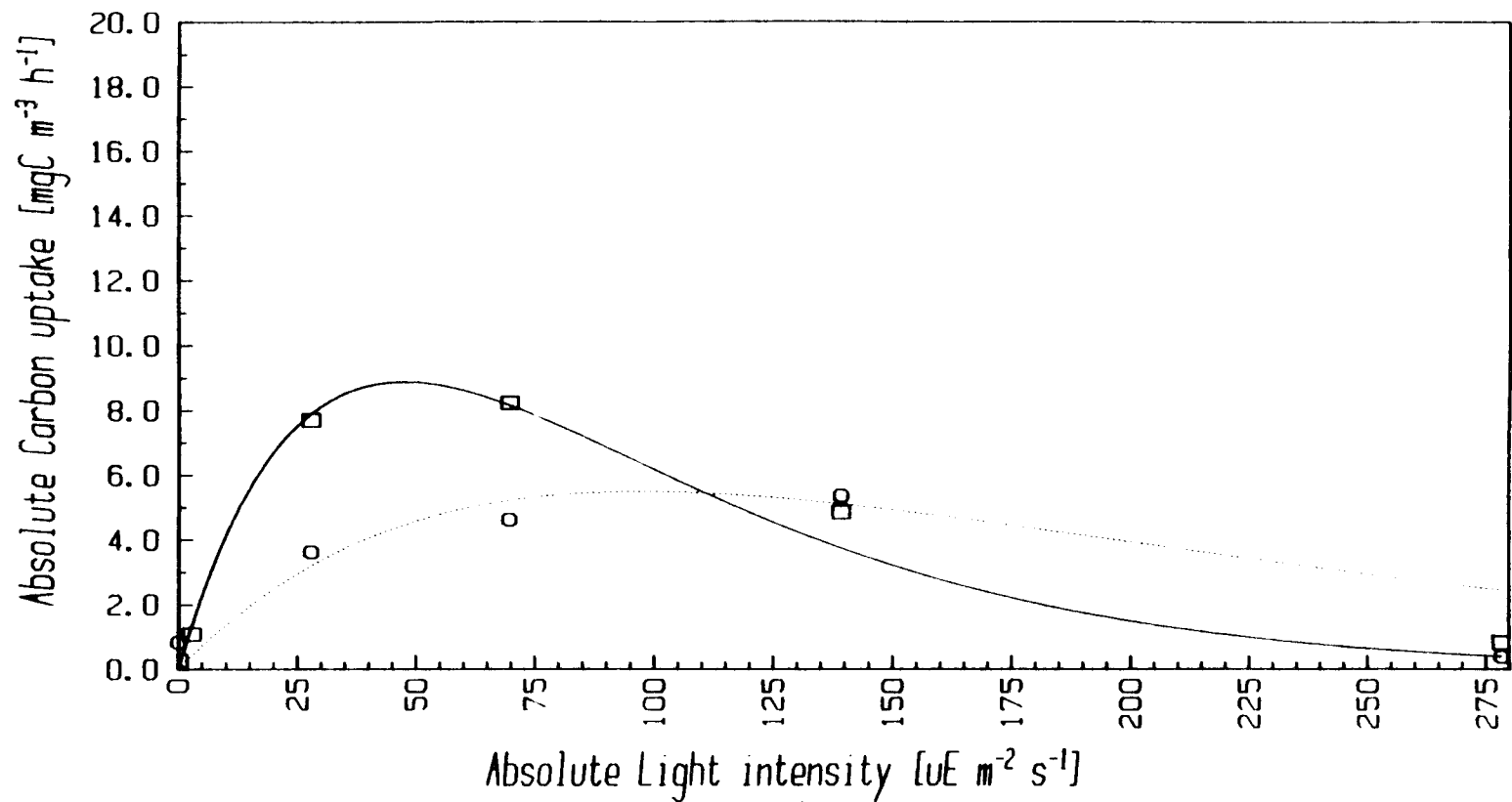
0 [m]:   o   Actual
              ....   Model
          (Gmax= 5.5 ; Iopt= 35 %SLI)

25 [m]:   □   Actual
              ————   Model
          (Gmax= 8.9 ; Iopt= 17 %SLI)

Figure 12.   Absolute carbon vs. irradiance curves, spring 1982.
Station: 025037.   Symbols are $^{14}CO_3$ incubation results.   Curves
represent Steele's (1962) model (see Methods).   Curves stop at on-deck
irradiances seen during incubation.   Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
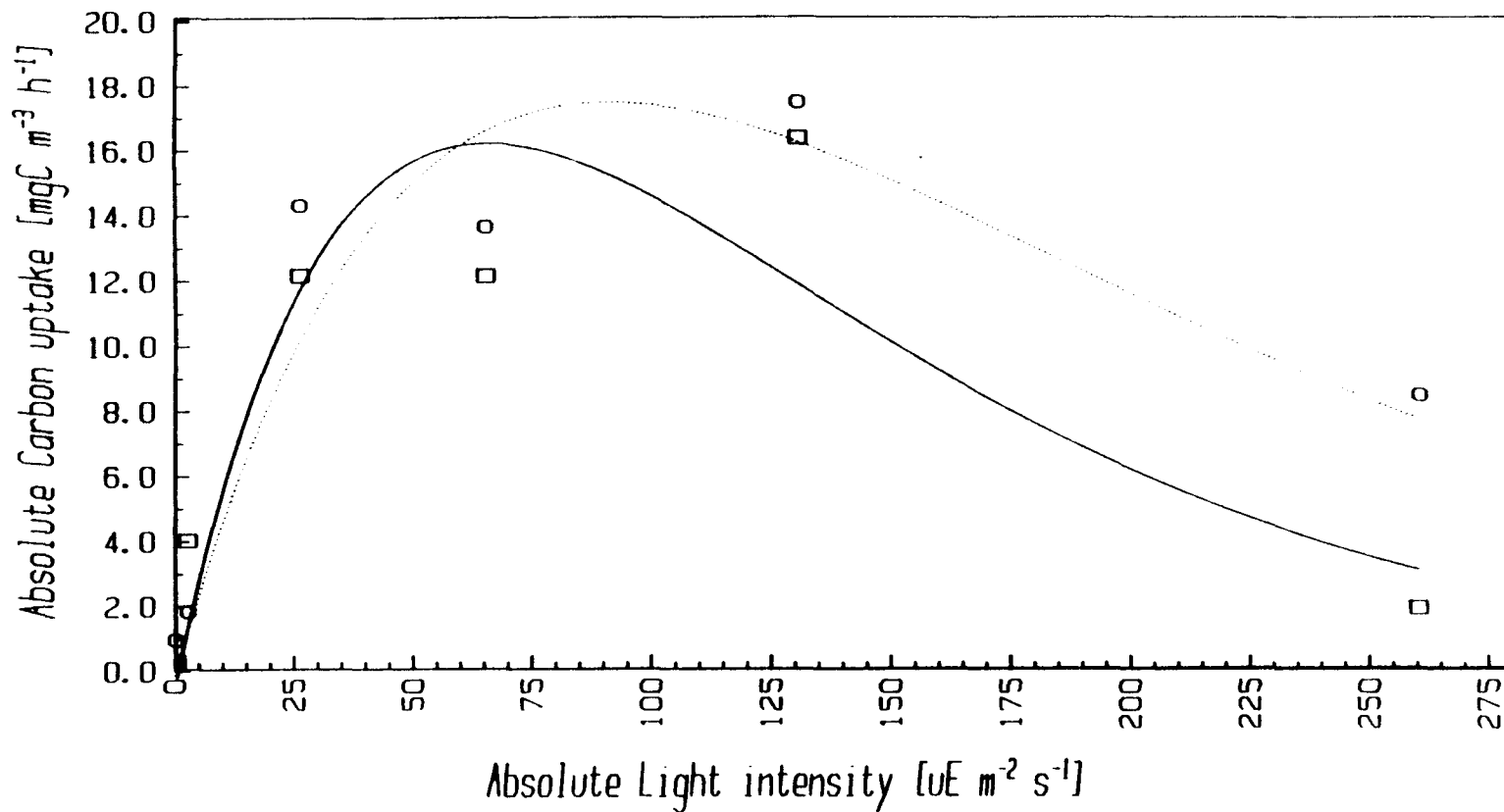
Figure 13. Absolute carbon vs. irradiance curves, spring 1982.
Station: 025045. Symbols are ${}^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
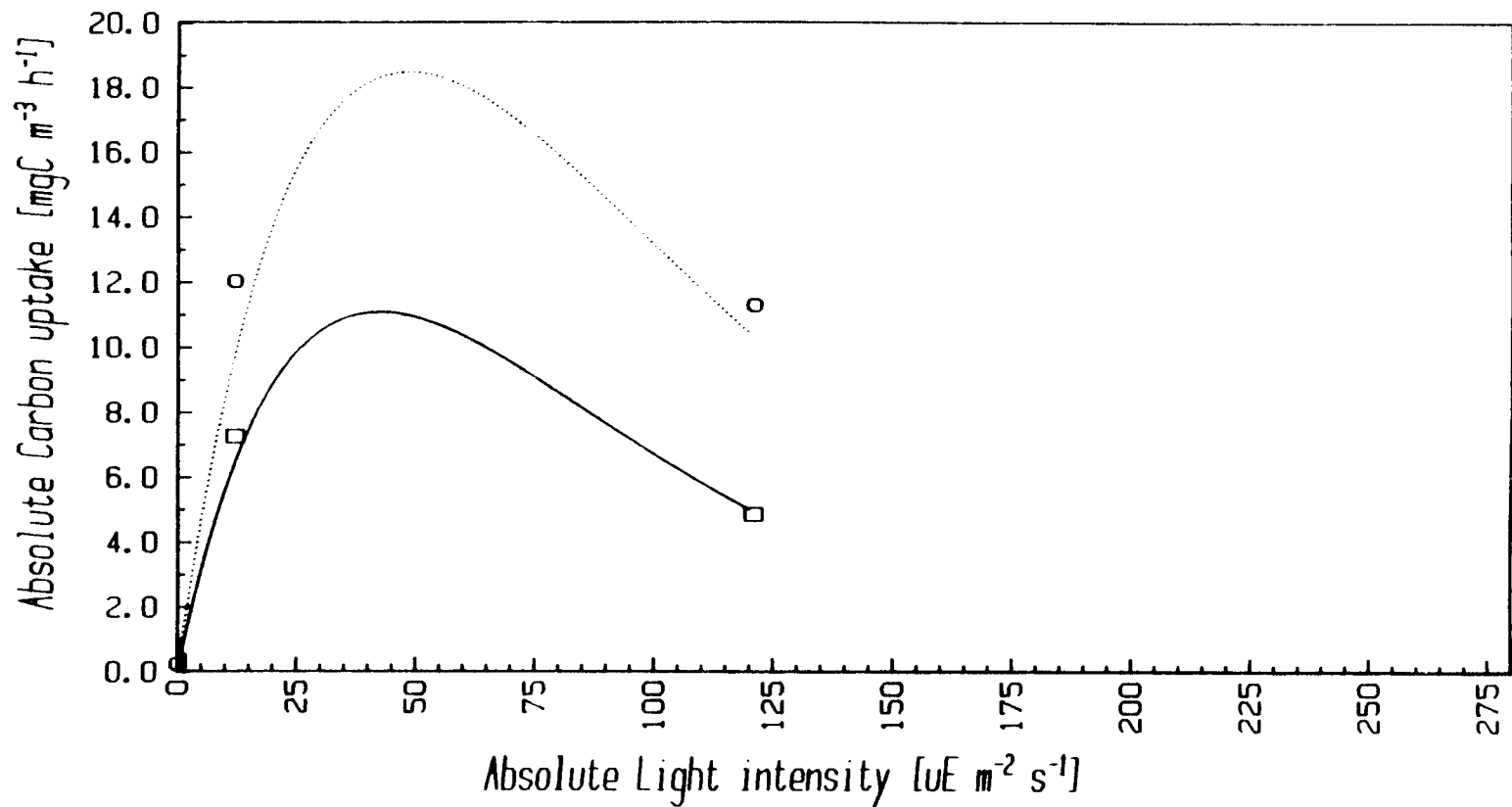
Figure 14. Absolute carbon vs. irradiance curves, spring 1982.
Station: 025057. Symbols are $^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.

Figure 15. Absolute carbon *vs.* irradiance curves, spring 1983.
Station: 043007. Symbols are $^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
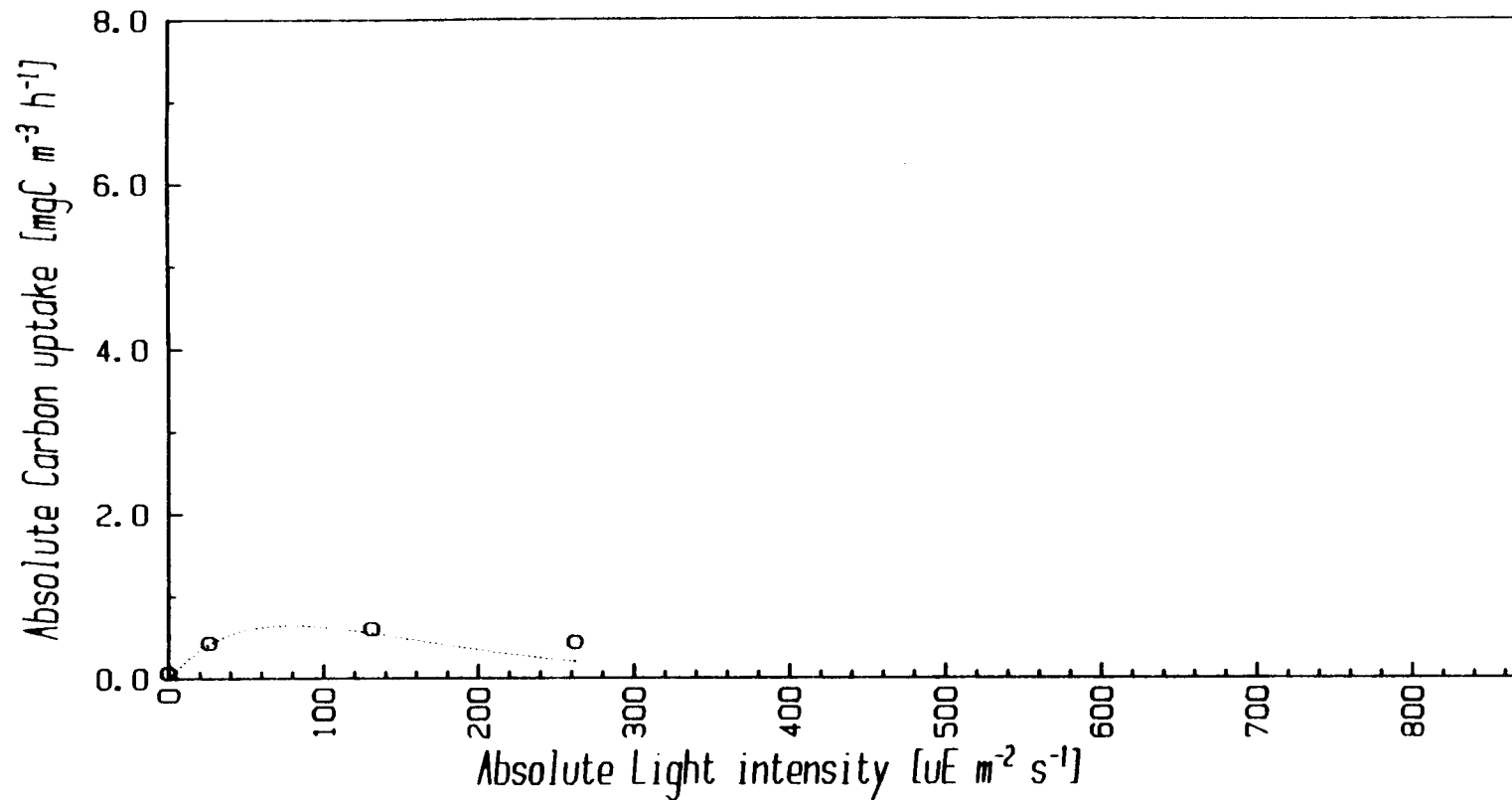
Figure 16. Absolute carbon *vs.* irradiance curves, spring 1983.
Station: 043029. Symbols are $^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
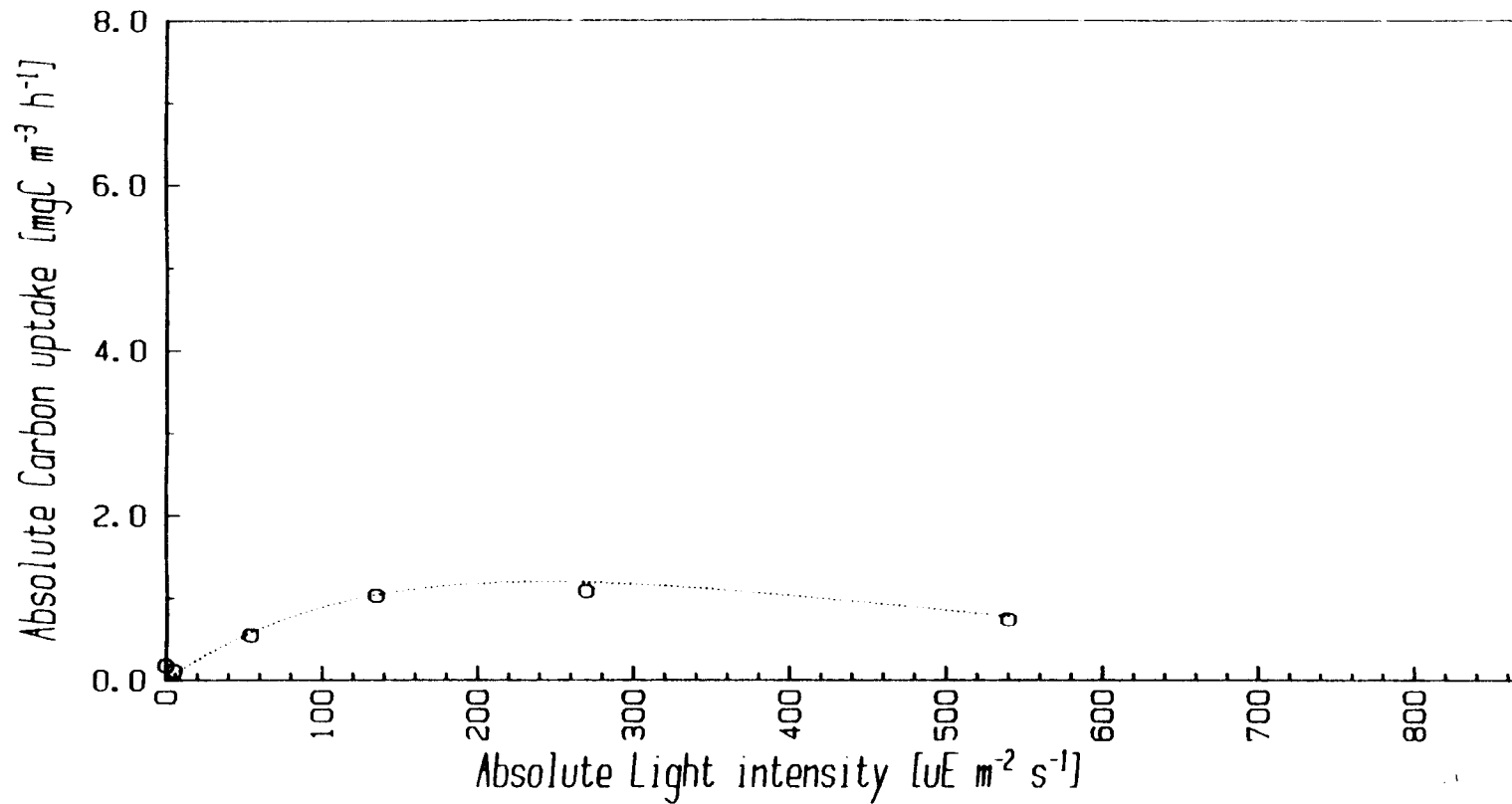
5 [m]:   o   Actual
        .... Model
    (Gmax= 1.2 ; Iopt= 45 %SLI)

Figure 17. Absolute carbon *vs*. irradiance curves, spring 1983.
Station: 043042. Symbols are $^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
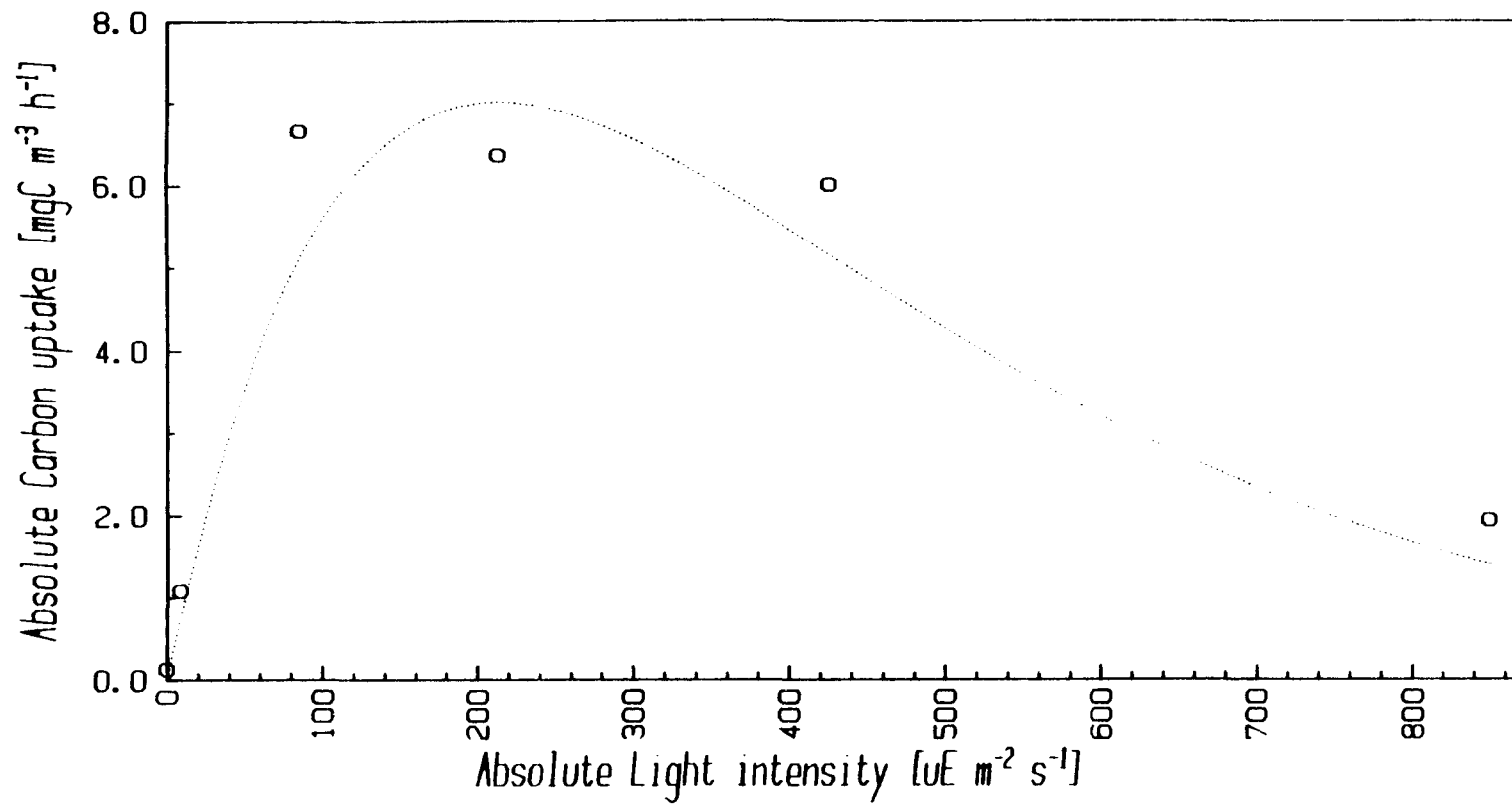
15 [m]:   o   Actual
             .... Model
      (Gmax= 7 ; Iopt= 25 %SLI)

Figure 18.   Absolute carbon *vs.* irradiance curves, spring 1983.
Station: 043050.   Symbols are $^{14}CO_3$ incubation results.   Curves
represent Steele's (1962) model (see Methods).   Curves stop at on-deck
irradiances seen during incubation.   Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
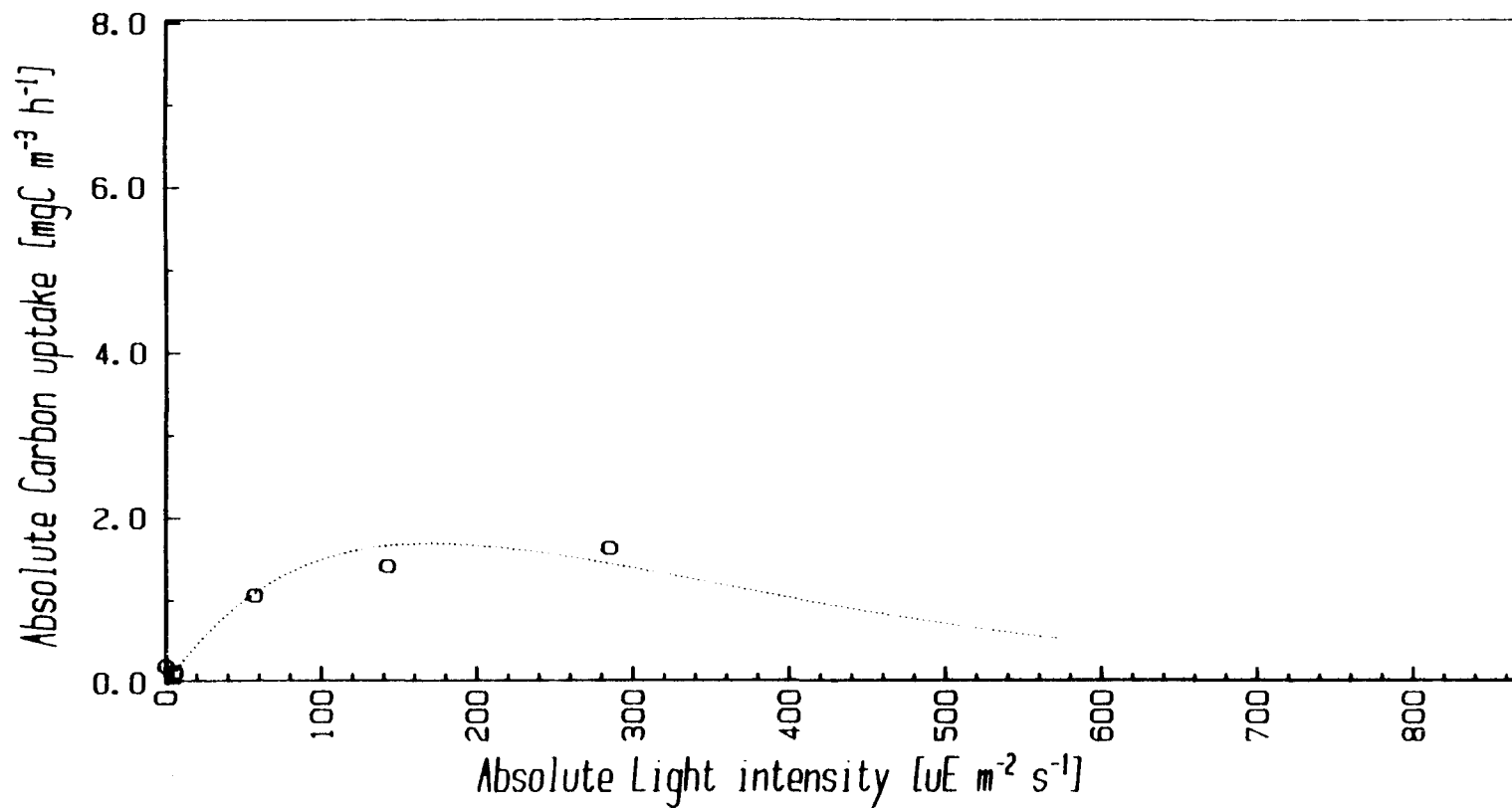
5 [m]:   o   Actual
....   Model
(Gmax= 1.7 ; Iopt= 30 %SLI)

Figure 19. Absolute carbon vs. irradiance curves, spring 1983.
Station: 043056. Symbols are $^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
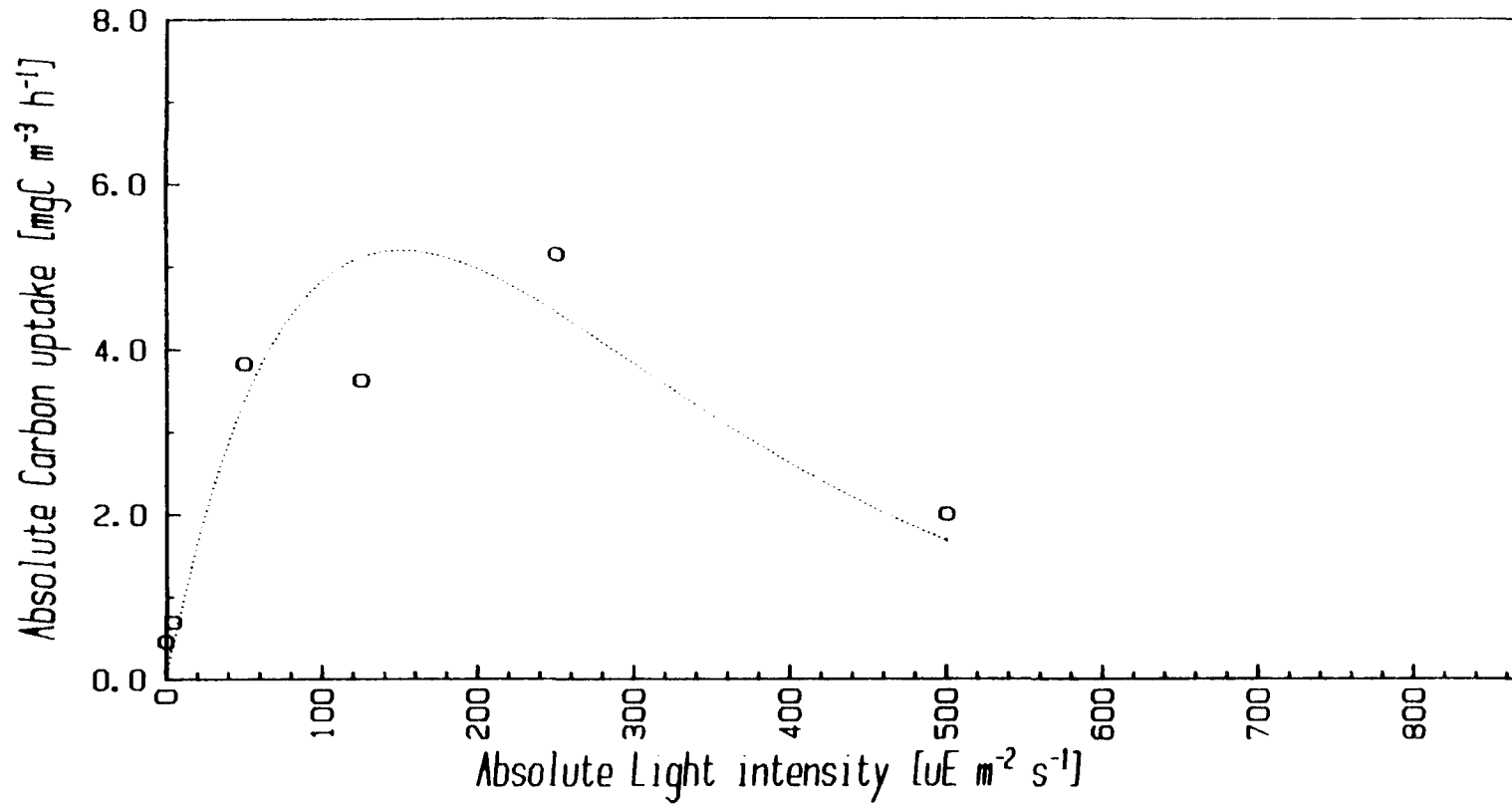
30 [m]:   o   Actual
.... Model
(Gmax= 5.2 ; Iopt= 30 %SLI)

Figure 20.   Absolute carbon vs. irradiance curves, spring 1983.
Station: 043059.   Symbols are $^{14}CO_3$ incubation results.   Curves
represent Steele's (1962) model (see Methods).   Curves stop at on-deck
irradiances seen during incubation.   Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
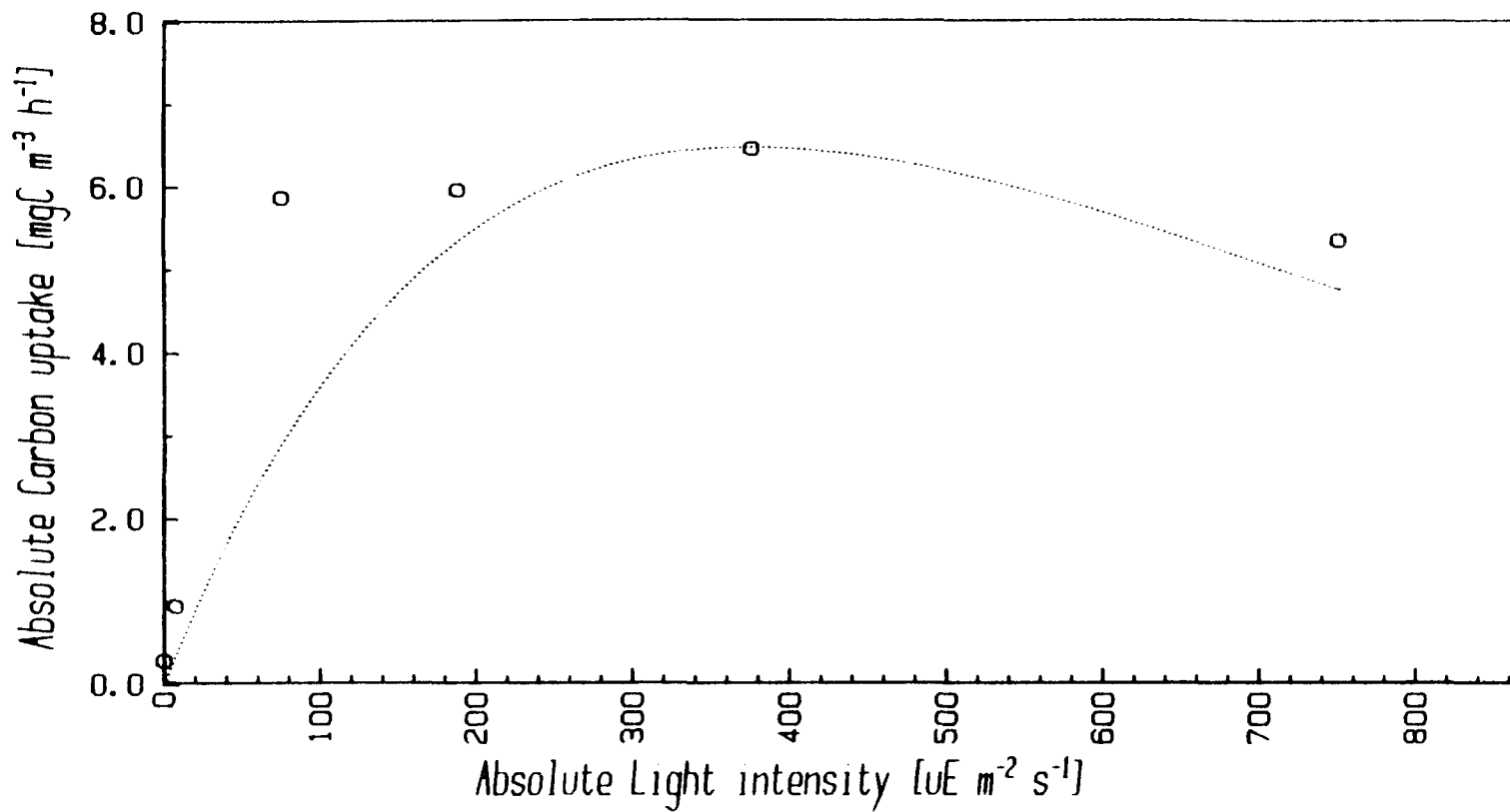
Figure 21. Absolute carbon *vs.* irradiance curves, spring 1983.
Station: 043074. Symbols are $^{14}CO_3$ incubation results. Curves
represent Steele's (1962) model (see Methods). Curves stop at on-deck
irradiances seen during incubation. Gmax=maximum photosynthetic rate.
Iopt=optimum irradiance.
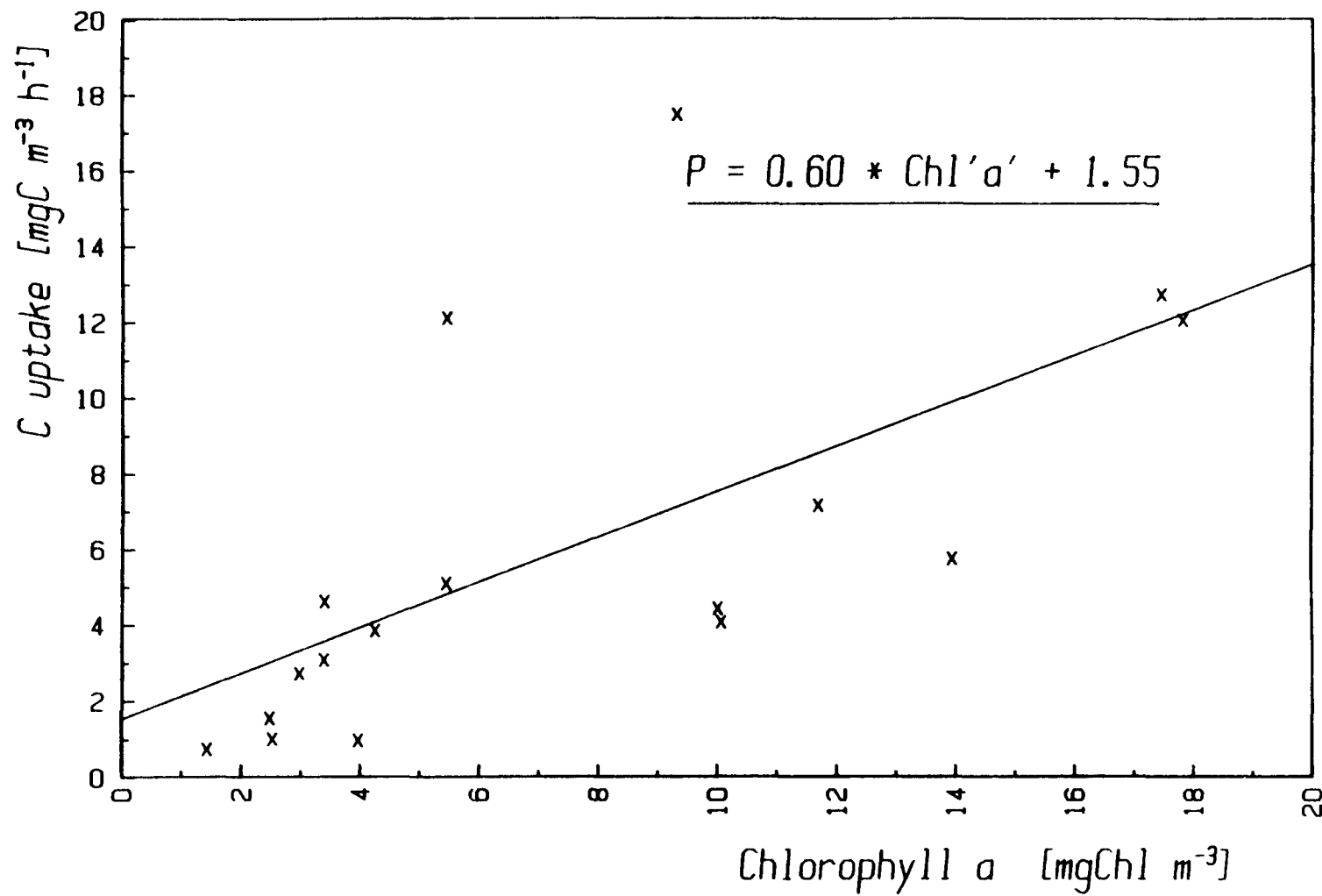
$$P = 0.60 * Chl'a' + 1.55$$

Figure 22.   Chlorophyll a vs. absolute carbon uptake rate.   Spring 1982
samples incubated at simulated in situ irradiance.   Regression line: P
= 0.60 * Chla + 1.55,   r=0.65.
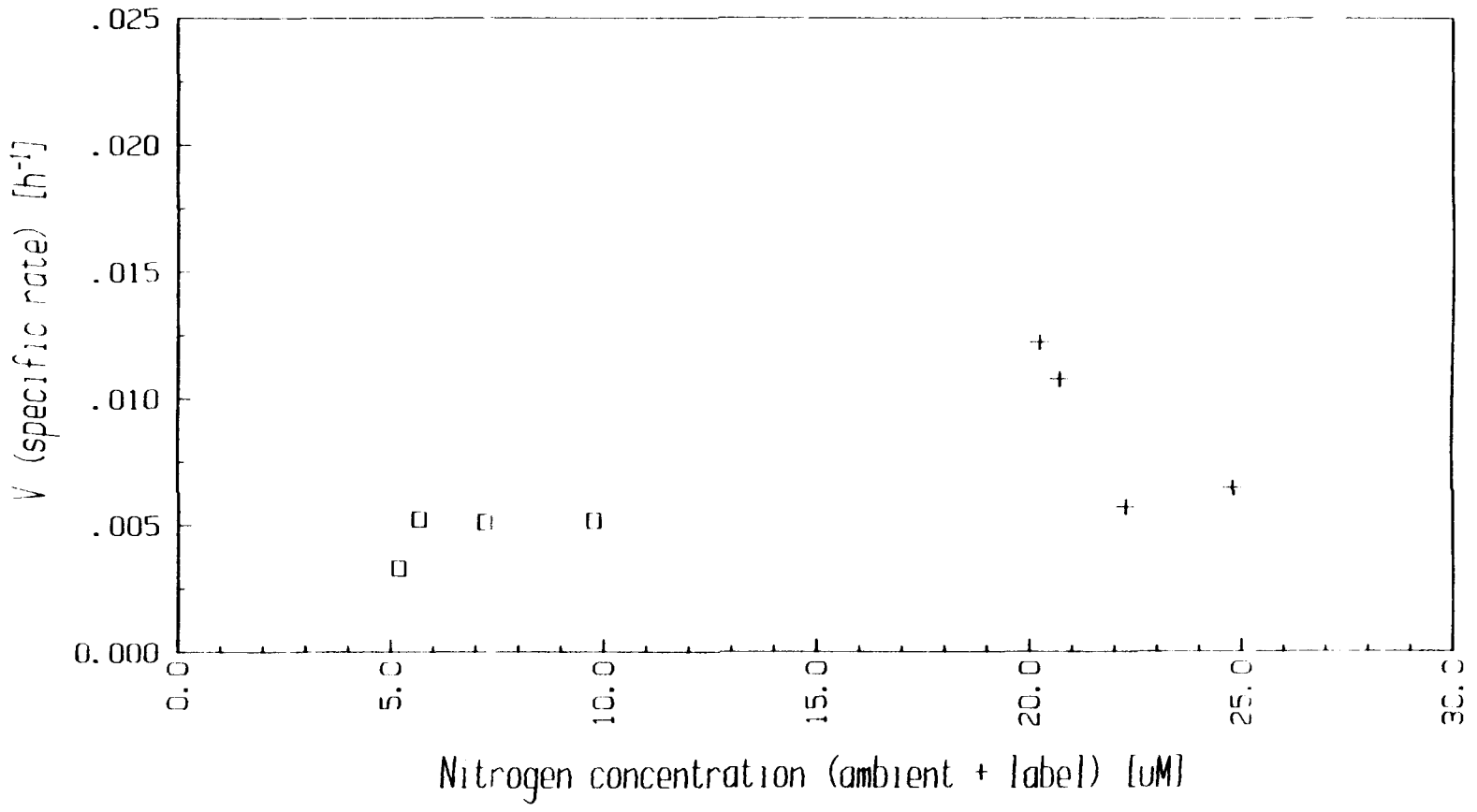
Figure 23. 1982 nitrogen concentration *vs.* nitrogen specific uptake
rates. Station: 025030. Surface sample incubated at 100% surface
irradiance. Squares = NH_4-N incubations. Crosses = NO_3-N incubations.
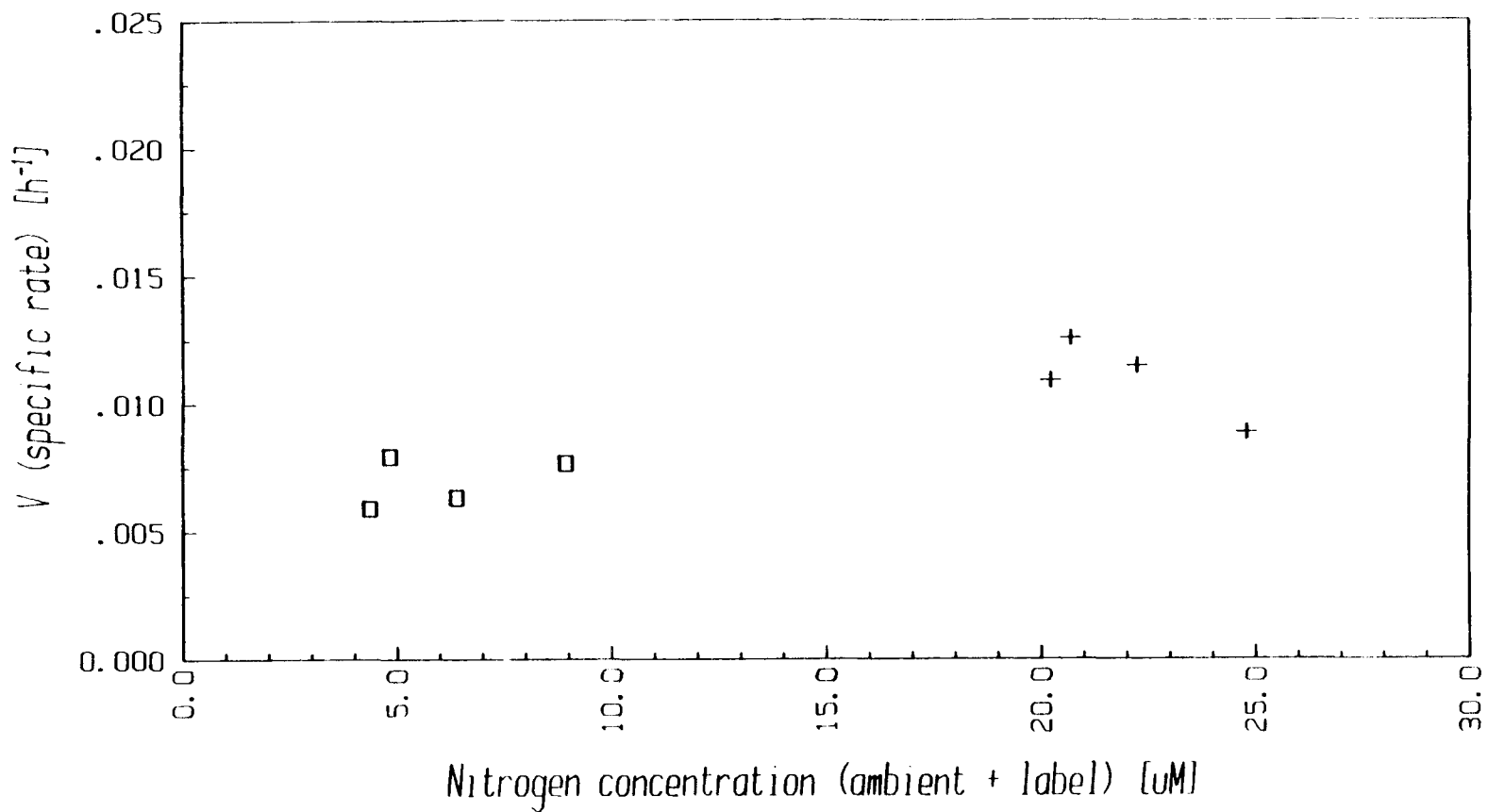
Figure 24. 1982 nitrogen concentration *vs*. nitrogen specific uptake
rates. Station: 025030. Surface sample incubated at 10% surface
irradiance. Squares = NH₄-N incubations. Crosses = NO₃-N incubations.
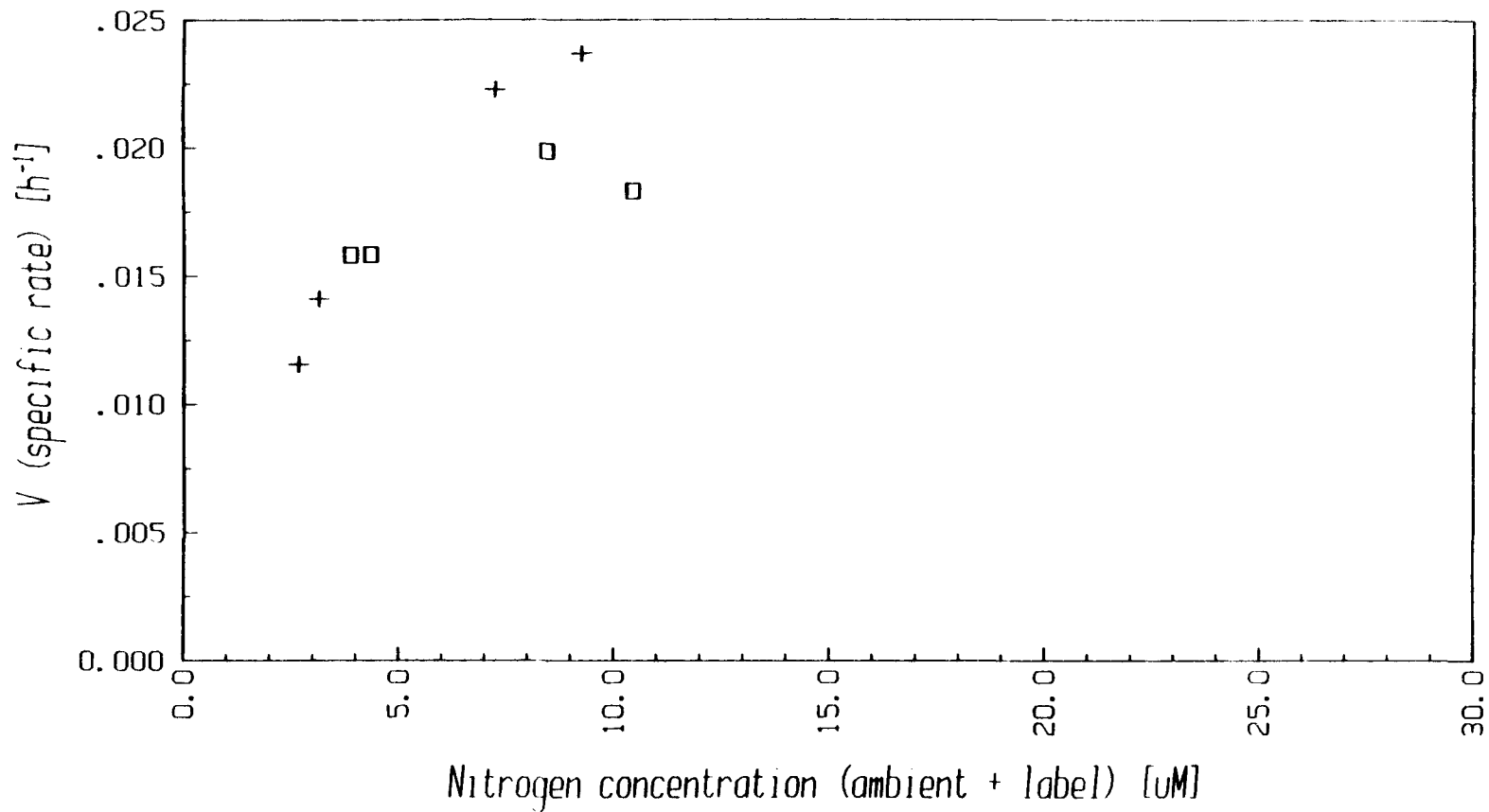
Figure 25. 1982 nitrogen concentration *vs*. nitrogen specific uptake rates. Station: 025068. Surface sample incubated at 50% surface irradiance. Squares = NH_4-N incubations. Crosses = NO_3-N incubations.

1III. Nitrogen dynamics at the Bering Sea ice edge in spring: a
budgetary approach.

Meltwater-driven stratification of the water column develops in the
first days of May in the Bering Sea ice-edge zone, inducing an ice-edge
bloom as described by Marshall (1957) and Niebauer et al (1981). The
development with time of physical (temperature, salinity, sigma-t),
biological (chlorophyll a) and nitrate structures in the April - May
1982 Bering Sea ice-edge zone is discussed in Niebauer and Alexander (in
prep.). Except for an initial lag, mixed-layer integrated chlorophyll a
appeared to increase linearly over time (table 9). Losses to deeper
water were observed on May 9 (station 58, figures 10d, 27-28), after
which the rate of chlorophyll a increase may have been slightly curbed
(table 9).

At the onset of the bloom, mixed layer (15-20 m) nitrate
concentration decreased from pre-bloom levels of over 20 μgat l^{-1} to
1.0-1.7 μgat l^{-1} in less than 7 days (figure 27). ^{15}N-nitrate uptake
rate measurements conducted during April-May 1982 suggest that as the
bloom develops in the surface mixed layer behind the retreating ice
edge, NO_3-N depletion could occur in 1.5-10 days (see rates in tables 8,
9).

The 1982 time series (Niebauer and Alexander, in prep.; figures
26-28) shows that NO_3-N concentrations in the surface meltwater layer
stabilized at 1.0-1.7 μgat l^{-1}. These nitrate levels are similar to
published NO_3-N half-saturation constants for marine phytoplankton
(Eppley et al, 1969; MacIsaac and Dugdale, 1969; Carpenter and

Guillard, 1971; Collos and Slawyk, 1980), and, therefore, suggest that inorganic nitrogen may become limiting to the ice-edge habitat bloom.

In contrast with the initial rapid decrease in nitrate concentration, NH₄-N seemed to decrease only slightly over a 5-8 day period in the surface layer and then increase again (figure 28). Mixed-layer integrated ammonium levels at the onset of stratification were similar to values observed toward the end of the cruise. Ammonium depletion was not detected in the ice-edge habitat.

^{15}NH₄-N specific uptake rate estimates averaged 0.0071 h^{-1} in 1982 (table 5), at stations featuring a wide range of characteristics. Stations were chosen from 1982 transects in which there was a completely mixed water column (station 30), stability with no evidence of upwelling (station 50), and from sections in which upwelling may have taken place (stations 39, 44). I consider these estimates to be between saturated V_{MAX} (about 0.018-0.024 h^{-1}, 1982 ice-edge cruise cruise; 0.020 h^{-1}, Sambrotto, 1983) and N-limited rates (<0.001 h^{-1}, HX022 fall 1981 ice-edge cruise; Sambrotto, 1983). Isotopic additions in the experiments (table 5) amounted to 1% (station 30), 32% (stations 39 and 44) or 71% (station 50) of the *in situ* ammonium concentration. If these rates were sustained over 24 hours (Glibert *et al*, 1982; Harrison, 1983), the daily ammonium requirement of an early bloom phytoplankton community would be about 0.744 μgat l^{-1}. Advanced bloom ammonium uptake rates (table 6) were calculated assuming constant specific uptake rate (V) and PN:chlorophyll a ratios. The mixed layer depth was defined where a difference greater than 0.02 sigma-t units from surface density was detected.

Table 5. Cruise: HX025 (26 April - 16 May, 1982). Phytoplankton ammonium uptake rates: specific (V), absolute (ρ) and mixed-layer integrated (Q).

Station	Ammonium uptake rate			Ambient	MLD
	V	ρ	Q(MLD)	spike	
025030	0.0052	0.0118	1.441	5.6	5
025039	0.0075	0.0235	8.460	4.1	15
025044	0.0113	0.0760	45.600	4.0	25
025050	0.0044	0.0128	1.536	2.4	5
Averages:	0.0071	0.0310	14.259		

Units: $V=(h^{-1})$; $\rho=(\mu gat\ l^{-1}\ h^{-1})$; $Q(MLD)=(mgat\ m^{-2}\ d^{-1})$, 24 h days; Concentration=$(\mu gat\ l^{-1})$; mixed layer depth=(m)

Table 6. Ammonium uptake rates: time series stations.

Station	3	23	42	52	58	78
time (d)	0	1.7	4.7	6.7	8.3	11.7
MLD (m)	20	20	15	15	20	20
Σ NH₄	115	84	32	32	56	119
Σ Chl a	87	74	184	272	359	397
ρ	11.65	9.91	24.63	36.42	48.06	53.15
Time-integr. ρ	0.00	18.32	70.14	131.19	198.77	370.84
dNH₄/dz	0.00	0.00	0.02	0.02	0.10	0.06

Units: Σ NH4=MLD integrated $(mgat\ m^{-2})$; Σ Chl$\underline{a}$=$(mg\ m^{-2})$; $\rho=(mgat\ m^{-2}\ d^{-1})$, based on constant $V=0.0071\ h^{-1}$, PN:Chl$\underline{a}$=11.0 and 24 h; Time-integrated ρ=(mgat gained in elapsed time m^{-2}); dN/dz at MLD=$(mgat\ m^{-4})$.

Water-column ammonium levels, in view of the rates presented in tables 5 and 6, should have decreased rapidly (e.g. depleted after 20 days at station 30, 7 days at station 39, 2 days at station 44 and 7 days at station 50), had there been no inputs.

Below I will use the following mass balance equation to estimate nitrogen input to the meltwater "dish" at the ice edge: (Nitrogen concentration change in the water) = (Supply) - (Uptake). I have two knowns in this equation, namely the change in the concentration of the

nutrient (nitrate or ammonia) in the water, and the absolute (ρ) nitrogen uptake rate by phytoplankton. Ammonium requirement of the phytoplankton is taken as the average uptake at stations 52, 58 and 78 (table 6), where stability had developed (average MLD=18 m, $\rho(NH_4-N)=45.9$ mgat m^{-2} d^{-1}).

There are at least seven mechanisms which may provide nitrogen to the physical structure described above and nourish the phytoplankton bloom. These can be regarded as the unknown variables in a budgetary approach:

1) Atmospheric precipitation: Arctic air is unlikely to be a major source of nitrogen (Dugdale and Toetz, 1961; Barsdate and Alexander, 1975; S. Whalen, pers. comm.).

2) Fishes and marine mammals: There is no information available on the impact of these animals on nutrient cycling. However, their nitrogen excretion may be neglected for purposes of productivity estimates on a scale of tens of kilometers and over a period of days.

3) Temporal or spatial aggregations of net zooplankton: Estimates of zooplankton ammonium excretion have been obtained by Smith and Whitledge (1972: small neritic animals = 0.107 μg-at l^{-1} mg dry wt^{-1} day^{-1}), Gardner and Scavia (1981: the freshwater crustacean *Daphnia magna* = 11-44 nmol mg dry wt^{-1} h^{-1}), Biggs (1982: Antarctic mixed zooplankton of specific gravity 1.1 = 1.6 μgat g wet wt^{-1} h^{-1}; *Thysanoessa* spp at 10°C = 2.4-2.7 μgat g wet wt^{-1} h^{-1}). Jawed (1969,

1973), Takahashi and Ikeda (1975), Ikeda and Motoda (1978) and Dagg *et al* (1982) provide estimates of roughly similar magnitude.

Cooney and Coyle (unp. data, table 7) conducted grazing experiments and zooplankton biomass measurements in the spring ice-edge habitat during 1982 and 1983. Grazing by neritic copepod (*Calanus marshallae, Pseudocalanus* spp., *Acartia longiremis*) and mixed copepod and euphausiid (*Thysanoessa raschii*) communities amounted to less than 1% of the daily photosynthetic carbon fixation (table 7). 1983 data suggest that over deeper water (>100 m) W of St. Matthew Island the larger oceanic copepod *Metridia lucens* was present, but no estimates of the potentially higher grazing rates for this species were obtained. These observations are consistent with previous studies (Cooney and Coyle, 1982). Copepod biomass in the spring Bering Sea ice-edge habitat (table 7) was too small to contribute significantly to the 1982 mixed layer ammonium pool (excretion was estimated as described in Methods). Zooplankton biomass was highest at stations where *Thysanoessa raschii* was present (stations 6, 50, table 7). Ammonium released by the euphausiid community in a 55 m water column (4×10^{-5} to 5×10^{-5} µgat l^{-1} h^{-1}) amounts to less than 0.05% of mixed layer phytoplankton NH_4-N requirements (table 6).

Table 7. HX025 zooplankton biomass, community type and grazing pressure data (Cooney and Coyle , unp. data).

Station	Depth of tow m	Type of community	Bio- mass	Grazing rate (%)	P
025006	60	Mixed	601.7	1.09	2981
025010	60	Copep	247.3	0.35	4286
025025	50	Copep	157.0	0.50	2116
025027	50	Copep	100.8	0.27	2601
025031	50	Copep	132.5	0.38	2382
025035	50	Copep	117.3	0.39	2046
025044	60	Copep	96.8	0.23	2880
025045	60	Copep	146.6	0.29	3471
025050	50	Mixed	1115.1	0.67	2019
025072	40	Copep	427.1	0.75	3932
025074	45	Copep	210.5	0.23	4321

Note: Community is Mixed if it contains copepod and euphausiid species and Copep if only copepods. Zooplankton biomass is in mg dry wt m^{-2}. Grazing rate given as % of $H^{14}CO_3$ primary production. P = approximated primary productivity in mgC m^{-2} d^{-1} fixed by algae over 30m in 13 h.

The vertical structure of *Thysanoessa* communities has not been resolved (Coyle, pers. comm.). Apparently, in the spring, young animals tend to congregate in layers exhibiting horizontal patchiness. The population may migrate vertically, seeking an optimum light and food level. Older organisms seem to be well adapted for benthic suspension feeding (Mauchline, 1966; Cooney and Coyle, pers. comm.). Green guts in young *Thysanoessa* specimens collected in 1982 and 1983 (guts were not examined microscopically) suggest that these organisms may occasionally congregate in the vicinity of the mixed layer depth (cf. figure 6c) during daylight hours, where chlorophyll a maxima are found. The *Thysanoessa* may be confined to a 5-10 m layer at the MLD during the day and move vertically in unison at night. If mixed community biomass is undersampled by 50-90% by using 333 µm mesh, 1 m diameter nets (Cooney, pers. comm), the above zooplankton nitrogen output (4×10^{-5} to 5×10^{-5} µgat 1^{-1} h^{-1}) is an underestimate. Correcting for animals that

were not collected, a mixed zooplankton community may provide up to 1.04 mgat m^{-2} d^{-1}, or about 3% of the ammonium needs of the algae. This is higher than what is estimated for Ross Sea mixed zooplankton communities (about 2% of the NH_4-N requirements of the phytoplankton, Biggs, 1982), but horizontal patchiness of euphausiid communities in the ice-edge zone is high.

4) Ice melting: Inorganic nitrogen input from melting ice will vary depending on ice cover, ice nutrient concentration and ice thickness. Ammonium levels in the ice are variable. During the winter when biological activity in the ice is at a minimum, bulk ice (ice plus brine) nutrients amount to about 10-20% of the concentration present in underlying waters (Schell, pers. comm.). In the spring, thawed ice samples showed nitrate concentrations <0.6 μgat l^{-1} and ammonium values ranging from 2.7 to 5.1 μgat NH_4-N l^{-1}. Ice in the Bering Sea ice edge is 0.5-2 m thick, thus thawing ice would not contribute more than 3% to the daily phytoplankton ammonium requirements. Grainger (1977) further discusses nutrient dynamics in the ice environment.

5) Eddy diffusion, mixing and ice-edge upwelling: Nitrate and ammonium productivity integrated through the mixed layer and over the 1982 time series period exceed the upper 25 m integrated NO_3-N and NH_4-N levels initially present in the marginal ice zone (tables 6, 9). Specific NO_3-N uptake rates obtained during 1982 (table 8) are comparable to pre- and peak-bloom rates measured over the southeastern Bering shelf (<0.001 h^{-1} to $V_{max}(NO_3$-N$)=0.0434\pm0.0025$ h^{-1}, Sambrotto, 1983). Nutrient supply mechanisms must be present to sustain the plant growth observed.

The rapid depletion of nitrate in the upper water column (table 9) suggests that nitrogen mass transport across the horizontal gradient at the bottom of the mixed layer may be slow in supplying nutrients to the bloom. Advective processes over the Bering Sea shelf are also slow (Kinder and Schumacher, 1981; Coachman and Walsh, 1981) in relation to the ice-edge bloom development. A more effective nutrient-supply mechanism may be ice-edge tidal or wind-driven upwelling (Alexander and Niebauer, 1981; Niebauer and Alexander, in prep.). An estimate of the magnitude of upwelled nitrogen can be obtained by examining nitrate sources and sinks in the ice-edge zone.

Nitrification is a potential source of nitrate. Ammonium oxidation (nitrification) rates measured in the central Pacific, Bering Sea and surface waters of Skan Bay (Unalaska Island, Alaska) have been low (Hattori and Wada, 1972; Hattori et al, 1978; 0.0-0.07 μgat l^{-1} d^{-1}; Hattori and Goering, 1981). Schell (1974b) estimated nitrification rates of 0.13 μgat l^{-1} d^{-1} when samples from northern Alaskan rivers and coastal lagoons were stimulated by NH_4-N additions. At the ice edge, bacterial nitrification is probably negligible since water

temperatures are low, but Haines *et al* (1981) suggest that nitrification

may be important in Bering Sea sediments. Denitrification (Goering,

unp.) may also be neglected in these oxygenated waters.

Evidence of upwelling along the Bering Sea ice edge was found in

1982 and 1983. The spatial continuity of the stable meltwater layer

appears to have been disrupted by upwelling on May 4, 1982 (figure 5a,

b, c, f). The isopycnals intersected the surface in the vicinity of the

50 m isobath. This feature was evident through May 11 (figure 6a, b, c,

d, f). Stations 42, 58 and 78 (time series in Niebauer and Alexander,

in prep.; table 9) were located in the central part of the isolated

"dish", each about 20-40 Km south of the upwelling area. Upwelling

close to the 50 m isobath may be a continuous process and not an "event"

(Niebauer, pers. comm.), which can seal off the meltwater "dish" on both

its open ocean and its ice flanks, creating a structure with two

physical vertical fronts (figure 6c). Upwelled water may then

presumably invade the dish structure by mixing across the upwarped

front. Phytoplankton in the vicinity of these frontal structures could

be exposed to higher NO_3 levels. As long as there is continuous ice

melting or/and high insolation at the surface under relatively calm

weather conditions, the buoyancy of the stratified layer may survive the

upwelling process.

The ice-edge system is treated below as a two-dimensional system.

The "dish" of figure 6c is thought of as an infinite water "band" of

reduced salinity, with no nutrient sources or sinks in the third

dimension. Austausch coefficients (=eddy coefficients or K_z, table 8)

were calculated as suggested by King and Devol (1979) and Eppley *et al*

(1979), namely as MLD integrated absolute nitrate uptake rates divided by the nitrate gradient across the MLD. This assumes that all the nitrate taken up by phytoplankton was supplied by diffusion (at the stations in table 8). Therefore, K_z values may be overestimates.

The eddy diffusion coefficients decrease with decreasing mixed layer depth (tables 5, 8), suggesting an inverse relationship with increasing stability. Similar calculations with data collected along the Bering Sea ice edge in 1983 suggest that even in a mixed water column K_z does not exceed 20 cm^2 s^{-1}. This may be an artifact since absolute nitrogen uptake rates measured in spring 1983 were lower than the 1982 rates by about 30%, presumably due to deeper ice-edge MLD (figures 8-11) and lower particulate nitrogen (PN) concentrations. Nevertheless, a deepening of the mixed layer and an increase in mixing across the pycnocline as observed in 1983 may have been caused by increased storm frequency during April - May 1983. These conditions allow for increased input of nutrients to the mixed layer from below.

Table 8. Cruise: HX025 (26 April - 16 May, 1982). Specific and absolute nitrate uptake rates at selected stations. Eddy diffusion coefficients (K_z) calculated according to King and Devol (1979, see text).

Station	Nitrate uptake rate			dNO_3/dz	K_z
	V	ρ	Q(MLD)		
025030	0.0108	0.0243	0.124	0.02	17.2
025039	0.0239	0.0752	1.128	0.60	5.2
025044	0.0358	0.2403	6.007	2.68	6.2
025050	0.0127	0.0366	0.183	1.20	0.4
Averages:	0.0208	0.0941	1.861		

Units: $V=(h^{-1})$; $\rho=(\mu gat\ l^{-1}\ h^{-1})$; $Q=(mgat\ m^{-2}\ h^{-1})$; NO_3 gradient at $MLD=(mgat\ m^{-4})$; $K_z=(cm^2\ s^{-1})$.

The flux of a nutrient form across a gradient can be calculated by multiplying $K_z*(dN/dz)$. The ammonium gradient across the pycnocline was small at all times (figure 28, table 6), indicating that NH_4-N flux across the pycnocline may be neglected.

The NO_3-N MLD diffusive flux (Diff.Flux[1,2], table 9: see Notes for definition of terms and superscripts) can be bracketed using K_z values of 0.1 and 3.0 $cm^2\ s^{-1}$. Diff.Flux[2] probably represents an overestimate because of the high K_z used. Even such high diffusive fluxes cannot account for the time-integrated $\Delta(\rho(NO_3-N))$ at stations 52, 58 and 78 (table 9).

Upwelling rates were calculated using a balance between diffusive NO_3-N flux and growth in the mixed layer, but PN losses (May 9, figure 27) were not accounted for. Thus, upwelling rates may have been underestimated (see negative values, table 9) by the amount of NO_3-N lost or the diffusion overestimate.

The following relationship was used to calculate the upwelling fluxes:

$$\text{Upwelling}^{1,2} = \Delta(NO_3) - (K_z)*(dNO_3/dz)*\Delta t + \Delta(\rho),$$

where Upwelling[1,2] is the NO_3-N flux (mgat m^{-2}) over a particular time period (Δt) estimated using either low (1) or high (2) eddy diffusion coefficients. Dependent and independent variables are defined in table 9 (Notes).

Upwelling velocities calculated in table 9 compare well with vertical velocities of 10^{-3} cm s^{-1} reported by Coachman (1982) at the mid-shelf front. Hood and Kelley (1976) also computed vertical velocities of 3.1×10^{-3} cm s^{-1} in Samalga Pass, in the Aleutian Islands (between Umnak Island and Islands of Four Mountains). Upwelling rates of this magnitude meet the nitrate demand of the ice-edge bloom. NH_4-N must be brought into the MLD via upwelling as well. At depth, the ammonium concentration is 2-5 μg-at l^{-1} (figure 28) which, using the vertical velocity estimates of table 9, would result in a transport of up to 26 mgat m^{-2} d^{-1} or from 0 to 57% of the ammonium requirements of the phytoplankton (table 6). Thus, time/depth-integrated $\rho(NH_4$-N) may exceed initial MLD ammonium by a factor of 1.5 or more. This agrees with values presented in table 6.

6) Bird excretion: Bédard et al (1980) measured ammonium content in excreta from several species of seabirds. The average ammonium excretion rate was 15-30 μgat g^{-1} bird d^{-1}. Divoky (pers. comm.) estimated sea-bird densities along the Bering Sea ice edge to be on the order of 200 to 600 Kg Km^{-2}. A bird-derived input of ammonium to the

MLD would be 0.3-1.8 mgat m^{-2} d^{-1} or approximately 0.7-3.9% of phytoplankton requirements (table 6). In shallow mixed layers (<10 m) this mechanism could supply 100% of phytoplankton ammonium requirements (table 5). Abundance of birds was striking at some of the stations along the ice edge in 1982 and 1983 but there was a high degree of patchiness and they were not present at all stations. This patchiness may be associated with the highly irregular distribution of the euphausiid *Thysanoessa raschii*.

Birds may be viewed as an efficient pumping mechanism by which nutrients from below the pycnocline may be brought to the bloom above, allowing potential export of food from the mixed layer without net nutrient losses (Dugdale and Goering, 1967; Eppley and Peterson, 1979). Again, it is emphasized that the mixed layer in the ice-edge zone cannot be regarded as a closed system, as it may in the deep ocean.

ERRATA TO:

'LOWER TROPHIC LEVEL STUDIES IN THE MARGINAL SEA ICE ZONE'
MS thesis by Frank Müller-Karger, UAF May 1984

The following table replaces Table 9, p. 91, of the MS thesis. An order of magnitude error was copied into the unit conversion from $Kz=[cm2\ s-1]$ to $Kz=[m2\ s-1]$ in the formula for variables 'Diff.Flux' 1 and 2 in the original table. This formula also incorrectly used 12 h instead of 24 h days. The table below reflects appropriate unit conversion factors. These new values propagate down the table, which gives new results to be taken into account when reading the discussion of the Nitrogen budget at the ice edge (pp. 89-93). The correct results are discussed in Müller-Karger and Alexander, 1987 (Continental Shelf Research, Vol. 7, No. 7, pp. 805-823).

Table 9. Nitrate uptake at time series stations and ice-edge upwelling estimates (corrected).

Independent variables

$V(NO3)=[h-1]$ 0.0208		PN:chla (wt)		11
Daylength [h] 13		Pool NO3 [uM]		15.2
Kz(1)=[cm-2 s-1]	0.1			
Kz(2)=[cm-2 s-1]	3			

Station	3	24	42	52	58	78
Date: May [days]	1.00	2.70	5.70	7.70	9.30	12.70
MLD [m]	-20.00	-20.00	-15.00	-15.00	-20.00	-20.00
MLD∫NO3	427.00	304.00	33.00	22.00	53.00	47.00
MLD∫Chla	87.00	74.00	184.00	272.00	359.00	397.00
dNO3/dz	0.00	0.00	0.94	1.19	0.66	1.39
d(NO3)	0.00	123.00	271.00	11.00	-31.00	6.00
p	18.48	15.72	39.09	57.79	76.27	84.35
Accum. N-uptake	0.00	29.07	111.30	208.18	315.42	588.47
dp betw dates	0.00	29.07	82.22	96.88	107.25	273.05
Diff.Flux1	0	0	0.81	1.03	0.57	1.20
dFlux1	0.00	0	1.22	1.84	1.28	3.01
SFlux1	0.00	0.00	1.22	3.06	4.34	7.35
Diff.Flux2	0.00	0	24.36	30.84	17.11	36.03
dFlux2	0.00	0	36.55	55.21	38.36	90.33
SFlux2	0.00	0.00	36.55	91.76	130.12	220.45
zAdvect1	0.00	152.07	352.00	106.04	74.97	276.04
zAdvect2	0.00	152.07	316.67	52.67	37.89	188.72
w1 [m d-1]	0.00	3.33	11.58	4.36	1.45	-1.43
w2 [m d-1]	0.00	3.33	10.42	2.17	0.73	-0.98

Frank Müller-K.

Table 9. 1982 time integrated nitrate uptake and ice-edge upwelling rate estimates.

Independent variables:

$V(NO_3)$ (h^{-1})	=	.0208	PN:Chl a (wt)	=	11
Daylength (h)	=	13	Pool NO_3 μM	=	15.2
$K_z(1):cm^2 s^{-1}$	=	.1	$K_z(2):cm^2 s^{-1}$	=	3

Station	3	24	42	52	58	78
Time (days)	0	1.7	4.7	6.7	8.3	11.7
MLD (m)	20	20	15	15	20	20
$\Sigma NO3$	427	304	33	22	53	47
$\Sigma Chl\underline{a}$	87	74	184	272	359	397
dNO3/dz (MLD)	0.00	0.00	0.94	1.19	0.66	1.39
$\Delta(NO3)$	0.00	123.00	271.00	11.00	-31.00	6.00
ρ	18.48	15.72	39.09	57.79	76.27	84.35
$\Sigma(\rho)$	0.00	29.07	111.30	208.18	315.42	588.47
$\Delta(\rho)$	0.00	29.07	82.22	96.88	107.25	273.05
Diff.Flux[1]	0.00	0.00	4.06	5.14	2.85	6.00
ΔFlux[1]	0.00	0.00	6.09	9.20	6.39	15.06
ΣFlux[1]	0.00	0.00	6.09	15.29	21.69	36.74
Diff.Flux[2]	0.00	0.00	73.09	92.53	51.32	108.09
ΔFlux[2]	0.00	0.00	109.64	165.63	115.08	270.99
ΣFlux[2]	0.00	0.00	109.64	275.27	390.36	661.35
Upwelling[1]	0.00	152.07	347.13	98.68	69.85	263.99
Upwelling	0.00	152.07	243.58	-57.75	-38.84	8.06
w[1] (m/d)	0.00	5.89	7.61	3.25	2.87	5.11
w[2] (m/d)	0.00	5.89	5.34	-1.90	-1.60	0.16

Notes:

ΣNO_3 = (mgat m^{-2})

$\Sigma Chl\underline{a}$ = (mg m^{-2}),

dNO$_3$/dz=(mgat m^{-4}) at mixed layer depth.

ρ = (mgat m^{-2} d^{-1}). ρ(NO$_3$-N) were obtained from chlorophyll a concentrations assuming invariant V(NO$_3$-N) = 0.0208 h^{-1} (table 8) and PN/Chl$\underline{a}$=11.0 (per wt.). Daily NO$_3$-N uptake based on 13 h/day calculations. PN/Chl$\underline{a}$=9.0 (wt.) in 1983.

$\Sigma(\rho)$ = cumulative mgat m^{-2} gained by plankton.

$\Delta(\rho)$ = (mgat m^{-2}) gain in plant N over Δt.

Diff.Flux[1,2] = NO$_3$-N flux across pycnocline (K$_z$*dN/dz) assuming 1) K$_z$=0.1 $cm^2 s^{-1}$, 2) K$_z$=3 $cm^2 s^{-1}$ respectively, in (mgat m^{-2} d^{-1}), acting over 24 h.

ΔFlux[1,2] = K$_z$*(dNO$_3$/dz)*Δt (mgat m^{-2}), mean diffusive flux estimated over Δt.

ΣFlux[1,2] = cumulative diffusive flux (mgat NO$_3$-N m^{-2}).

Δ(NO$_3$) = MLD integrated NO$_3$-N difference over Δt (mgat m^{-2}).

Upwelling[1,2] = flux in (mgat NO$_3$-N m^{-2}).

w[1,2] = vertical velocity = Upwelling[1,2]/(Pool NO$_3$-N*Δt) = (m d^{-1}), Pool NO$_3$-N (mgat m^{-3}) is assumed constant in the water column outside the "dish".

7) Flagellate (nanoplankton: 2-20 μm, Dussart, 1965) and bacterial cycling: Phytoplankton samples collected from the Bering Sea ice-edge habitat for algal species identification suggest that at times nanoplankton and bacteria may greatly exceed the phytoplankton in numbers. No attempt was made to classify the <<20 μm organisms in the ice-edge zone. Nanoplankton and bacteria seem to be even more abundant, relative to diatoms, in ice samples than in water samples. Phytoplankton, nanoplankton and bacterial communities seem to develop simultaneously, as samples collected in waters covered by ice show few of either.

To obtain an estimate of the combined nanoplankton and bacterial cycling of nitrogen in the mixed layer, I will assume steady state, since ammonium levels in the water changed little over the course of a week (figure 28):

$$(dN/dt) = 0 = Supply - Uptake - Nitrification$$
$$Supply = A + F + Z + I + D + U + B + R$$
$$A, F, I = 0$$
$$Z + D + U + B + R = Supply = Uptake + Nitrification$$
$$N = 0$$
$$R = Uptake - Z - D - U - B$$

Where A = atmospheric N input; F = fish + mammal N; N = nitrification; Z = zooplankton N; I = ice N; D = eddy difusive flux; U = upwelling N; B = bird excretion; R = nanoplankton N, so that:

Microbial regeneration = (Uptake) - ((*Thysanoessa* spp. excretion) + (Diffusion) + (Upwelling) + (Bird excretion))

Regeneration rates by microorganisms are estimated as ranging from 0 to 25 mgat NH_4-N m^{-2} d^{-1} (0-55% of phytoplankton requirements). The

estimated microbial regeneration rate is low compared to rates measured
in tropical systems (i.e. 0.162 μgat l^{-1} h^{-1} for organisms <0.035 mm
in Hawaiian waters, Caperon et al, 1979). Sorokin (1981) and Azam *et
al* (1983) review the role of microheterotrophs in marine trophic
structures.

According to the above estimates, most NH_4-N taken up by
phytoplankton can be supplied by physical processes (eddy diffusion and
upwelling). Bacterial and flagellate regeneration may contribute up to
80% of the ammonia taken up by the phytoplankton in an ice-edge bloom,
if stability is strong ($K_z << 0.1$ cm^2 s^{-1}), the mixed layer depth is
greater than 10 m and upwelling is slow ($w << 5.0$ m d^{-1}). At shallower
MLD other mechanisms may suffice (i.e. bird excreta or larger
zooplankton concentrations), in addition to microflagellate nitrogen
remineralization.

Preliminary look at 1983 nitrogen dynamics:

The bloom observed on 5 May 1983 developed because stratification
occurred in nutrient rich waters (stations 71-76, figure 11c, d). As
mentioned previously, these stations were occupied as part of an
oceanographic time series. Stations 2, 7, 17 and 72 correspond to the
same geographical location (figure 7). Changes in oceanographic
parameters at stations 6 and 73 can also be compared over time. ^{15}N
uptake measurements were conducted at station 74.

Water-column-integrated inorganic nitrogen (table 10) decreased
between 22 April 1983 (stations 2 and 7) and 27-28 April (station 17) by
about 600 mgat m^{-2}. This would be equivalent to about 1000 mgChl$\underline{a}$ m^{-2},

given no losses (assuming PN:Chl$\underline{a}$=9.0 wt.). The actual increase

measured was only of about 200 mgChl$\underline{a}$ m^{-2}. This suggests that advection

may have carried an excess chlorophyll away in the period of a week, or

that a different water mass with lower nutrient levels invaded the area

by April 27, 1983. Such a bloom may have also sunk before our

observations were made. An underestimation of the PN:Chl$\underline{a}$ ratio may

also partially account for the discrepancy.

Table 10.   1983 time series water column integrated nitrogen (mgat m^{-2}) and chlorophyll $\underline{a}$ (mg m^{-2}).

Date	Station	Bottom depth	Σ NO3	Σ NH4	Σ Chl$\underline{a}$
21 April '83	2	62	65⁻	362	56
22 April '83	7	60	634	274	20
27 April '83	17	63	231	79	267
5 May '83	72	63	261	155	400
21 April '83	6	63	596	218	120
5 May '83	73	64	316	164	238

    The decrease in water column nitrogen between stations 6 (April 22,

1983) and 73 (May 5) suggests an increase in chlorophyll of about 520 mg

m^{-2} (PN:Chl$\underline{a}$=9.0 wt.). The observed increase is 118 mgChl$\underline{a}$ m^{-2} (table

10). Not even by using a higher PN:Chl$\underline{a}$ (<20 wt.) can I account for the

apparent nutrient level changes in terms of observed chlorophyll $\underline{a}$. The

differences in NH$_4$-N between April 27 (station 17) and May 5 (station

72), suggest fast nitrogen regeneration. These calculations indicate

that the mixed water column conditions during the 1983 sampling season

precluded straightforward inferences on bloom dynamics.
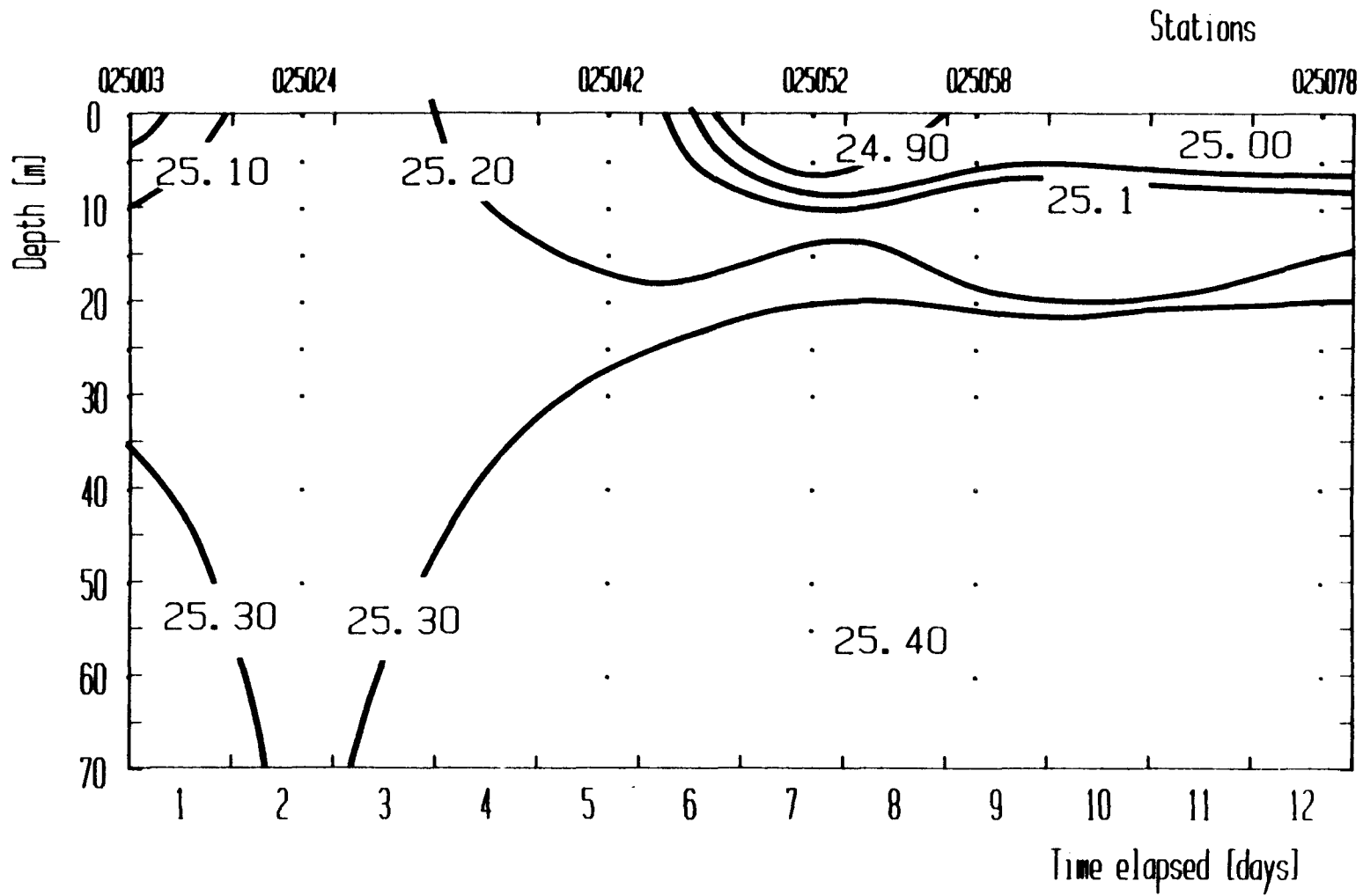
Figure 26.   1-12 May 1982 ice edge: Sigma-t time series.
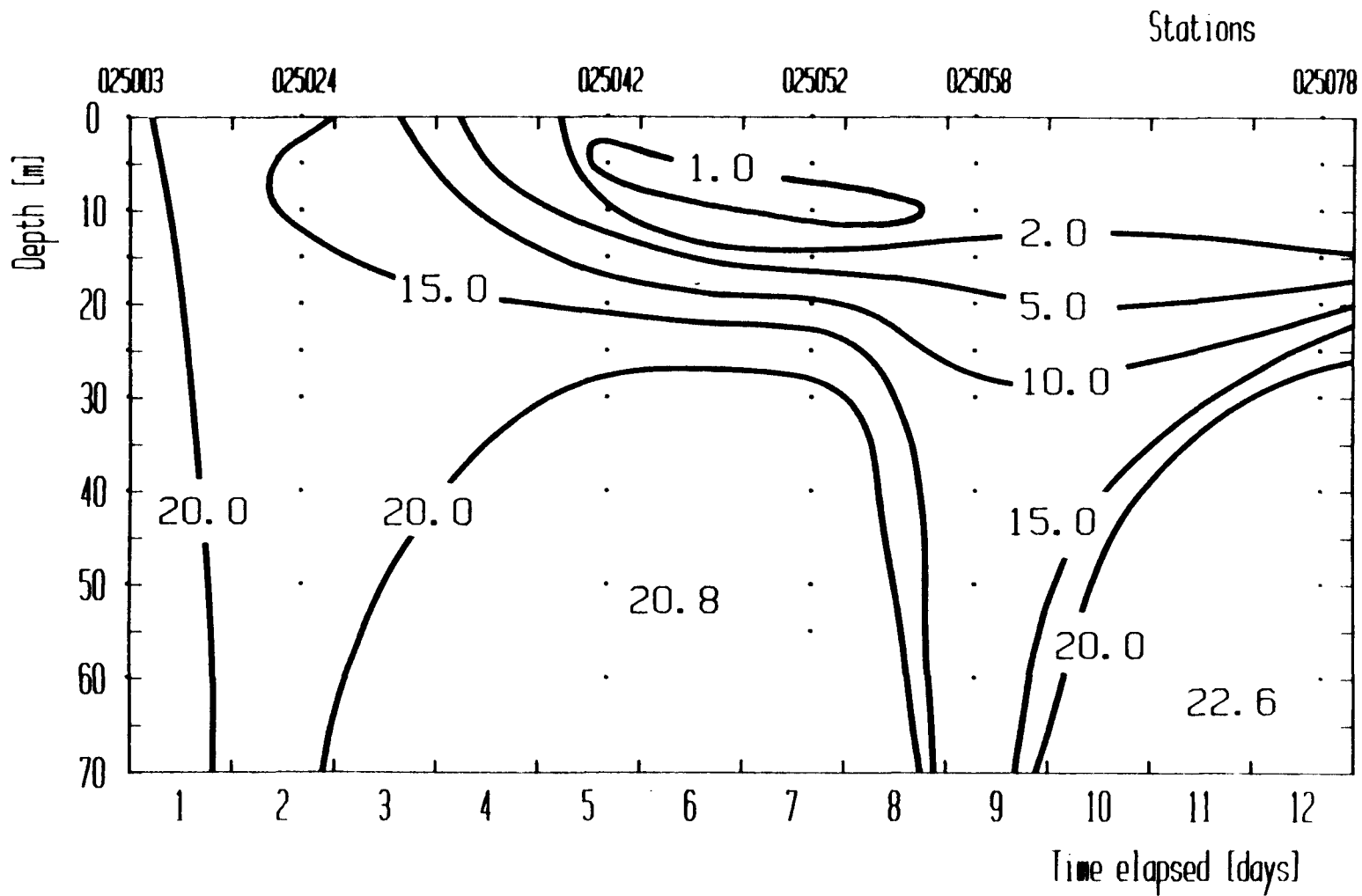
Figure 27. 1-12 May 1982 ice edge: Nitrite + nitrate time series.
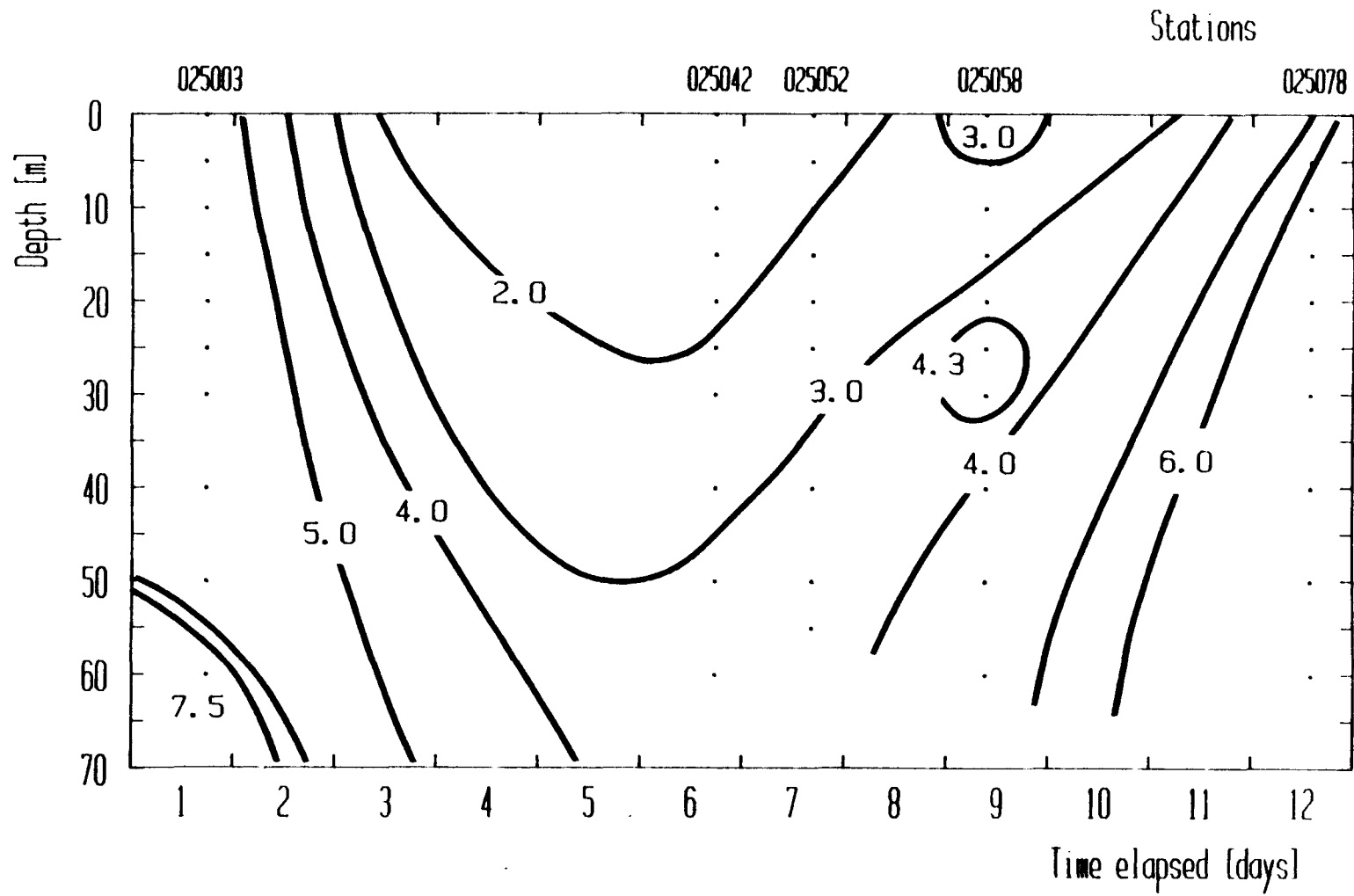
Figure 28.   1-12 May 1982 ice edge: Ammonium time series.

IV. <u>Annual</u> <u>carbon</u> <u>and</u> <u>nitrogen</u> <u>budget</u> <u>for</u> <u>the</u> <u>Bering</u> <u>Sea</u> <u>ice-edge</u>
<u>habitat</u>.

Arctic explorers noted the presence of algae and other
microorganisms in sea ice (Horner, 1977 and references therein) and
phytoplankton blooms associated with melting sea ice in early spring
(Marshall, 1957; McRoy and Goering, 1974a, b; Niebauer and Alexander,
in prep.). Observations made on these phytoplankton communities in the
Bering Sea since 1970 (McRoy *et al*, 1972; Alexander, 1980) indicate
that there is interannual variability in total organic matter produced.
Biological oceanographers are just beginning to understand the magnitude
and the nature of this variability, by developing annual nutrient and
carbon budgets which address the nutritional requirements of primary
producing communities.

A budget calculated for the southeastern Bering Sea (Sambrotto,
1983) allocates to phytoplankton an annual carbon production of
approximately 166 ± 80 gC m^{-2}. an estimate that does not include
ice-related production since it was obtained during years of reduced ice
extent (1978-1981).

McRoy and Goering (1974b) estimate that the late winter (February -
April: 61 days) ice-related primary production is about 19% of the
total Bering Sea shelf annual production (McRoy and Goering, 1974b;
table 5). This represents a contribution of about 27 gC m^{-2} y^{-1}. This
estimate was based on a measurement conducted before the ice-edge bloom
reached its maximum potential productivity.

Based on three years of primary production data (1975-1977)
collected in waters over the St. George Basin (outer continental shelf
between the Pribilof Islands and Unimak Island, figure 1), Alexander
(1980) estimates that about 136 gC m^{-2} are produced between January and
mid May (calculated from Alexander, 1980: figure 3). This represents
about 40% of her annual shelf production estimate (339 gC m^{-2}).

Several problems arise in the construction of a nutrient budget for
the Bering Sea. The Bering Sea is notable for interannual variability
in oceanographic parameters. The spatial or temporal distribution of
epontic algae over the Bering Sea shelf in spring (late February - May)
is not known (Alexander and Chapman, 1981), and productivity patterns at
any one time along the ice are probably patchy. The presence of other
microorganisms in addition to the photosynthesizing algae in sea ice and
the marginal ice zone further complicates the problem, and to date no
quantification of nanoplanktonic and bacterial productivity has been
attempted. These problems make it difficult to estimate the total
contribution of the early spring primary productivity to the annual
Bering Sea carbon and nutrient balance. Below I construct a nitrogen
and carbon budget from data collected in the marginal sea-ice zone
during the spring of 1982 and 1983. The budget is assumed valid for the
early part of 1982 and 1983 and only for the ice-affected central Bering
shelf regions deeper than 40 m, since shallower waters were completely
mixed.

For purposes of discussion, three environments in the marginal sea

ice zone have been identified (tables 11 and 12):

    1.- Epontic algal community.
    2.- Water column under the ice.
    3.- Ice-edge bloom.

Table 11. 1982 nitrogen and carbon productivity budget. 1) Epontic (1983), 2) Water column under the ice, 3) Ice-edge bloom productivity. (Units: Thickness=m, Period=days, p=mgat N m^{-2} y^{-1}, P=gC m^{-2} y^{-1}, P:p(NH$_4$+NO$_3$)=atoms).

Stations	Thickness	Period	pNO3	pNH4	P	P:p(N+N)
1) HX043028	0.2	40	36.8	95.8	11.3	7.1
2) 37, 50	25	15	178.4	115.2	25.3	7.2
3) 19, 68	20	15	673.7	700.9	41.1	2.5
1)+2)+3)		70	888.9	911.9	77.7	

Table 12. 1983 nitrogen and carbon productivity budget. 1) Epontic, 2) Water column under the ice, 3) Ice-edge bloom productivity. (Units: Thickness=m, Period=days, p=mgat N m^{-2} y^{-1}, P=gC m^{-2} y^{-1}, P:p(NH$_4$+NO$_3$)=atoms).

Stations	Thickness	Period	pNO3	pNH4	P	P:p(N+N)
1) 28	0.2	40	36.8	95.8	11.3	7.1
2) 42, 56	25	15	89.9	27.6	6.8	4.8
3) 50, 59, 74	30	15	146.9	93.8	31.9	11.0
1)+2)+3)		70	273.5	217.2	50.0	

An analysis of the contribution to the annual Bering Sea shelf

productivity by each of these components follows.

    1.- Epontic algal community: The algal community forming brown

colored ice can be found from mid-February (McRoy *et al*, 1972) to

mid-May in Bering Sea ice, in a layer in the submerged parts of ice

floes. The layer was not seen to grow larger than 35 cm and could be

absent altogether. Epontic productivity in February and March is low
(McRoy and Goering, 1974a) compared to rates found in April and May
(table 12). The algae are released to the water, where some seed the
ice-edge bloom and some presumably sink out of the water column
immediately. The brown ice layer was not observed during the 1982
sampling season, presumably due to prior decay of the ice. The 1983
sampling season started a week earlier than the previous year, and brown
ice was found at all ice stations. It was not possible to estimate the
patchiness of the epontic community due to limited areal coverage by the
ship.

Absolute nitrogen uptake rates in the epontic algal layer as
measured in 1983 appear high on a volume basis as a result of the very
high concentration of algae (70 to 130 mgChl$\underline{a}$ m^{-3}). On an areal basis,
epontic algae (14-26 mgChl$\underline{a}$ m^{-2}) assimilated about 37 mgat NO$_3$-N m^{-2}
y^{-1}, 96 mgat NH$_4$-N m^{-2} y^{-1} and fixed 11 gC m^{-2} y^{-1} in 1983 (table 3).
The greater dependence on ammonium of this community (f=.28) is to be
expected from the numerical dominance of flagellates and bacteria (unp.
data), the high NH$_4$-N concentrations, and the very low nitrate levels in
bulk ice (ice + brine).

The estimated Bering Sea ice-edge epontic productivity
(approximately 11 gC m^{-2} y^{-1}) is higher than that estimated for coastal
Arctic ice algal communities (2.4 gC m^{-2} y^{-1} in ice near Barrow's shore,
calculated from Matheke, 1973 and Matheke and Horner, 1974; 5.0 gC m^{-2}
y^{-1}: Clasby et al, 1976; 0.7 gC m^2 y^{-1}: Horner and Schrader, 1981,
1982; 1-6 gC m^{-2} y^{-1}: Schell et al, 1982, being highest offshore in
the Beaufort Sea away from sediment laden ice).

2.- Water column under the ice: Primary productivity from late January to March in the water column immediately under the ice has been found to be limited (about 1.3 gC m^{-2} y^{-1}: McRoy et al, 1972). This study shows higher rates under the ice during late April - early May (6-25 gC m^{-2} y^{-1}, tables 11, 12). Productivity here is probably light limited in a completely mixed, cold water column.

Algae in the water under the ice in the vicinity of the ice edge appear to have contributed during 15 days in 1982 about as much to the production of the system as the ice-edge bloom did in 1983 (tables 11, 12). These algae, as mentioned above, are probably derived from the ice, but in contrast with epontic algae their contribution is based mainly on NO$_3$-N. It is expected that their productivity will rise with irradiance until photoinhibition occurs (figures 12, 16, 17).

3.- Ice edge: Variation in oceanographic and meteorological parameters allows for continuously changing ice-edge patterns. The one of interest here is common under mild and warm weather conditions: a stable melt water layer (15-25 m deep) along a uniform and relatively straight ice margin.

Algal growth in the water column along the ice edge begins in late winter (March - April: McRoy and Goering, 1974). At this time production is low due to poor water-column stability and low surface irradiance. The major ice-edge bloom lasts about two weeks in late April - May (Niebauer et al, 1981), though given adverse weather conditions the stable surface layer could be broken up and the organic material mixed throughout the water column. Conversely, mixing or turbulent events can extend the period of the bloom by the supply of

nutrients from below if thermal or salinity restabilization ensues. The main problem primary producers would encounter under stable conditions is nitrogen limitation (see previous section).

During the sampling effort in 1983, the ice-edge bloom did not develop fully and high chlorophyll a occurred only toward the end of the cruise (4-6 May, figure 11d). Even then the bloom was patchy and uptake rates low (figures 11d, 21). Low pressure systems seemed to extend the winter season in this apparently abnormal year, constantly mixing the water column and limiting surface irradiance levels. Ledbetter (1979) suggests that phytoplankton patchiness may develop as a response to turbulence generated under these conditions.

The strong water-column stability effect on ice-edge phytoplankton was evident in 1982 when high rates of nitrogen and carbon uptake were measured (table 11). Ammonium became more important as a nutrient source as nitrate levels diminished. Zooplankton were absent in quantities necessary to support the observed ammonium uptake rates and grazing accounted for less than 1% of primary production (R. Cooney and K. Coyle, pers. comm.). This suggests that other sources of nitrogenous nutrients were available (see above).

The annual productivity estimate for 1982 (table 11) does not include a direct estimate of epontic algal production. Adding the 1983 productivity estimate (component 1) to the 2+3 (1982) components, I obtain an estimated combined nitrogen (NH_4-N + NO_3-N) requirement of 1.8 gat N m^{-2} y^{-1} and a total carbon fixation of 77.7 gC m^{-2} y^{-1} for 1982. In turn for 1983, when the ice-edge blooms never developed to their full potential, nitrogen taken up was about 0.5 gat N m^{-2} y^{-1}, less than a

third the 1982 estimate. During this production period, also estimated

at 70 days, algae fixed an estimated 50 gC m^{-2} y^{-1}.

The carbon productivity values presented in tables 11 and 12 may be

underestimates of Bering Sea ice-related primary productivity, since it

was assumed that under-the-ice primary productivity and the ice-edge

bloom lasted only 15 days each. The estimates obtained previously by

McRoy and Goering (1974) for late winter primary productivity could be

added to the ones presented here. This would yield an approximated

annual input of 105 gC m^{-2} in 1982 and 78 gC m^{-2} in 1983 at the spring

Bering Sea ice edge.

I cannot explain the low C:N uptake ratios observed in the water

column in 1982 (4.9 per atoms, compared to 7.9 in 1983, for components 2

and 3 in tables 11, 12). It is possible that my depth-integrated

nitrate uptake rates were overestimated since no correction was applied

to account for decreased NO$_3$-N uptake at very low irradiances (below 10%

surface light intensity). MacIsaac and Dugdale (1972) attribute

discrepancies between the Redfield C:N ratio for deep-sea particulate

matter and C:N uptake ratios at least partially to the loose coupling

between photosynthesis and nitrogen uptake. Slawyk et al (1977, 1979)

point out that carbon and nitrogen uptake measurements may not be

directly comparable since the experimental techniques involved are

different. Donaghay et al (1978) noticed that there is great

variability in the C:N ratio of natural phytoplankton assemblages.

Their results also suggest that morning samples have a depressed C:N

ratio compared to evening samples. Goldman and McCarthy (1978) also

found it hard to draw conclusions from observations of this kind.

Sambrotto (pers. comm.) observed similar depressions in C:N uptake ratios in Bering Sea open shelf blooms in years of strong water-column stability and vigorous diatom growth. It may be that under these conditions the $H^{14}CO_3$ technique underestimates primary productivity. If the Redfield C:N ratio for deep-sea particulate matter (Redfield et al, 1963) is applied to the 1982 total N productivity (table 11), I obtain an ice related carbon input of approximately 143 gC m^{-2} y^{-1}, comparable to Alexander's (1980) estimate.

Another cause for the low overall 1982 C:N uptake ratio may have been high protein production rates (pure protein C:N=3.7 per atoms: Russell-Hunter, 1970; Morris, 1981). High incorporation of nitrogen into proteins seems to occur when nitrogen limitation is approached (DiTullio and Laws, 1983). During 1983 the total C:N uptake ratio was high compared to the Redfield ratio probably due to the unfavorable light history leading to inefficient nitrogen uptake. The 1983 C:N uptake ratios of epontic algae suggest that conditions were favorable for balanced growth (Eppley, 1981b), or that algae were growing at maximum specific growth rates (Shuter, 1979).

Nutrient data collected during February 1983 (Muench et al, 1983b) suggest that the average mixed layer depth (25 m) integrated nutrient concentrations were 332 mgat NO_3-N m^{-2} and 18 mgat NH_4-N m^{-2}. This amount of inorganic nitrogen is inadequate to support the phytoplankton nitrogen requirements in 1982 (table 11). Nitrogen inputs were necessary, as discussed above. February 1983 water-column-integrated (depths from 60-115 m) nitrogen levels were 1.4 gat NO_3-N m^{-2} and 0.05 gat NH_4-N m^{-2}, still less than the estimated 1982 combined (ammonium +

nitrate) N uptake (table 11). Higher ammonium concentrations and the annual ammonium absolute uptake values obtained for 1982 suggest that a certain amount of recycling occurs in the ice-edge zone. In 1983, primary producers may have grown for a considerable period without nitrogen limitation, given the slower uptake rates and lower biomass. Nitrogen limitation may have ensued as thermal stratification developed (figure 11a, b, c, f).

The values presented (tables 11, 12) are within the range suggested by previous estimates of ice-affected algal activity in the Bering Sea in spring. Variability in annual estimates of primary productivity in the ice-edge habitat may be related to ice extent and thus be closely tied to climatic variability (Niebauer, 1980). Possibly, ice-related production is not only linked to ice extent, but also to the rate and timing of ice retreat, and global events, in particular those leading to climatic oscillations such as El Niño, may cause productivity minima as observed in the Bering Sea in 1983.

My results support the conclusion of McRoy and Goering (1974b) and of Alexander and Chapman (1981) that even though the marginal sea-ice zone in the Bering Sea does not support extremely high sustained production rates such as those found in temperate upwelling regions, the system gains by extending the production season by 50 to 70 days.

Phytoplankton blooms occur in the spring in open shelf waters (away from the influence of the ice) as well (Sambrotto et al, in prep.). If nutrient depletion occurs in the surface mixed layer during the ice-edge bloom, open shelf productivity may become limited prematurely (Niebauer and Alexander, in prep.). Wind mixing, mixed-layer-depth turbulence or

upwelling events followed by melt water or heat-derived stratification stretch the shelf production season. Walsh *et al* (1978) studied the New York Bight primary productivity applying this concept. The effects of wind mixing on southeastern Bering shelf blooms are discussed by Sambrotto (1983), but the evolution of the ice-edge bloom to an open shelf bloom has not been investigated in this respect.

The budget discussed here shows that the ice system represents a significant but variable addition to the nutrient and carbon budget of the Bering Sea (50-136 gC m^{-2} y^{-1}, in addition to the 166 ± 80 gC m^{-2} y^{-1} suggested by Sambrotto, 1983). Previous conceptual models recognized the importance of this organic material to a water column and benthic-detritivore food web (Niebauer *et al*, 1981; Cooney and Coyle, 1982). The loss of particulates to the bottom in relatively shallow shelves has been noted elsewhere (Falkowski *et al*, 1983). The mechanism of nutrient supply to surface waters is the key question to address to understand annual central Bering shelf primary production.

Variations of the magnitude implied above in production regimes probably have great effects on Bering Sea fisheries, but the information available is insufficient to establish, for example, whether there is a relationship between a decline in the 1983 bottom crab fisheries in the central Bering Sea and lower overall production due to reduced ice cover.

CONCLUSIONS

1) Inorganic nitrogen specific uptake rates (V) along the advancing ice edge in the Chukchi Sea ranged: $V(NH_4-N)=0.71 \times 10^{-3}$ to 1.70×10^{-3} h^{-1}; $V(NO_3-N)=0.06 \times 10^{-3}$ to 1.89×10^{-3} h^{-1}) in October 1981. These rates were an order of magnitude less than rates measured at the spring ice edge in 1982 (tables 5, 6, 8 and 9) and 1983 (Appendix).

2) Part of the October Chukchi Sea phytoplankton community trapped in forming ice possibly overwinters. The similarity between the fall phytoplankton species (tables 3, 4), and spring epontic and ice-edge bloom species (pp. 35-36), suggests that epontic algae seed the April-May water column bloom. Many of the algal species seen are found in Pacific and northern North Pacific Ocean waters.

3) Epontic algal communities were common during the sampling period in 1983 (up to 35 cm thick layer on the under side of ice floes, 5-130 mg Chl$\underline{a}$ m^{-3}), but were absent in 1982, presumably due to previous loss by ice decay.

4) High ammonium concentrations in the ice-edge zone water column (>2 µgat NH_4-N l^{-1}) suggest rapid ammonification occurs in this habitat, as suggested by Niebauer *et al* (1981). High nitrogen recycling rates seem to occur in brown ice prior to, or concurrent with, the ice-edge

water column bloom. Nitrate uptake inhibition by the presence of
ammonium in the water was not seen, while phytoplankton preferred
ammonium over nitrate.

5)   Nitrogen could limit ice-related productivity in the spring under
strong stability conditions, but upwelling processes meet the
phytoplankton nitrogen demands for the duration of the bloom (2-3
weeks). Tidally driven upwelling along the 40-60 m isobath seems to be
the dominant type of upwelling affecting the ice-egde zone in the
central Bering shelf. Biological N-supplies, are usually small compared
to supplies by physical mechanisms. Both mechanisms may act
simultaneously.

6)   Neither phosphorus nor silica seem to limit the ice-edge bloom (late
winter water-column N:P=5.3 to 9.9 per atoms, 10-30 μgat Si(OH)$_4$-Si
l^{-1}).

7)   The frequency of wind-mixing events in the ice-edge zone was higher
in 1983 compared to 1982. Also, due to an early retreat of the ice edge
in April 1983, the ice-edge zone remained close to the 40-60 m isobaths
for a longer period, in the vicinity of a vertical front. Vertical
velocities are higher within this frontal structure (0 to ca. 10^{-2} cm
s^{-1}). The deeper mixed layer resulted in lower ice-edge zone primary
productivity in 1983 (approximately 50 gC m^{-2} y^{-1}, 0.5 gat N m^{-2} y^{-1},
epontic plus ice-edge water column), with respect to 1982 (approximately
78 gC m^{-2} y^{-1}, 1.8 gat N m^{-2} y^{-1}, epontic plus ice-edge water column).

The mechanism of nutrient supply to surface waters is key to
understanding annual primary productivity in the central Bering Sea in
spring.

8) Phytoplankton communities in the ice-edge zone are shade-adapted.
Photosynthetic rates of 8-18 mgC m^{-3} h^{-1} were observed at irradiances
<75 μE m^{-2} s^{-1}.

9) Ice-related primary productivity was photoinhibited at irradiances
found in the upper 0-1.5 m in the mixed layer at mid-day, while optimum
irradiances (I_{OPT}) coincide with subsurface chlorophyll a maxima.
Carbon uptake response to varying irradiance was modeled using Steele's
(1962) equation.

10) Maximum absolute photosynthetic rates varied directly with
chlorophyll a concentration ($P=0.60*Chla+1.55$, r=0.65). Assimilation
numbers were <<3.0 mgC mgChla^{-1} h^{-1} in 1982 and 1983. This supports the
idea that arctic phytoplankton may not utilize light very efficiently
(Platt et al, 1982).

11) Community succession (in time or space) between the ice-edge zone
and the open water shelf bloom may result in changes of nitrogen and
carbon uptake characteristics of the algal community. Early spring
phytoplankters may be susceptible to nitrate uptake photoinhibition.

12)   Oceanographic concepts developed for the deep ocean and associated

surface mixed layer nitrogen dynamics (e.g. King and Devol, 1979;

Dugdale and Goering, 1967) cannot be applied to a shallow shelf

ecosystem and its nitrogen budget.

RECOMMENDATIONS FOR FUTURE RESEARCH

IN THE ICE-EDGE ZONE

It is evident that a great deal is not known or understood about the influence of ice on the biota of subarctic and arctic marine environments. Discussions with Drs. V. Alexander, J. Kelley, J. Niebauer, H. Feder and J. Goering indicate that future studies of ice-edge zone productivity should address the following:

The importance of nutrients other than inorganic nitrogen has to be resolved. No measurements of organic nitrogen concentration or uptake rates exist in the ice-edge habitat. The importance of phosphorus as a potentially limiting nutrient cannot be neglected.

Light influence on nitrate uptake in early spring ice-related blooms is not clear.

Variations in nutrient uptake rate with ice-edge zone community structure changes may be important. Do the ammonium and nitrate uptake rates change with succession of species? Close examination of species assemblages and their nitrogen uptake rates may clarify such community characteristics, as attempted previously by Sambrotto (1983).

The relationship between epontic, ice-edge and Bering Sea spring algal species has to be resolved.

The timing of the onset, and the temporal and spatial patchiness of epontic and ice-edge blooms needs to be resolved.

The role of bacteria and flagellates associated with ice is unclear. Biomass and rates of nutrient mineralization by these organisms in the ice and ice-edge zone need to be measured.

Time series of fine resolution (once or twice a day) have to be conducted at the ice margin to resolve daily and weekly variations in primary productivity and nitrogen uptake rates. The interaction of the ice edge with shelf fronts should be followed in such time series as well.

Shear at the bottom of the water column is periodically caused by
    barotropic tidal flows. The interaction of the bottom mixed layer
    so created, and the surface wind-mixed layer, needs to be examined
    in shallow (<70 m) Bering shelf waters. This physical interaction
    may allow for nutrient-unlimited bloom development.

A three-dimensional understanding of the ice-edge zone has to emerge.
    Along-ice continuity of the 'dish-shaped' structure found in
    transects perpendicular to the ice (figure ?) must be examined. Is
    the structure continuous along the isobaths and 'band-shaped' or is
    it 'dish-shaped'?

The development of ice-edge blooms in the well-mixed waters shoreward of
    the 50 m isobath (coastal domain, Kinder and Schumacher, 1981) is
    not clear. Does an ice-edge bloom occur there, and are there
    adequate nutrient supplies to support it?

Sedimentation rates and elemental composition of suspended particulate
    matter need examination. Sediment traps may be useful tools to
    address this problem.

The ecological importance of the ice-edge bloom is still obscure. The
    relationship between the benthic communities and the ice-related
    production needs to be addressed. Are interannual productivity
    differences driving or contributing to fluctuations of Bering Sea
    bottom fisheries (e.g. crabs)?

Simplification, speed and accuracy of chlorophyll a measurements is
    important in the type of work proposed here. Slovacek and Hannan
    (1977) suggest the use of DCMU
    (3-(3,4dichlorophenyl)-1,1-dimethylurea) for *in vivo* fluorometry
    chlorophyll determinations to eliminate variability and obtain
    maximum fluorescence. The method may be useful in parameterizing
    photoadaptation (Lewis *et al*, 1984) or mixing history of
    phytoplankton (Harris, 1980; Vincent, 1980)

Sampling strategies need to be developed to enable examination of
    biological oceanographical processes at the ice edge from January
    on. This is important for characterizing interannual variability
    and mechanisms driving such variations.

Comparison of ice-affected, nutrient-unlimited areas (NW Bering Sea:
    Anadyr Gulf, waters around St. Lawrence Island and the Bering
    Strait) with ice-affected, potentially nutrient limited areas
    (central and SE Bering shelf) is necessary to weigh total Bering
    Sea primary productivity. In studying the NW Bering Sea, the
    effect of ice on early (February-March) ice-related primary
    productivity may be regarded from a light limitation perspective,
    and compared to winter algal growth in the open waters south of St.
    Lawrence Island.

Ice-edge oceanographic conditions close to the Soviet coast should be
    studied, and the effects of the proximity to the sharp shelf break
    examined.

Differences and similarities between the Bering Sea ice edge and other
    marginal ice zones around the world need comprehensive review.

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APPENDIX A

Inorganic nitrogen uptake data collected during Alpha Helix cruise HX025, in April - May, 1982. Data for a station and depth continues along rows on successive pages (first two columns are cruise-station number and depth). SUR.L.I.=Surface light intensity ($\mu E\ m^{-2}\ s^{-1}$). SIMLI%=Simulated % surface irradiance. K-EXT=extinction coefficient (m^{-1}). Chlorophyll a (mg m^{-3}). Particulate nitrogen (mgat-N m^{-3}).

Station	DEPTH	SUR.L.I	SIMLI%	K-EXT	Chlor.a	PN
025-019	0	172.8	100	.21	5.45	6.3
	0	172.8	100	.21	5.45	6.3
	0	172.8	100	.21	5.45	6.3
	15	172.8	10	.21	14.08	5.54
	15	172.8	10	.21	14.08	5.54
	15	172.8	10	.21	14.08	5.54
	15	172.8	10	.21	14.08	5.54
	15	172.8	10	.21	14.08	5.54
025-030	0	57.6	100	.38	2.98	2.26
	0	57.6	0	.38	2.98	2.26
	0	57.6	100	.38	2.98	2.26
	0	57.6	100	.38	2.98	2.26
	0	57.6	100	.38	2.98	2.26
	4	57.6	25	.38	3.39	2.28
	4	57.6	25	.38	3.39	2.28
	4	57.6	25	.38	3.39	2.28
	6	57.6	10	.38	3.39	2.28
025-039	5	112.09	50	NA	4.63	3.15
025-044	0	360.2	50	.56	6.65	6.71
	0	360.2	50	.56	6.65	6.71
	0	360.2	50	.56	6.65	6.71
025-050	0	187.28	100	NA	2.48	2.87
025-068	10	71.51	50	NA	10.19	4.76
	10	71.51	50	NA	10.19	4.76
	10	71.51	50	NA	10.19	4.76
	10	71.51	50	NA	10.19	4.76

Appendix A (cont.). Ambient inorganic nitrogen concentration and isotopic label addition or spike (μgat-N l^{-1}). NAT%ABN=estimated ^{15}N atom % natural abundance.

Station	DEPTH	NO$_3$	NH$_4$	SPIKE-NO$_3$	SPIKE-NH$_4$	NAT%ABN
025-019	0	7.92	4.6	.04762	.04762	.3989
	0	7.92	4.6	.09524	.09524	.3989
	0	7.92	4.6	.704	.704	.3989
	15	5.71	4.1	.04762	.05	.403366
	15	5.71	4.1	.09524	.09524	.403366
	15	5.71	4.1	.2	.2	.403366
	15	5.71	4.1	.505	.505	.403366
	15	5.71	4.1	.704	.704	.403366
025-030	0	19.74	4.7	.4762	.4762	.3964222
	0	19.74	4.7	.4762	.4762	.3964222
	0	19.74	4.7	.9524	.9524	.3964222
	0	19.74	4.7	2.502	2.502	.3964222
	0	19.74	4.7	5.05	5.05	.3964222
	4	19.74	3.9	.4762	.4762	.475726
	4	19.74	3.9	.9524	.9524	.475726
	4	19.74	3.9	2.502	2.502	.475726
	6	19.74	3.9	5.05	5.05	.475726
025-039	5	13.35	3.1	1	1	.388485
025-044	0	9	3	1	1	.4603708
	0	9	3	5	5	.4603708
	0	9	3	14	14	.4603708
025-050	0	8.12	1.4	1	1	.8755989
025-068	10	2.2	3.4	.4762	.4762	.6458023
	10	2.2	3.4	.9524	.9524	.6458023
	10	2.2	3.4	5.05	5.05	.6458023
	10	2.2	3.4	7.04	7.04	.6458023

Appendix A (cont.). Specific inorganic nitrogen uptake rates (h^{-1}) and absolute uptake rates (μgat-N l^{-1} h^{-1}. Incubation temperature (°C).

Station	DEPTH	VNO$_x$	VNH$_4$	ρNO$_x$	ρNH$_4$	Inc. T
025-019	0	.0312011	.0239543	.1965671	.1509118	-1
	0	.0145723	.0137146	.0918057	.0864022	-1
	0	.0115045	.0117521	.0724786	.0740382	-1
	15	.0327463	.0091517	.1814145	.0507007	-1
	15	.0108846	.0211622	.0603007	.1172386	-1
	15	.012175	.0145544	.0674495	.0806314	-1
	15	.0134365	.0104114	.0744383	.0576792	-1
	15	.0117097	.0099962	.0648717	.0553792	-1
025-030	0	.012204	.0032991	.0275810	.0074559	-.75
	0	.010751	.0052338	.0242973	.0118285	-.75
	0	.0056967	.0051225	.0128745	.0115768	-.75
	0	.0064545	.0051808	.0145873	.0117085	-.75
	4	.0190753	.0059238	.0434917	.0135064	-.75
	4	.012568	.0079479	.0286550	.0181211	-.75
	4	.0114887	.0063446	.0261941	.0144657	-.75
	6	.0088587	.0076776	.0201979	.0175049	-.75
025-039	5	.023885	.0074508	.0752378	.0234699	-.5
025-044	0	.035816	.0113336	.2403254	.0760483	-.4
	0	.0756774	.048233	.5077954	.3236434	-.4
	0	.0316144	.0400895	.2121326	.2690005	-.4
025-050	0	.012743	.0044484	.0365724	.0127669	-.3
025-068	10	.0115837	.0158353	.0551385	.0753760	-.75
	10	.0141304	.0158545	.0672608	.0754672	-.75
	10	.0222775	.0198591	.1060409	.0945293	-.75
	10	.0236986	.018321	.1128053	.0872080	-.75

Part 1.   Inorganic carbon (^{14}C) uptake corollary data collected during
Alpha Helix cruise HX025, in April - May, 1982. Data for a station and
depth continues along rows on successive pages (first two columns are
cruise-station number and depth). SUR.L.I.=Surface light intensity
($\mu E\ m^{-2}\ s^{-1}$). SIMLI%=Simulated % surface irradiance.
K-EXT=extinction coefficient (m^{-1}). Chlorophyll a (mg m^{-3}).

Station	DEPTH	SUR.L.I	SIMLI%	K-EXT	Chlor.a
025-019	0	172.8	100	.21	5.45
	0	172.8	0	.21	5.45
	5	172.8	50	.21	10.00
	5	172.8	0	.21	10.00
	10	172.8	25	.21	19.83
	10	172.8	0	.21	19.83
	15	172.8	10	.21	14.08
	15	172.8	0	.21	14.08
	20	172.8	1	.21	24.62
	20	172.8	0	.21	24.62
025-029	0	57.6	100	.39	5.65
	0	57.6	0	.39	5.65
025-030	0	57.6	100	.38	2.98
	0	57.6	0	.38	2.98
	2	57.6	50	.38	3.39
	2	57.6	0	.38	3.39
	4	57.6	25	.38	3.39
	4	57.6	0	.38	3.39
	6	57.6	10	.38	3.39
	6	57.6	0	.38	3.39
	12	57.6	1	.38	2.38
	12	57.6	0	.38	2.38
025-037	0	720	100	.39	3.39
	0	720	0	.39	3.39
	0	720	50	.39	3.39
	0	720	25	.39	3.39
	0	720	10	.39	3.39
	0	720	1	.39	3.39
	25	720	100	.39	3.96
	25	720	0	.39	3.96
	25	720	50	.39	3.96
	25	720	25	.39	3.96
	25	720	10	.39	3.96
	25	720	1	.39	3.96
025-045	0	720	100	.28	9.28
	0	720	0	.28	9.28

Appendix B (cont. part 1). See previous page for definition of abbreviations.

Station	DEPTH	SUR.L.I	SIMLI%	K-EXT	Chlor.a
025-045	0	720	50	.28	9.28
	0	720	25	.28	9.28
	0	720	10	.28	9.28
	0	720	1	.28	9.28
	20	720	100	.28	5.45
	20	720	0	.28	5.45
	20	720	50	.28	5.45
	20	720	25	.28	5.45
	20	720	10	.28	5.45
	20	720	1	.28	5.45
025-048	0	285.71	100	NA	1.42
	0	285.71	0	NA	1.42
025-049	0	291.82	100	NA	2.53
	0	291.82	0	NA	2.53
025-050	0	187.28	100	NA	2.48
	0	187.28	0	NA	2.48
025-051	0	92.76	100	NA	4.25
	0	92.76	0	NA	4.25
025-052	0	23.19	100	NA	13.84
	0	23.19	0	NA	13.84
025-055	0	107.32	100	NA	10.05
	0	107.32	0	NA	10.05
025-056	0	115.52	100	NA	17.43
	0	115.52	0	NA	17.43
025-057	0	120.93	100	NA	17.81
	0	120.93	0	NA	17.81
	0	120.93	10	NA	17.81
	15	120.93	100	NA	11.68
	15	120.93	0	NA	11.68
	15	120.93	10	NA	11.68

Appendix B (cont.). Part 2. April - May, 1982, carbon uptake rates
(mgC m⁻³ h⁻¹) and incubation temperature (°C). See corollary data in
Appendix B, part 1 (first two columns are cruise-station number and
depth).

Station	DEPTH	C.uptk	Inc. T
025-019	0	5.1857	-1
	0	.4665	-1
	5	4.529	-1
	5	.291	-1
	10	5.529	-1
	10	.8194	-1
	15	4.1	-1
	15	1.383	-1
	20	.235	-1
	20	.602	-1
025-029	0	1.393	-1.1
	0	.159	-1.1
025-030	0	2.825	-.75
	0	.462	-.75
	2	3.176	-.75
	2	.409	-.75
	4	-1.15	-.75
	4	6.157	-.75
	6	-.225	-.75
	6	4.891	-.75
	12	-.431	-.75
	12	3.1486	-.75
025-037	0	.476	-.9
	0	.9244	-.9
	0	5.463	-.9
	0	4.721	-.9
	0	3.7227	-.9
	0	.38	-.9
	25	.8013	-.9
	25	.2585	-.9
	25	4.83	-.9
	25	8.219	-.9
	25	7.684	-.9
	25	1.07	-.9
025-045	0	8.58	-.4
	0	1.07	-.4

Appendix B (cont. part 2). Carbon uptake rate (mgC m^{-3} h^{-1}) and incubation temperature ($^{\circ}$C).

Station	DEPTH	C. uptk	Inc. T
025-045	0	17.58	-.4
	0	13.76	-.4
	0	14.425	-.4
	0	1.942	-.4
	20	1.991	-.4
	20	.3407	-.4
	20	16.433	-.4
	20	12.192	-.4
	20	12.212	-.4
	20	4.081	-.4
025-048	0	.837	-1
	0	.164	-1
025-049	0	1.115	-.75
	0	.355	-.75
025-050	0	1.659	-.3
	0	.368	-.3
025-051	0	3.952	-.1
	0	.442	-.1
025-052	0	5.854	0
	0	.526	0
025-055	0	4.184	.6
	0	.55	.6
025-056	0	12.816	0
	0	.372	0
025-057	0	11.421	0
	0	.334	0
	0	12.142	0
	15	4.861	0
	15	.35	0
	15	7.27	0

APPENDIX C

Inorganic nitrogen and carbon uptake data collected during Alpha Helix cruise HX043, in April - May, 1983. Data for a station and depth continues along rows on successive pages (first two columns are cruise-station number and depth). SUR.L.I.=Surface light intensity (μE m^{-2} s^{-1}). SIMLI%=Simulated % surface irradiance. K-EXT=extinction coefficient (m^{-1}). Chlorophyll a (mg m^{-3}). PC meas=measured particulate carbon (mg m^{-3}).

Station	DEPTH	SUR.L.I	SIMLI%	K-EXT	Chlor.a	PC meas	
43028	0	262.5	50	NA	124.08	5475.98	Brown
	0	262.5	10	NA	124.08	5475.98	Ice
43042	5	540	50	.155	1.495	133.5	
	5	540	50	.155	1.495	133.5	
	5	540	10	.155	1.495	133.5	
	5	540	10	.155	1.495	133.5	
43050	15	850	50	.186	8.023	370.36	
	15	850	50	.186	8.023	370.36	
	15	850	10	.186	8.023	370.36	
	15	850	10	.186	8.023	370.36	
43056	5	570	50	.134	3	195.23	
	5	570	50	.134	3	195.23	
	5	570	10	.134	3	195.23	
	5	570	10	.134	3	195.23	
43059	30	500	50	NA	7.604	175.32	
	30	500	50	NA	7.604	175.32	
	30	500	10	NA	7.604	175.32	
	30	500	10	NA	7.604	175.32	
43074	10	750	50	.275	10.33	326.42	
	10	750	50	.275	10.33	326.42	
	10	750	10	.275	10.33	326.42	
	10	750	10	.275	10.33	326.42	

Appendix C (cont.). PN meas=measured particulate nitrogen (mgat-N m⁻³).
Ambient inorganic nitrogen concentration and label addition or spike
(mgat-N m⁻³)

Station	DEPTH	PN meas	NO$_x$	NH$_4$	NO$_x$Spike	NH$_4$Spike
43028	0	57.49	.56	3.2	5.05	5.05
	0	57.49	.56	3.2	5.05	5.05
43042	5	1.35	6.1	1.86	.4762	.4762
	5	1.35	6.1	1.86	5.05	5.05
	5	1.35	6.1	1.86	.4762	.4762
	5	1.35	6.1	1.86	5.05	5.05
43050	15	3.69	9.53	.01	.4762	.4762
	15	3.69	9.53	.01	5.05	5.05
	15	3.69	9.53	.01	.4762	.4762
	15	3.69	9.53	.01	5.05	5.05
43056	5	1.86	12.31	.24	.4762	.4762
	5	1.86	12.31	.24	5.05	5.05
	5	1.86	12.31	.24	.4762	.4762
	5	1.86	12.31	.24	5.05	5.05
43059	30	1.33	10.99	1.43	.4762	.4762
	30	1.33	10.99	1.43	5.05	5.05
	30	1.33	10.99	1.43	.4762	.4762
	30	1.33	10.99	1.43	5.05	5.05
43074	10	3.87	1.7	.89	.4762	.4762
	10	3.87	1.7	.89	5.05	5.05
	10	3.87	1.7	.89	.4762	.4762
	10	3.87	1.7	.89	5.05	5.05

Appendix C (cont.). Approximate ^{15}N natural abundance (atom %).
Inorganic nitrogen uptake rates: specific rates (V: h^{-1}), absolute
rates (ρ: μgat-N l^{-1} h^{-1}).

Station	DEPTH	NAT%ATN	VNO_3	VNH_4	ρNO_3	ρNH_4
43028	0	.3984	.0065255	.0090533	.3751510	.5204742
	0	.3984	.005777	.0082972	.3321197	.4770060
43042	5	.55039	.008957	.0027369	.0120920	.0036948
	5	.55039	.0025472	.0016222	.0034387	.0021899
	5	.55039	.0112006	.0037433	.0151208	.0050535
	5	.55039	.0015707	.0014539	.0021204	.0019627
43050	15	.64704	.005252	.0014195	.0193799	.0052380
	15	.64704	.01102	.0039309	.0406638	.0145050
	15	.64704	.010363	.0011036	.0382395	.0040723
	15	.64704	.0098867	.005069	.0364818	.0187046
43056	5	.58407	.010642	.0016075	.0197941	.0029900
	5	.58407	.0070324	.0022144	.0130803	.0041188
	5	.58407	.016401	.0011534	.0305059	.0021453
	5	.58407	.0060968	.003036	.0113400	.0056470
43059	30	.48513	.01296	.004609	.0172368	.0061300
	30	.48513	.008236	.0051138	.0109539	.0068014
	30	.48513	.02188	.0044077	.0291004	.0058622
	30	.48513	.0066602	.0060772	.0088581	.0080827
43074	10	.48761	.007563	.0043708	.0292688	.0169150
	10	.48761	.007653	.0046997	.0296171	.0181878
	10	.48761	.00787	.0045529	.0304569	.0176197
	10	.48761	.0075996	.0043093	.0294105	.0166770

Appendix C (cont.). Carbon uptake rate (P=mgC m^{-3} h^{-1}, averaged in 4 h incubations). Inorganic nitrogen uptake experiments incubation time (h) and incubation temperature ($^{\circ}$C).

Station	DEPTH	P	IncTime	Inc.Temp.
43028	0	113.23	6.75	-1.5
	0	145.86	6.75	-1.5
43042	5	1.124	7.5	-1
	5	1.124	7.5	-1
	5	.5864	7.5	-1
	5	.5864	7.5	-1
43050	15	6.0468	7.33	-.5
	15	6.0468	7.33	-.5
	15	6.7	7.33	-.5
	15	6.7	7.33	-.5
43056	5	1.6696	8.58	-.75
	5	1.6696	8.58	-.75
	5	1.1004	8.58	-.75
	5	1.1004	8.58	-.75
43059	30	5.1846	6.75	-.5
	30	5.1846	6.75	-.5
	30	3.867	6.75	-.5
	30	3.867	6.75	-.5
43074	10	6.499	7.8	0
	10	6.499	7.8	0
	10	5.9066	7.8	0
	10	5.9066	7.8	0

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